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ABSTRACT BOOKLET

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Table of Contents

NCM 2019 Poster Abstracts

Poster Session 1

A – Control of Eye & Head Movement

1-A-1 Microsaccades in blindsight monkeys

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Patients with damage to the primary visual cortex (V1) demonstrate residual performance on laboratory visual tasks despite the denial of conscious seeing (blindsight). Macaque monkeys with a unilateral V1 lesion have been used as an animal model for blindsight. Previously, we have demonstrated that blindsight monkeys retain some cognitive and attentional capacities including visual-spatial memory (Takaura et al 2011) and endogenous attention (Yoshida et. al. 2017). Here we examined whether a unilateral V1 lesion affects microsaccades, which are small, unconscious, fixational eye movements. Our first question was whether microsaccades during fixation are affected. After a surgical lesion in the left side of V1 in two monkeys, the number and/or amplitude of leftward microsaccades (towards the normal visual field) were larger than those of rightward microsaccades (towards the affected visual field). Analysis of horizontal eye positions at the onset of microsaccades (Tian et. al. 2018) revealed that the average horizontal eye position of blindsight monkeys was shifted towards the affected (right) visual field, suggesting that the increased number and/or amplitude of leftward microsaccades compensated for a lesion-induced rightward eye-position shift. We then asked whether microsaccades during peripheral and central cueing were affected. Before the V1 lesion, in a memory-guided saccade task (Takaura et al 2011), peripheral cue onsets transiently decreased the number of microsaccades. A rebound in frequency followed, and most rebound movements were directed away from the cues, consistent with our previous finding in monkeys and humans (Tian et. al. 2016). After the V1 lesion, the overall patterns of inhibition and rebound were not affected. However, the number of cue-directed microsaccades occurring <120 ms after cue onset ("express microsaccades", Tian et. al. 2018) increased for leftward microsaccades and was almost completely abolished for rightward microsaccades. In a Posner task with informative central cues (Yoshida et. al. 2017), the number of express microsaccades was also affected in a similar manner to the peripheral cues. These results suggest that: 1) V1 lesions affect the balance of leftward and rightward microsaccades, which is consistent with the push-pull equilibrium model of microsaccade dynamics (Hafed 2011); and 2) V1 is not necessary for transient inhibition of microsaccades after peripheral cues. These results help constrain models of microsaccade dynamics after peripheral and central cueing, and they highlight how V1 can contribute to such dynamics, in addition to visual-oculomotor areas such as FEF and the superior colliculus.

1-D-2 Exploring microsaccade-induced visual reafferent responses in macaque superior colliculus neurons

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Rhesus macaque superior colliculus (SC) neurons exhibit feature tuning to individual spatial frequencies (Chen et al., 2018). However, the impacts of microsaccades on visual reafferent responses to a continuously presented spatial frequency grating are not known. Here we recorded SC activity from two monkeys while they fixated and we presented Gabor gratings of 0.56, 2.22, or 4.44 cycles per deg (cpd). The gratings remained visible for at least 800 ms, meaning that there were frequent microsaccades while the gratings were visible. Grating location and size were always matched to response field (RF) location and size, and our sampled neurons were all extra-foveal. The gratings were always vertical. We compared SC visual responses after grating onset (similar to Chen et al., 2018) to visual reafferent responses after microsaccades subtly jittered the images of the gratings over the neurons' RF's. For the latter, we aligned neural responses to microsaccade onset, and we grouped neurons according to their preferences to different spatial frequencies. After stimulus onset, our neurons showed stronger and earlier visual responses to low spatial frequencies, consistent with (Chen et al., 2018), and the great majority of neurons preferred either 0.56 or 2.22 cpd as opposed to 4.44 cpd. Relative to microsaccade onset, we compared activity before movement onset to activity 50-100 ms after movement onset. Approximately half of the neurons did not show a post-movement increase in activity relative to before (i.e. no reafferent response). The remaining neurons showed a visual reafferent response. Neurons that preferred 0.56 cpd at stimulus onset also preferred 0.56 cpd in the reafferent responses, but the responses after microsaccades were strongly muted; only reaching approximately 1/3-1/4 of the stimulus-evoked responses. For neurons preferring intermediate spatial frequencies (2.22 cpd) after stimulus onset, the visual reafferent responses were less clearly tuned, and they were always similarly weak compared to stimulus-evoked responses. In all cases, the visual reafferent responses were not faster than stimulus-evoked responses. Our results demonstrate that microsaccades only cause subtle visual reafference in SC neurons, suggesting that the often-large impacts of these movement on perceptual performance might arise through additional mechanisms.

1-A-3 cTBS increases narrow-band gamma bursts and theta-band phase synchronization in the contralateral pre-frontal cortex in a primate model of rTMS

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Repetitive modes of TMS (rTMS) modulate behaviour in both humans and non-human primates (NHP). Although widely used in basic and clinical neuroscience, a precise understanding of the neurophysiological effects of rTMS in brain networks, and how such effects influence behaviour, is lacking, particularly when rTMS is applied to an interconnected network. To address this gap in knowledge, we have developed an NHP model of rTMS, focusing on the well-studied oculomotor network. Here, we report the effects of continuous theta-burst-stimulation (cTBS) to the right prefrontal cortex (PFC) on neuronal activity in the left PFC during performance of an oculomotor task. Our hypothesis is that cTBS disinhibits neural activity in the callosal target. We recorded neural activity from the left PFC (area 8Ar) with a Utah array during performance of an intermixed memory pro- and anti-saccade task. After a first block of 200 trials, we delivered 600 pulses of cTBS (50Hz bursts of 3 pulses, inter-burst frequency of 5 Hz) above motor threshold, followed by a second block of trials. In one monkey, we have analyzed changes in behavior and neural activity across cTBS applied to either the right PFC (15 sessions), M1 (a brain control; 10 sessions), or above the head (an AIR control, 11 sessions). Behaviorally, we observed significantly shorter leftward reaction times for anti-, but not pro-saccades, after cTBS-PFC compared to controls. Surprisingly, we observed no evidence for disinhibition of overall spike rates, as cTBS to the PFC, M1, or air produced a diversity of effects. However, we observed an increase in the rate of narrow-band oscillatory bursts in the low-gamma (40-80 Hz) that selectively increased following cTBS-PFC on left anti-saccade trials. This increase lasted ~10 minutes after cTBS-PFC, resembling the behavioural effect. We also observed an increase in theta-band phase synchronization within the contralateral PFC. Our results suggest that the behavioural effects of cTBS may be brought about by changes in network oscillations, suggesting that these, rather than a direct effect on firing rates, may be the neuronal signatures of contralateral disinhibition in the PFC. To our knowledge, this is the first study showing both behavioural and neurophysiological effects at the network level following cTBS.

1-A-4 Visual accuracy constraints do not influence saccade kinematics

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The stereotyped relationship between the amplitude, duration and peak velocity of saccades, the so-called main sequence, has been proposed to reflect a speed-accuracy optimization in the presence of signal-dependent noise in the control signals (Harris & Wolpert, 2006; van Beers, 2008). If so, visual accuracy constraints might influence the main sequence. To test if this is the case, we examined the amplitude-duration-peak velocity relationship for saccades towards Gaussian-blurred visual targets of 1, 3, and 5° in diameter (±3σ). The theory suggests that movements to smaller targets could be slower than amplitude-matched saccades to larger targets as smaller targets require more precise motor control. Five human subjects (1 male) participated. Each trial started with fixation of a central fixation point for 300-1000ms. As soon as the fixation point disappeared, a peripheral target was flashed to the left or right. Targets were only presented for 100ms to exclude visual feedback during the movement. Target eccentricities ranged from 5-21°. Stimulus conditions were randomized across blocks of 270 trials. Subject performed 6-10 blocks each. Eye movements were measured with an Eyelink 1000 at 500Hz. In line with previous studies, endpoint variability increased with target eccentricity. Furthermore, the largest target sizes induced more scatter in the saccade endpoints whereas saccades made to the smaller targets at the same location were more precise. Yet, we found no significant differences between the main sequence relations in the three different target size conditions. The saccade gains were not affected by target size either. These results indicate that saccade kinematics are conserved regardless of visually-imposed precision constraints. There was, however, a difference between the main sequence of the saccades that had latencies of ~200ms - the majority of responses - and those that had significantly longer reaction times. Indeed, the reaction times show a skewed bimodal distribution with most saccades occurring around 200ms and a set of later responses occurring closer to 300ms. The late saccades of this distribution had longer durations and lower peak velocities than the early saccades. The apparent dissociation between endpoint variability and saccade kinematics may be explained by assuming that the saccadic motor system plans an optimal movement to the saccade goal (as proposed by Goossens & van Opstal, 2012), while noise in the sensory representation of the visual target results in variability of the planned saccade goal, thus adding to the net variability of the saccade endpoints due to noise in the control signals which induces variable differences between the planned and the actual movement. The effect of saccade latency on the main sequence indicates, however, that the principle of minimizing the consequences of motor noise alone is not enough to explain the main sequence relations. Funded by EU Marie-Curie ITN: HealthPAC #604063

1-A-5 Encoding and decoding strategies of natural self-motion in the vestibular pathway

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The vestibular system generates reflexes that are vital for gaze and posture stabilization, as well as for accurate spatial perception and motor control. Yet, most previous studies of self-motion processing by vestibular neurons have used artificial (e.g., sinusoidal) stimuli whose properties fundamentally differ from those experienced during natural everyday activities. Here we investigated how neurons in the vestibular nuclei (VN) encode naturalistic self-motion and how this information is decoded by downstream brain areas. Previous studies have shown that different cell classes within the VN project to different downstream areas and mediate reflexive versus perceptual behavioral responses. Specifically, vestibular-only (VO) neurons project to the ventral posterolateral (VPL) nucleus of the Thalamus, thereby mediating self-motion perception, as well as to the spinal cord, mediating vestibulo-spinal reflexes. In contrast, position-vestibular-pause (PVP) as well eye-head (EH) neurons project to eye motoneurons within the abducens nucleus and mediate reflexive behaviors such as the vestibulo-occular reflex (VOR). Our results show that coding strategies in VN were matched to natural stimulus statistics such as to optimally encode them through temporal whitening, irrespective of cell type. Interestingly, how optimal coding was achieved did differ across cell types in VN. Specifically, we found that the tuning properties of PVP neurons were sufficient to account for temporal whitening. However, this was not the case for EH neurons as both neuronal variability and tuning were needed to account for optimized coding, similar to results previously obtained VO neurons (Mitchell et al. 2018). We then investigated how information optimally encoded by VO neurons is actually decoded in downstream areas by recording the activities of VPL neurons within the Thalamus to natural self-motion stimuli. We found that, contrary to VN neurons, the response power spectra of VPL neurons decayed with increasing frequency, indicating that they do not perform temporal whitening. In order to explain this surprising result, we built a model that incorporates the known response properties of VO neurons. Our model reproduced experimental data and showed that information transmitted by VO neurons is optimally decoded by VPL. Specifically, the large variability displayed by VO neurons is detrimental at high frequencies, thereby reducing the neuronal response power. Our findings suggest that optimal coding strategies change throughout vestibular pathways and suggests that they are adapted to the function that a specific brain area serves (i.e., reflexive or perceptual). To further test this hypothesis, recordings from downstream structures that mediate reflexes (i.e., Abducens nucleus) will be needed. These studies, will have important implication in our understanding of how self-motion experienced during everyday activity is processed to sustain accurate behavior and perception.

1-A-6 Spatiotemporal tuning of ocular following response can be acquired by statistical machine learning of visual images during daily self-movements

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Visual motion has crucial roles for quickly adjusting posture, eyes, and limbs in dynamic interactions with environments. Ocular following response (OFR), which is induced by a suddenly applied visual motion [Miles et al 1986; Kawano et al. 1986], is highly sensitive for the visual moition of low spatial and high temporal frequency (under 0.1 cpd and over 10 Hz) [Miles et al 1986; Gomi et al. 2006]. In addition, OFR gradually increased with stimulus size, whereas it gradually decreased with increasing size of the visual center mask [Gomi et al. 2013]. We here examined as to whether these OFR tuning characteristics are acquired by the natural statistics of the visual motion and self-movements. To reduce the retinal slip caused by self-motion, eye should move in the opposite direction to the self-motion which always occurs in daily movements. Based on this functional assumption, we developed a convolutional network which estimates translational velocities and angular velocities of self-motion from time-sequential images by a statistical learning. The data of images were taken by a head-mounted camera during several kinds of daily human movements (walking outside and inside, playing a ball, watching a poster, etc). The 95% upper limits of distributions of simultaneously recorded head movements were 0.53 [m/s] in the lateral direction and 61.8 [rad/s] around the vertical axis. High correlation coefficients for the test dataset after learning ($r = 0.907 \pm 0.002$ for 6-DoF) indicate a successful estimation of self-motion from the time-sequential images. Next, we quantified the spatiotemporal frequency tuning characteristics acquired by the learning, by feeding sinusoidal grating patterns with various temporal frequency and spatial frequency into the learned network, as done in the human experiments. When the low spatial frequency grating pattern was moved with high temporal frequency in the transversal direction on the front parallel plane, the outputs corresponding angular velocity around the vertical axis and translational velocity along the transversal axis exhibited a relatively great values. On the other hand, those outputs did not for the high spatial frequency patterns. Additionally, for the low-spatial and high-temporal frequency patterns, those outputs gradually increased as the stimulus area became larger. Those spatiotemporal frequency tunings and size tunings are qualitatively similar to those of OFR. These results would suggest that the area MST, which contributes to generate OFR, acquires the analysis to encode the visual motion considering the self-motion statistics, rather than the statistical nature for motion perception. This work was supported by KAKENHI (JP16H06566)

1-A-7 Neural substrate for coordinated and uncoordinated pupil and saccade responses

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The appearance of a salient stimulus evokes a series of responses including eye movements and pupil dilation to orient the body for appropriate action, and the intermediate layers of the midbrain superior colliculus (SCi) has been hypothesized to coordinate this orienting response. Although the role of the SCi on saccade and pupil dilation has been separately established, whether these responses are coordinated is still unknown. Moreover, the SC receives luminance signals directly from the retina, whether these signals can modulate saccade and pupil responses coordinated by the SCi is yet to be explored. Here, we investigated the role of the SCi in coordinating saccade and pupil responses, and in modulating luminance effects through SCi microstimulation by varying stimulation frequency and background luminance. Stimulation frequency systematically modulated saccadic and pupillary responses, with the trial-by-trial correlation between two responses. Background luminance, however, only modulated pupil, but not, saccade responses. In summary, our results demonstrate an integrated role of the SCi in coordinating correlated saccade and pupil responses, and characterize luminance independent modulation in the SCi, together elucidating the differentiated pathways underlying this behavior.

1-A-8 The effect of different visual conditions on gaze behaviors during a ball-catching task

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There is a close relationship between ball-catching skills and visual strategy. Eye and head movements have been used as parameters to evaluate visual search strategy during ball tracking. For example, infielders in baseball/softball can focus not only a ball but also other things such as runners or other players, and they change their gaze patterns according to the situation. In such cases, head and eye movements are limited during tracking a ball. However, it is still uncertain whether different visual environments during ball catching influence gaze behaviors using head movements. Therefore, the purpose of this study was to determine the effect of different visual conditions on head movements during a ball-catching task. Subjects were female college students who belong to a softball team. Subjects were asked to sit at a distance of 9 m from a tennis ball-shooting machine. They performed a one-handed catching task under normal vision condition (normal condition) and when vision of the catching hand was occluded by an opaque screen (occlude condition). We tested two different ball speeds (slow and fast conditions) and 10 trials were performed at each catching task. We detected peak head velocity (PHV) by a gyroscope and evaluated their catching performance with success rate of catching a ball, The results showed that the success rate of catching was lower in the fast condition than the slow condition and lower in the occlude condition than the normal condition. Similarly, the peak head velocity (PHV) during catching was lower in the fast condition than the slow condition and lower in the occlude condition than the normal condition. These results showing lower PHV in the occlude condition could be due to that subjects might change their allocation of attention to the invisible hand to adjust their hand position. Furthermore, the results showed that PHV has a positive correlation between the normal condition and the occlude condition. Therefore, each subject might have a common visual strategy in either condition. We also categorized subjects into two groups according to the success rate of catching in the occlude condition (high-rate and low-rate groups). The result showed that in the high-rate group, PHV showed a lower value for the occlude condition than the normal condition. In contrast, PHV in the low-rate group showed no difference between occlude and normal conditions. These results suggest that the subjects who have high success rate of catching in the occlude condition could change their visual strategy according to the condition.

B – Fundamentals of Motor Control

1-B-9 Retinal eccentricity modulates visuomotor feedback gains along the movement

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Goal directed reaching movements are guided by a combination of visual feedback of the hand and target. Errors that arise during the reach are corrected by visuomotor feedback responses. The magnitude of these responses to shifts in the visual representation of the hand exhibits state dependent evolution [1, 2], specifically with decreases for perturbations far from the target. Traditionally this modulation is well explained by optimal feedback control [3], but more recent research has shown visuomotor feedback gain modulation with gaze location [4], albeit with gaze locations fixated outside of the movement. Here we test to what extent gaze location within the movement modulates these feedback gains. Participants performed ballistic reaching movements from the home position to a target while grasping a robotic manipulandum. Visual feedback of the cursor, home and target positions was provided in the plane of movement via a mirror. In order to examine the effect of the gaze location participants were asked to fixate on one of the locations (38% or 100% of movement distance) for the entire reach. On the majority of trials, a visual perturbation shifted the cursor location by 2 cm left or right at different distances in the movement. On half of these trials this perturbation was maintained until the end of the movement requiring active correction to reach the target. The other half of these trials were performed in a mechanical channel in order to measure the feedback responses. On these trials, no lateral correction was required as the perturbation was only maintained for 250 ms. The results confirm our hypothesis that visuomotor feedback gains are modulated by retinal eccentricity. Specifically, we observe upregulation of the feedback gains closer to visual fixation, and downregulation away from visual fixation. Moreover, we see additional regulation of overall feedback gains that may be related to target certainty [5]. These findings could be explained by a model of visuomotor feedback gains depending on both retinal eccentricity and target certainty. In general, our results provide new insight into the regulation of visuomotor feedback gains and might further explain differences in visuomotor feedback control of the hand and target. 1. Dimitriou M, Wolpert DM, Franklin DW (2013) The Temporal Evolution of Feedback Gains Rapidly Update to Task Demands. J Neurosci. 33:10898-10909 2. Franklin DW, Reichenbach A, Franklin S, Diedrichsen J (2016) Temporal Evolution of Spatial Computations for Visuomotor Control. J Neurosci. 36:2329-2341 3. Liu D, Todorov E (2007) Evidence. for the Flexible Sensorimotor Strategies Predicted by Optimal Feedback Control. J Neurosci. 27:9354-9368 4. de Brouwer AJ, Gallivan JP, Flanagan JR (2018) Visuomotor feedback gains are modulated by gaze position. J Neurophysiol. 120(5):2522-2531 5. Izawa J, Shadmehr R (2008) On-Line Processing of Uncertain Information in Visuomotor Control. J Neurosci. 28(44):11360-11368

1-B-10 Control of visually guided reaching: Can the sensorimotor control system independently modulate feedback from the hand and target?

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Successful visually guided reaching to an object requires locating the object and the hand, planning the reach, initiating the movement, and adjusting online for any disturbances during the reach. One prominent theory suggests that the sensorimotor control system calculates a difference vector between the hand and target and uses this signal to compute the required motor commands (1). However, recent studies have shown that this model fails to predict the nature of rapid visuomotor feedback during reaching (2). Instead, online control has been suggested to occur through independent visuomotor feedback loops - one for hand control and one for target acquisition. Previous work has shown modulation of the rapid visuomotor feedback gains by changing the task-relevancy of the visual environment (3, 4). Here we test whether these two feedback loops are independent by determining whether cursor and target feedback gains can be independently modulated. Specifically, we test if participants can upregulate their feedback gains to cursor motion while simultaneously downregulating the feedback gains to target motion (and vice versa). Participants grasped a robotic manipulandum and made reaching movements to place a cursor into a target. During the reach the cursor would undergo task-relevant motion, that is, lateral motion that had to be corrected to intercept the target, while the

target would undergo task-irrelevant motion. On random movements probe trials (brief perturbations of the cursor or target) were introduced to measure the visuomotor feedback gains. Participants performed one session of 2800 trials over two days, followed by a second 2800 trial session where the task-relevancy between the cursor and target was switched. The order of these two sessions was randomized across participants. Our results examine to what degree these two systems can be independently regulated and provide new insight into the online visual control of reaching movements.
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1-B-11 Visual error and internal model uncertainty contributes to visuomotor feedback gains

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When humans adapt to novel dynamics, large increases in their visuomotor feedback gains are observed during early adaptation. We have proposed that this increase might be due to internal model uncertainty. That is, when we experience large errors we have increased uncertainty in our ability to predict the environment, and therefore increase feedback gains and co-contraction as a coping mechanism. In order to test this hypothesis, we conducted two experiments. In experiment 1, we examined how these visuomotor feedback gains change during adaptation to abrupt or gradual introduction of a force field. In experiment 2, in order to separate internal model uncertainty from visual error signal contributions to this feedback gain increase, we tested the same protocol in the absence of visual error information. Participants grasped the end of a robotic manipulandum while making forward reaching movements. After initial movements in a null field, a force field was introduced either abruptly or gradually. Throughout the entire experiment, probe trials (mechanical channel with a visual perturbation of the cursor) were used in order to measure the visuomotor feedback response. In addition, in experiment 2 all non-probe trials were performed in a visual channel where the cursor always moved straight to the target regardless of lateral error. In experiment 1, abrupt introduction of the force field produced large increases in feedback gain, which gradually decreased to a plateau over the course of learning. In the gradual condition, these visuomotor feedback gains slowly increased until they reached the same plateau as abrupt condition. Experiment 2 showed a similar pattern, but with suppressed visuomotor feedback gains in both conditions throughout the experiment. The removal of this visual error information inhibited the visuomotor feedback gains, but increased co-contraction, demonstrating that visuomotor feedback responses are independent from the level of co-contraction. We have demonstrated a direct connection between learning and predictive visuomotor feedback gains, independent from the visual error signals. Overall, this work supports our hypothesis that internal model uncertainty drives initial increases in feedback gains.

1-B-12 Muscle activation strategy during fatigue

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It is well known that during sustained or repeated voluntary contractions, the amplitude of motor unit force twitches decrease as fatigue develops, and the excitation to the motoneuron pool increases both the firing rates and recruitment of motor units to compensate for the decreasing force-generating capacity and sustain muscle force, [1]. While previous investigations have verified these adaptations to fatigue in the vastus lateralis muscle of the leg [2-3], contradicting observations have been reported in the first dorsal interosseous (FDI) muscle of the hand [4]. Because voluntary human movement is typically generated through coordinated patterns of muscle activation, we set out to investigate whether adaptations in inter-muscle activation during a fatigue protocol of repeated contractions in the FDI muscle may explain the contrasting observation. Five healthy (22-34 years old) subjects performed voluntary isometric contractions of the FDI sustained for 10 s at 50% maximal voluntary contraction force and repeated to the endurance limit. Motor unit action potentials and firing times were measured directly from recorded surface electromyographic (sEMG) signals using decomposition technology [5]. To monitor the contribution of coactive muscles to index finger abduction force during each contraction, we recorded additional sEMG signals from the flexor carpi radialis, extensor carpi radialis, and pronator teres muscles. Overall, we observed that FDI motor unit firing rates increased and recruitment threshold decreased by the end of the contraction series. However, in four subjects the increasing trend in FDI motor unit firing rates was not observed throughout the entire contraction series, but instead increased primarily throughout the first portion of the contraction series and then decreased as the subjects approached their endurance limit. This decrease in FDI motor unit firing rates during this later phase of the fatigue protocol was associated with increased sEMG root-mean-square (RMS) from the FDI muscle and decreased sEMG RMS from coactive muscles. Our findings provide evidence that increased excitation to the motoneuron pool of the FDI muscle leads to increased motor unit firing rates and recruitment to compensate for decreases in motor unit force-generating capacity during fatigue [6]. Importantly, our experiments indicated that occasional decreases in motor unit firing rates were likely a result of changes in inter-muscle activation strategy during fatigue to increase activation of coactive muscles leading to decreased activation of the fatiguing muscle, while the underlying motor unit control properties and responses to common excitation remained unchanged. References: [1] Bigland-Ritchie et al. J Physiol 1986 [2] Contessa et al. J Neurophysiol 2016 [3] DeRuiter et al. Eur J Appl Physiol 2005 [4] Enoka et al. J Neurophysiol 1989 [5] Nawab et al. Clin Neurophysiol 2010 [6] Adam and De Luca. J Appl Physiol 2005

1-B-13 Planter flexors activities during human upright standing are determined by cosine tuning

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Human bipedal stance is inherently unstable. The soleus (SOL) and medial gastrocnemius (MG) synergistically play a key role in stabilizing bipedal stance, but their activation patterns are quite different; MG tends to be more phasic and SOL is more tonic. It is unknown how the central nervous system controls the activation levels of these plantar flexors; however it is often thought that physiological differences in muscle fibre types and the size of motor units between these two muscles account for this difference in the activation pattern. For thigh muscles, it has been shown in an isometric leg force exertion that the muscle activity levels can be predicted by a combination of knee and hip joint torques, in a cosine tuning manner (i.e., thigh muscle activation is proportional to the orthogonal project from the knee-hip torque linear summation to the muscle's preferred torque direction (PTD), which is a representation on the torque plane where the muscle activation has the greatest sensitivity) (Nozaki D, et al. Journal of Neurophysiology, 93:2614-24, 2005). Here we tested whether cosine tuning can predict the unique activation pattern of each planter flexor muscle during standing. We hypothesized that the plantar flexors' activities can be similarly represented by the linear summation of the ankle/knee joint torques. Nine healthy adult males (20.7 ± 3.4 years; 174.1 ± 7.8 cm; 70.6 ± 7.0 kg) were asked to stand quietly with their eyes open. Their 3D body kinematics, kinetics as well as electromyography (EMG) signals from the MG and SOL were recorded. We found that the ankle/knee joint torques combination predicted the general trend of the measured EMG data using a multiple linear regression (correlation coefficient between the predicted and measured EMGs: r = 0.659 ± 0.093 and 0.558 ± 0.232 for MG and SOL, respectively). We also found that PTDs of the two muscles were -62.5° ± 18.6° and 12.9° ± 24.6° for MG and SOL muscles, respectively (i.e. -45° is equal ankle extension and knee flexion, 45° is equal ankle extension and knee extension). These differed from their mechanical torque directions based on physiological moment arms of each muscle with respect to their joints, which are -30° and 0° for MG and SOL muscles, respectively. These results suggest that the MG is more sensitive to knee flexion than ankle plantarflexion, and that the SOL muscles despite being a monoarticular muscle is sensitive to both ankle plantarflexion and knee extension, a joint it does not span. The ankle/knee joint torques combination as well as the PTDs account for the phasic activity of MG and for the tonic activity of SOL. Thus, the unique muscle activation patterns of MG and SOL can be accounted for by cosine tuning. Consequently, the central nervous system determines the muscle activation patterns based on the mechanics of muscles instead of their physiological characteristics.

1-B-14 Analysis of fixation points before and during writing a line

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When a person make a voluntary movement, it is known that he/she makes a motion plan before the movement depending on visual information. When drawing a line under the condition that the target path can be seen only before drawing the line and cannot be seen during drawing, more information for motion execution is needed before the movement because online feedback control is difficult. Even when tracing the target path, that is, the target path can be seen during tracing, it is expected that a certain degree of motion plan is made before tracing. Therefore, gaze analysis before the movement is important to investigate the motion planning of the voluntary movement. Many studies on eye-hand coordination often measured arm and eye movement during drawing, but there is few report on the experiment of measuring the gaze before drawing. In this study, we measure the eye movement before and during drawing or tracing a line and investigate what kind of information is obtained before the movement and how the information on the trajectory obtained before drawing or tracing is used for motion control. In this experiment, eye position and pen tip were simultaneously measured before and during the drawing or tracing task using Tobii Pro X3-120 and touch display. The measurement was performed in the dark room, and they fixed their head on a chinrest, and drew the target paths presented on the touch display 60cm away from the eyes. Ten subjects were required to draw or trace

32 kinds of paths consisting of sine wave, triangular wave, sawtooth wave, square wave. They performed drawing task and tracing task in different day. As a result of the analysis, the number of fixation points and scan path length before the movement in the drawing task were significantly more than the tracing task. It is suggested that the subjects confirmed the entire target path before drawing. During the movement, although there was no significant difference in scan path length, the number of fixation points during tracing was significantly more than drawing. Therefore, when tracing, online corrective feedback control seems to be performed more frequently. At last, in order to investigate how the information acquired before the movement is used during the task, fixation points during the movement at which subjects looked before the movement were examined. As a result, the ratio in the drawing task of the fixation points during movement corresponding to the fixation points before movement was larger than in the tracing task. In addition, pen position error at the corresponding fixation points that is the distance between the pen position and the target path was significantly smaller than the error at the other fixation points in the drawing task. These results suggest that in drawing task, a human search feature points on the target path before start drawing and controls own hand so as to pass through these points.

1-B-15 A stable, long-term cortical signature underlying consistent behavior

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For learned actions to be executed reliably, the brain must integrate sensory information, establish a motor plan, and generate appropriate motor outputs to muscles. Animals, including humans, readily perform such behaviors with remarkable consistency, even years after acquiring the skill. How does the brain achieve this stability? We explored this fundamental question by observing the behavior of populations of cortical neurons. Recent work suggests that the building blocks of neural function may be the activation of population-wide activity patterns, the neural modes, rather than the independent modulation of individual neurons. These neural modes, the dominant co-variation patterns of population activity, define a low-dimensional neural manifold that captures most of the variance in the recorded neural activity. We refer to the time-dependent activation of the neural modes as their latent dynamics. We hypothesize that the ability to perform a given behavior in a consistent manner requires that the latent dynamics underlying the behavior also be stable. We developed a simple linear method to examine the stability of the underlying latent dynamics despite the unavoidable changes in the set of neurons recorded when using chronically implanted microelectrode arrays. We used the sensorimotor system as a model of cortical processing, and analyzed the recorded activity of neural populations, approximately one hundred neurons at a time, in each of three different cortical areas: dorsal premotor cortex (PMd), primary motor cortex (M1), and primary somatosensory cortex (S1), as monkeys performed an instructed-delay reaching task. This allowed us to probe the stability of latent dynamics during the three main aspects of movement generation: movement planning, movement execution, and feedback processing. Despite steady turnover in the recorded neurons, the latent dynamics in all three areas, PMd, M1, and S1, remained stable for up to two years of recordings. Remarkably, the "aligned" latent dynamics were almost as stable across different days as they were across subsets of trials within the same day. Such stability allowed reliable decoding of behavioral features with a fixed decoder for the entire timespan, whereas performance degraded substantially when using the unaligned recorded activity as inputs. Decoders based on the aligned latent dynamics were virtually as accurate as decoders

based on the full neural population when trained and tested on the same day. We posit that latent cortical dynamics within the neural manifold are the fundamental and stable building blocks underlying consistent behavioral execution. This observation argues for the development of Brain-Computer Interfaces based on latent dynamics as opposed to recorded neural activity. The periodic alignment of the latent dynamics would achieve accurate performance through months or even years of neural turnover. * Study available as bioRxiv preprint https://doi.org/10.1101/447441

1-B-16 Proactive and reactive modulation of cortical excitation and inhibitory mechanisms during selective stopping of a planned bimanual action

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Stop signal tasks have proved invaluable in our understanding of inhibitory function. However, many tasks require rapid cancellation of one component of an action, while continuing to execute other action components. Reaction time (RT) delays of ~100ms in such tasks suggests that such 'selective inhibition' relies on a global stopping mechanism followed by re-initiation of the required (non-cancelled) action. Here we used dual-site transcranial magnetic stimulation (dsTMS) to investigate the interhemispheric mechanisms of selective inhibition. 21 healthy adults (19-41 y) responded to an imperative stimulus (IS) with simultaneous button presses with the left (L) and right (R) index fingers. On 1/3 of trials the IS was followed by a stop-signal (SS) requiring cancellation of only the L or R response. To assess the extent to which expectation can influence inhibitory function, a cue preceded the IS in some trials informing participants as to which hand might be required to stop. dsTMS assessed corticospinal excitability (CSE) and distinct interhemispheric inhibitory (IHI) pathways between the primary motor cortices (M1). While cues reduced the RT delay by 21 ms (p=0.002), selective stopping was less efficient in cued trials as indicated by a 10 ms increase in SSRT (p=0.031). During the movement preparation period (prior to IS), CSE was lower in both hands in cued, relative to uncued, conditions (p=0.002) irrespective of which hand potentially had to inhibit its response. During the same period, IHI mediated by direct pathways between M1s was unaffected by cues; however, a greater release of IHI mediated by indirect (frontal) pathways (and thus affected by cognitive components of the task) was observed in cued trials in both hands (p=0.025). The data suggest proactive control of selective stopping may result in activation of an indirect stopping network which has independent effects on M1 excitability and inhibitory mechanisms.

1-B-17 Shocking discoveries: The effect of penalty modality on decision making and movement trajectories

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The use of cognitive penalties, such as monetary loss, have been widely used in decision-making research, however there is less research involving how physical penalties, such as pain, affect decision making and risk taking. Physical penalties may be especially relevant for action selection type tasks where one of the actor's aims is to avoid injury. The purpose of the present study is to compare the evolving selection process between when people must choose between options that either differ based on physical or cognitive penalties. Participants were presented with two targets that were each overlapped by a penalty region. Participants are asked to select a target by rapidly reaching to touch it while their reach trajectory was recorded. When hit, the target yielded a monetary reward. When the penalty region was hit the participant would receive a monetary loss (cognitive penalty) or a cutaneous electric shock (physical penalty). Notably, each penalty type had a high and low-value version, allowing for observation of the effect of the magnitude of the penalty. The results revealed individual differences where participants employed one of four possible strategies when making decisions with regard to which target/penalty configuration to choose: those who preferred cognitive penalties; those who preferred physical penalties; and those who changed their preference based on the magnitude of the penalty; those who were indifferent of the form of penalty presented. In brief, analysis comparing movement trajectories between groups suggest that groups that have a clear preference for one mode of penalty have more direct movements than those who are less decisive about the mode of penalty they are willing to risk. Furthermore, if participants select their non-preferred penalty, their movements are also less direct.

1-B-19 Bilateral motor synergies and interlimb force coordination in older adults

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Aging progression may impair an ability to modulate bilateral actions. The purpose of this study was to examine age-related changes in interlimb coordination by quantifying bilateral motor synergies based on the uncontrolled manifold hypothesis approach. Ten older adults and 10 young adults participated in this study. Participants executed 12 bilateral force control trials at 5% of their maximum voluntary contraction level under two different vision conditions (i.e., with and without visual feedback). Two-way mixed model (Group x Vision Condition; 2 x 2) ANOVAs with repeated measures on the last factor were used for statistical analyses. The findings showed that older adults produced an increase in mean force from vision to no vision condition and more symmetrical force variability between hands (non-dominant hands > dominant hands) collapsed across vision conditions than those in the young adult group. Finally, bilateral motor synergies in the older adult group was significantly lower than in the young adult group in the vision condition. In summary, the current findings indicated that aging progression may interfere with bilateral movement execution as well as coordination patterns across multiple trials.

1-B-20 Enhancing motor sequence consolidation using anodal tDCS at primary motor cortex during a repetitive practice format

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Learning a number of motor sequences simultaneously is facilitated by using an interleaved as opposed to repetitive training schedule typically manifest as superior consolidation and long-term retention. Emergence of greater functional connectivity of dorsal premotor region (PMd) and primary motor cortex (M1) during interleaved (IP) compared to repetitive practice (RP) has been reported to be associated with IP learning benefits. Moreover, M1 has been reported to be central to consolidation of motor memories. Interestingly, low- frequency rTMS following IP, used to disrupt consolidation, failed to reduce IP retention gains. The present work was an initial attempt to modify the involvement of M1 during as opposed to after IP and RP. Specifically, participants were exposed to cathodal transcranial direct current stimulation (tDCS) at M1 of 2 mA during approximately 20-min of IP or anodal tDCS while practicing within a RP. In addition, IP and RP sham conditions were included as controls. Our working hypothesis was that cathodal or anodal stimulation would suppress or facilitate recruitment of M1 respectively. As a result, it was expected that suppressing M1 activity during IP should hinder performance especially consolidation that occurs immediately after practice. Less clear however was if facilitating M1, via anodal stimulation, could enhance the effectiveness of RP resulting in gains in retention performance. Performance of the trained skills was determined prior to and immediately after practice, as well as 6-hr, 24-hr, 48-hr, and 72-hr later for all participants. Results revealed the typical outcome for training and test performance following the sham stimulated IP and RP participants. That is, RP led to superior performance immediately after practice finished yet IP led to significantly more success at the test administered 72-hr after practice. This was a result of stable performance across the first 6-hr and further improvements presumably due to sleep-dependent consolidation. While application of cathodal tDCS during IP impaired performance in the presence of the stimulation, the offline improvements remained. As anticipated, RP with sham stimulation revealed significant forgetting in the initial 6-hr reflecting a lack of time-dependent consolidation as well as modest improvement across the next 72-hr. Importantly, application of anodal tDCS during RP mitigated the forgetting that is typically associated with this practice format during the initial 6-hrs as well as enhancing subsequent overnight improvements. Thus, upregulating M1 activity during RP resulted in improved time-and sleep-sensitive consolidation processes that are effectivity supported during IP.

1-B-21 Neuromuscular adaptation subserving independent control of finger movements in musicians

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Human hand dexterity enables various tool-use such as typing a computer keyboard and manipulating a smartphone. Through further training, human can acquire exceptionally dexterous motor skills such as playing a musical instrument and surgery (Furuya et al. 2014), in which the fingers move highly independently. Yet, even trained musicians cannot move their fingers completely independently (Furuya et al. 2011). Two factors limit independent movement control across fingers (Lang and Schieber 2004). One is active neuromuscular constraints within the nervous system, whereas the other is passive mechanical coupling between the fingers via the internal anatomical binding within the hand and forearm. In musically untrained individuals (i.e. non-musicians), passive mechanical coupling limits the independent movement control across fingers to a larger extent than active neuromuscular constraints (Lang and Schieber 2004). However, it is unclear how these features are altered in pianists being capable of moving their finger independently. The purpose of this study is firstly to define differences associated with independent movement control across fingers between pianists and non-musicians, and secondly to identify an association between the finger movement independence and dexterous motor skills. To these aims, two studies were conducted. The first study assessed differences in neuromuscular and biomechanical features of the fingers between pianists and non-musicians. The result showed no group differences in biomechanical characteristics such as mechanical constraints on independent control of the fingers and the finger abduction-adduction range of motion. By contrast, pianists moved their middle finger more independently particularly when moving fast compared with non-musicians. In addition, neuromuscular constraints on independent control of the middle finger movement were reduced in the pianists than non-musicians. These results indicate enhancement of the finger movement independence through neuromuscular adaptation in pianists who underwent extensive musical training. The second study assessed factors explaining individual differences in motor skills across pianists. The result showed no relationship of the maximum finger tapping speed with both finger movement independence and neuromuscular constraints. Intriguingly, the tapping speed covaried with the maximum force level, the range of motion, and biomechanical constraints. For example, the tapping speed of the middle finger covaried negatively with biomechanical constraints on the index finger, and positively with the maximum force level for the ring finger flexion. These results suggest that the individual differences in the fast finger movements across trained pianists were explained not by finger movement independence, but by biomechanical characteristics of the hand. Taken together, these implicates that effective training on the dexterous finger movements depends on musical expertise.

1-B-22 Motor decision-making in the face of competing descending control

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Descending signals from the brain are responsible for controlling behavior features including the order of movement sequences, their timing, or their amplitude, giving rise to different actions. These descending signals in some cases are carried by so-called "command" neurons which - in many species including cats, rodents, stick insects, cockroaches and flies - are sufficient to drive specific behaviors including walking and grooming. Understanding how populations of descending neurons and this special class of "command" neurons work together to orchestrate multiple behaviors is a fundamental requirement for understanding movement control. Drosophila melanogaster is a valuable model organism for the study of descending control: It has a powerful genetic toolkit enabling the targeting of individual, or populations of descending neurons. Genetic screens have revealed a number of different "command" neurons that drive, for example, backward walking (Moonwalker Descending Neurons or MDNs), or antennal grooming (antennal Descending Neurons or aDNs). These genetic reagents provide a powerful means of testing how different commands are resolved in the context of action selection (i.e., what to do next in the face of competing and conflicting stimuli). In my poster, I will describe a series of experiments aiming to uncover a simple decision-making process: executing a single motor action in the face of multiple descending commands. Specifically, I am using a GAL4/UAS binary system to optogenetically activate MDNs and/or aDNs. A novel automated robotic behavioral screening system was developed and different optogenetic stimulation intensities were tested to explore the range of decision-making outcomes. Finally, a pose estimation deep network was used to quantify multiple limb and body features across datasets and these data were classified to quantify the degree to which backward walking and/or grooming behaviors were expressed in this conflicting command scenario. Following up on these studies, I will also present preliminary data for future experiments, aiming to exploit 2-Photon-based spatially resolved optogenetic stimulation to further dissect how animals decide on what to do in the face of conflicting descending signals.

1-B-23 Modulation of event-related spectral perturbations in the μ band during a position matching task: a study about neural correlates of upper limb position sense

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Proprioceptive information allows us to perform smooth coordinated movements by constantly updating us with knowledge of the position of our limbs in space. How this information is combined and centrally processed to form conscious perceptions of limb position is still relatively unknown. μ oscillations across the cortex have been used to characterize the neural dynamics associated to motor control and behavior. What has proven more elusive is pinpointing the contribution of proprioception in the cortical activity related to motion. The goal of the present study was to develop an experimental protocol that would combine EEG activity and a robot-based proprioceptive test, with the specific objective to compare the pattern of neural activity between active movements performed with and without visual feedback, under visuo-proprioceptive and proprioceptive condition respectively. To this aim, we collect EEG from a group of 23 healthy individuals while they performed a robotic position matching task in which they had to replicate a target position with the upper limb. We examined the cortical representation, in terms of event-related spectral perturbation (ERSP) in the μ band. We then compared the cortical activations in the two feedback conditions. We observed increased μ band activity in the left motor area and left somatosensory area, contralateral to the moving limb. In contrast, parietal and occipital regions, identifying association and visual brain area respectively, showed similar activation in the two hemispheres. Different activation in the μ band emerged in the two conditions, predominantly at movement's offset, due to an increased μ band activity in the visuo-proprioceptive condition. Such effect scaled with the brain region, with the highest difference in the visual and association areas decreasing in the hand motor and somatosensory areas. Our results suggest that when movements are performed relying only on proprioceptive feedback, a different cortical activity is entailed, with respect to the case in which visual information is provided. We offer evidence that feedback condition affects mostly the desynchronization at movement's offset with low or no influence at the onset of movement. Further, the brain area modulates the difference in the μ power under the two feedback conditions with less evidence in motor and somatosensory areas. We believe that a comprehensive study of upper limb position matching including, at the same time, its neural correlates during an active matching task is needed to better understand how the brain processes the limb position sense information and if there are differences with respect to the visual processing of active movements. Moreover, a deeper investigation of proprioception can improve the comprehension of human physiology and motor control, but will also allow to move forward in the understanding of how to help the brain recover from an injury and restore the proprioceptive sense in prosthetics.

1-B-24 Continuous neural and whole-body kinematic recordings across the rodent behavioral repertoire

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A longstanding goal of neuroscience has been to understand how different brain areas contribute to the acquisition and control of movement. In support of this goal, techniques for large-scale neural recordings have made rapid progress in recent years, however complementary techniques for characterizing motor behavior have yet to emerge. As a result, experiments probing the relationship between neural activity and movement often do so across a limited range of motor behaviors, preventing a general understanding of the relationship between movement and brain activity. To address this, we developed a new behavioral monitoring system, CAPTURE, that combines motion capture and deep learning to track in 3D twenty points on a rat's trunk and appendages, continuously, across the full repertoire of home-cage rodent behavior. We validated CAPTURE's ability report the known kinematics, sequential organization, and circadian modulation of grooming and locomotor behaviors. CAPTURE can identify >1000 distinct movement elements, and additionally revealed unanticipated variability in the kinematics and sequencing of behaviors commonly assumed to be stereotypic, such as grooming. CAPTURE also revealed previously undescribed perturbations in movements and behavioral organization following pharmacological challenges and in animal models of disease. Analysis of behavioral organization revealed that rodent home-cage behavior is comprised of long-timescale behavioral states, common across animals, that modulate the kinematics and sequencing of a shared set of behaviors. We combined CAPTURE with continuous neural recordings in the dorsolateral striatum, a brain region with an often debated role in controlling diverse aspects of movement kinematics, action selection, and behavioral sequencing. Preliminary analyses of striatal recordings revealed that neurons are active across multiple behaviors, involving disparate poses and appendage movements. However analyses at longer timescales revealed that striatal neurons were preferentially active during individual long-timescale behavioral states, suggesting behavioral context may strongly influence movement encoding in the brain. Overall, CAPTURE should enable new efforts in phenotyping, studies of behavioral organization, and significantly advance our understanding of how the brain underlies motor behavior.

1-B-25 Optimal force production via flexible neural control of motor units

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Roughly 102-103 motor units (MUs) control each muscle, providing myriad ways to generate a particular force profile. Nevertheless, MUs are believed to obey an orderly recruitment process, the 'size principle' (SP), wherein small MUs are recruited before larger MUs. Intriguingly, several studies report deviations from the SP during dynamic movements, but whether such deviations are instances of a broader phenomenon remains unclear for three reasons: the lack of a hypothesis predicting when deviations should be observed; an inability to directly document deviations given the challenge of isolating single MU spikes; and uncertainty regarding whether supra-spinal mechanisms could utilize additional degrees of freedom. We used mathematical optimization to develop predictions regarding MU recruitment. We tested those predictions using a new experimental paradigm and novel spike-sorting methods. Finally, we asked whether cortical recruitment of MUs extends beyond the single degree of freedom associated with the SP. Predictions were derived from the recruitment strategy that best matched actual force to desired force. We modeled an idealized motor pool of five MUs of varying size. As observed empirically, larger MUs had briefer twitch responses. Optimization predicted that recruitment should obey the SP for steady forces, but deviate from the SP for rapidly changing forces. Specifically, there should be preferential recruitment of larger MUs, whose briefer twitch responses are better suited for rapid force fluctuations. We trained a monkey to generate a variety of force profiles (steps, ramps, sinusoids, and chirps) via isometric contractions of the anterior deltoid, whose activity we recorded using 8 modified percutaneous electrodes. We leveraged Bayesian nonparametrics and optimal filtering to decompose EMG into the spike times of single MUs. For steady forces, MU activity lay on a 1-dimensional nonlinear manifold (as predicted by the SP), but departed from this manifold for higher frequency (>1 Hz) forces. MU activity in both steady and dynamic regimes were consistent with our model. Our theoretical and empirical results suggest that MU recruitment depends both on instantaneous and future force commands. The need to consider the future suggests supra-spinal structures may play a role in recruitment. To test this, we used microstimulation of sulcal motor cortex, via a 32-channel linear array, combined with simultaneous EMG recordings as described above. Microstimulation produces artificial activation under experimenter control, yielding the potential to reveal degrees of freedom that are available but rarely used, and might be difficult to otherwise observe. We found that stimulation recruited MUs in ways that often deviated from the 1-dimensional manifold observed during steady force production. Thus, MU recruitment is flexible, force-profile specific, and can be influenced by descending control.

1-B-26 Motor cortex mediates forelimb antagonist muscle cocontraction using a distinct control strategy

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During limb movement, spinal circuits ensure the alternating activation of antagonist flexor and extensor muscles. Many movements, however, require cocontraction of antagonist muscles, as when preparing to oppose a load or learning precision movements. The neural mechanisms that enable antagonist cocontraction remain unclear. Certain results suggest that during cocontraction, flexion- or extension-related neurons in motor cortex (M1) are coactivated via a decrease in intracortical inhibition. Other results suggest that cocontraction requires a distinct form of cortical influence that suppresses reciprocal inhibition between antagonist spinal circuits. Corticospinal neurons synapse onto spinal interneurons capable of such suppression, suggesting that M1 may regulate cocontraction through these connections. To test whether cocontraction is mediated by inhibitory gating or a distinct control scheme, we first developed a behavioral paradigm in which head-fixed mice are trained to turn a small wheel with their forelimb, which involves biceps-triceps alternation, then to isometrically cocontract these muscles. M1 inactivation with muscimol severely degrades performance of both tasks. We performed multi-electrode array recordings in M1 output layers as mice behaved in this paradigm, aggregating recordings from hundreds of neurons in individual mice. Using waveform width to infer neuronal identity, we found that inhibitory and pyramidal cells show reduced activity during cocontraction relative to alternation. Furthermore, during cocontraction, almost all inhibitory interneuron firing rates increased in proportion to excitation, suggesting a balance between the two rather than inhibitory gating. To assess the relationship between M1 activity and motor output during both tasks, we then fit linear models of trial-averaged neural activity to muscle activity. Models trained with alternation data poorly fit data from cocontraction, indicating the relationship between neural and muscle activity varies between contraction modes. Moreover, principal components that capture most neural variance during alternation capture very little during cocontraction, suggesting that cocontraction does not rely on a summation of flexion and extension-related neural activity. We then used two-photon calcium indicator imaging to measure activity in corticospinal neurons during both tasks and observed that the above findings hold specifically for this population. Currently, we are using a transsynaptic rabies-based approach together with calcium indicator imaging to examine whether corticospinal neurons that specifically target spinal interneurons implicated in mediating cocontraction are preferentially recruited during our cocontraction task. Collectively, our results indicate that M1 uses a specialized control strategy during antagonist muscle cocontraction.

1-B-27 Differential impact of interhemispheric inhibition on motor mirroring in the aged brain

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With advancing age, various changes in the brain take place and their behavioral impact is of pivotal interest and relevance especially in the view of the increase in average life expectancy. Older adults have been shown to recruit larger areas of the brain such as bilateral primary and secondary motor cortical areas during unimanual tasks. These age-related changes are often discussed as adaptive processes, likely supporting the successful processing of motor tasks. However, the recruitment of additional bilateral cortical activity might have behavioral "cost"; it is thought to lead to activation of the corticospinal tract bilaterally, resulting in involuntary mirror activity in the contralateral side. Transcallosal inhibition is hypothesized to be of particular importance in the prohibition or manifestation of mirror activity. Based on previous studies showing larger mirror activity in older adults, age-related changes of transcallosal inhibition are thus expected. Here, we investigated transcallosal inhibition and its functional relevance for mirror activity in young and older adults. Transcallosal inhibition was assessed in two states, resting and active conditions, using a well-established double-pulse transcranial magnetic stimulation paradigm (Ferbert et al., 1992) in 14 young (26.3 ± 3.4 years, mean ± standard deviation) and 15 older (69.9 ± 4.6 years, mean ± standard deviation) participants. None of the participants had a history of serious medical, neurological, psychiatric illnesses, or any contraindications for transcranial magnetic stimulation. Mirror activity was assessed with a modified version of a bimanual motor task used in previous studies (Mayston et al.1999; Hübers et al. 2008). In agreement with previous studies, the amount of mirror activity observed in the young and older group was different: the older group demonstrated larger mirror activity than the young group. However, in contrast to our hypothesis, the degree of transcallosal inhibition did not differ between the groups. In the young group, the degree of transcallosal inhibition was associated with the amount of mirror activity; however, the same association was not found in the older group. Our results point towards a lack of functional efficacy of transcallosal inhibition in older adults. A possible underlying mechanism is defective task-related modulatory capacity of transcallosal inhibition observed in the older group. This suggests an altered neuronal system suppressing activity of the contralateral side with respective behavioral consequences, i.e., increased mirror activity.

1-B-28 Reticulospinal drive with a flexor bias can be detected as alpha-band shared neural drive during voluntary tasks in healthy individuals

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There is growing evidence suggesting that synchronized activity between muscles at ~10 Hz (α-band), quantified by coherence analysis, reflects their shared neural drive arising from the reticulospinal pathway. This α-band shared neural drive can be observed, for example, across muscles in response to acoustic startle, which is transmitted via the reticulospinal pathway. Interestingly, muscles involved in pathologic flexion synergy post stroke also show exaggerated α-band shared neural drive. This is consistent with a previous suggestion that inappropriate activation through the reticulospinal pathway is an important for expression of such pathologic synergies. However, little is known whether or not such drive exists in healthy individuals during voluntary actions. To test this possibility, we measured intermuscular coherence between the muscle pairs driving isometric wrist torque in 4 directions (flexion and extension, and radial and ulnar deviation). As present in flexion synergies post stroke, we expect that flexor muscles receive stronger reticulospinal drive, and therefore stronger α-band shared neural drive, compared to extensors. Conversely, corticospinal drive may play the predominant role in the control of radial/ulnar deviation. Thus, we expect a lack of α-band shared neural drive between muscles during those actions. We first asked twelve consenting participants to produce constant, isometric wrist flexion or extension torque at 20% MVC, and calculated pair-wise EMG coherence across synergistic wrist flexors and extensors. We found that wrist flexors showed significantly higher α-band coherence compared to the extensors ($p < 0.01$). This was not altered by error augmentation in visual feedback, nor related to force variability during the isometric holds (both of which can alter proprioceptive feedback). Since the relative strength of reticulospinal drive may increase with contraction level, we then asked three of the participants to perform the wrist flexion task at 5% and 30% MVC. In them, coherence in the α-band increased with contraction level ($p < 0.01$). Finally, to confirm the dominance of corticospinal drive in radial-ulnar deviation torques, we asked a subset of participants ($n = 2$) to perform those actions. We found no significant α-band coherence between radial deviators (FCR and ECR) nor ulnar deviators (FCU and ECU). Our results strongly suggest that intermuscular coherence reflects the differential contribution of corticospinal vs. reticulospinal pathways during voluntary actions by healthy individuals. The impactful corollary to this result is that intermuscular coherence can be used to assess re-organization of cortico- and reticulo-spinal pathways that results in pathologic synergies.

1-B-29 Nerve-specific sensory attenuation during muscle contraction

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BACKGROUND AND AIM: For motor control, sensory information plays an important role, but if the information is too much and not regulated, it would be difficult to use the information effectively. The sensory weighting hypothesis is proposed, which screens the sensory information depending on importance relating to the willing movement, allowing humans to plan and execute movements efficiently. A lot of research has shown that the transmission of somatosensory signals to the primary somatosensory cortex is suppressed during active movement. Somatosensory evoked potentials (SEPs) is one way to measure this attenuation phenomena. Those measurements were performed mainly by median nerve stimulation. Median nerve is a mixed nerve with cutaneous and proprioceptive nerve. If the importance of the information alters depending on nerve types, the attenuation of SEPs would show different modulation. Therefore, the purpose of this study was to investigate the difference of modulation of SEPs during muscle contraction from different nerve types. METHODS: Ten healthy subjects (all right-handed) participated. We electrically stimulated one of three nerves to obtain SEPs; median nerve (MED: mixed nerve), superficial radial nerve (SR: cutaneous nerve) and deep radial nerve (DR: proprioceptive nerve) on the right arm. We tested on three conditions on wrist joint; at rest, isometric contraction of palmer flexion (PF) and isometric contraction of dorsiflexion (DF). Isometric contraction was 20% of maximal voluntary contraction, hold for 30 seconds with visual feedback. Electroencephalographic (EEG) signals were recorded with 63 electrodes and separated into brain activity, blink, eye movement, and other artifacts by using independent component analysis. The SEP amplitude was calculated on the component of P14-N20 and N20-P27 at CP3, the electrode contralateral to the side of the stimulation. RESULTS: The first component of SEP amplitude on all three nerves demonstrated no attenuation. The second component of SEP amplitude on MED suppressed during isometric contraction both DF and PF. On SR, the second component suppressed only on DF compares to rest condition. However, the amplitude On DR showed no suppression on isometric contraction. These results show that the attenuation of SEPs is occurred not only on MED but also SR

which is a cutaneous nerve. On the other hand, DR which is a proprioceptive nerve showed no attenuation, suggesting proprioceptive information might be needed for the task of holding the muscle activity on a certain level and keeping the wrist joint at a certain angle. CONCLUSION: The present study demonstrated the possibility of different sensory gating mechanism with certain nerve types. The somatosensory input from cutaneous nerve is suppressed during muscle contraction in order not to disturb motor command whereas proprioceptive input might favor the somatosensory information to plan and execute movements.

1-B-30 Role of Mesencephalic Locomotor Region in modulating locomotor modules in the lumbosacral spinal cord.

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Given the huge number of muscles to control when performing a movement, the central nervous system uses a simplifying strategy to quickly and accurately select motor commands without sacrificing too much behavioral diversity. It has been proposed that spinal interneurons are organized in "motor modules" that activate specific groups of muscles that can be linearly combined, allowing the generation of diverse behavioral patterns with a small number of modules. Here, we investigate how hindlimb locomotor motor modules encoded in the murine lumbosacral spinal cord are activated by supraspinal structures. Indeed, stimulation of the lumbosacral grey matter activates motor modules that generate locomotor patterns. These patterns can be triggered and modulated by the descending control system that involves the midbrain. In particular, the Mesencephalic Locomotor Region (MLR) plays a fundamental role in initiating and modulating locomotion. Recent findings showed that locomotor functions are regulated by two distinct MLR nuclei - the cuneiform (CnF) and pedunculopontine (PPN) nuclei, involved in fast escape responses and slow explorative behaviors, respectively. Our aim is to examine to what extent the MLR regulates locomotor behaviors by activating and modulating the motor modules in the lumbosacral spinal cord. We optogenetically stimulated the MLR (N=4) and lumbosacral spinal cord (N=9) in two separate groups of anesthetized Thy1-ChR2 transgenic mice in which ChR2 is expressed in excitatory neurons. Motor modules were represented as light-evoked isometric ankle forces across different workspace locations. In the MLR group, either the contralateral CnF or PPN was stimulated (duration of 100, 200, 500 or 1000 ms at 20, 100, or 150 Hz, at 3 laser intensities in 3% increments from minimum). In the spinal group, force fields along the entire length of the ipsilateral lumbosacral cord were elicited by successive rostral-to-caudal repositioning of the laser in 0.1 mm increments; the minimum laser intensity that evoked an observable force (200 ms; 100 Hz) was used. The MLR force fields were then compared against the spinal fields. We first assessed the force-field dimensionality using principal component (PC) analysis, which showed that 3 PCs explained 95% of the spinal data, but 9 PCs explained only 81% of the MLR data. We then used a gradient descent algorithm to extract fundamental force fields underlying all spinal fields. Four fundamental fields explained the spinal data at R2=77%, but the same spinal fields explained the MLR data (through a least squares fit) only at 44-63%. This spinal-to-MLR fit also showed that the activation magnitude of one spinal field increased with increasing MLR stimulation intensity. Our data suggest that the MLR regulates locomotion by modulating at least a subset of spinal modules, but the lumbosacral modules are not sufficient in explaining the diversity of hindlimb behaviors that can be triggered by the MLR.

1-B-31 Acute effect of blood flow restriction on muscle activation and force fluctuations during repetitive low load exercises

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Objective. Recent studies demonstrated that blood flow restriction (BFR) in combination with low load exercise is beneficial to increase muscle strength after a long-term training. However, acute effects of BFR during repetitive low load exercise are less investigated. With muscle oxygen saturation (SmO2) monitored, this study contrasted characteristic differences in surface electromyography (EMG) and force fluctuation with and without BFR during repetitive low-level isometric wrist extensions contraction. Methods.Nine healthy participants (age :26.6±1.8 yrs; 4 men and 5 women) were included in this study. Under visual guidance, they conducted eight successive contraction trials of 44-second isometric wrist extensions contraction at 20% of maximum voluntary (MVC) in the BFR and no restriction (NR) conditions. The order for the two conditions was randomized, and the two conditions were separated at least 48 hours. SmO2, force output and multi-electrode surface EMG were collected during the experiment. MVC was determined immediately before and after the repetitive low-level isometric wrist extensions contraction. Force and EMG parameters in the late phase of the exercise (the 7th and 8th trials) were normalized to those in the early phase of the exercise (1st and 2nd trials) for both the BFR and NR conditions. Paired t statistic was used to examine hypoxia-related declines in contraction capacity, by contrasting those normalized variables (the late phase relative to the early phase) between the BFR and NR conditions. Results. Normalized MVC decreased significantly in the BFR condition (82.2±2.1 %) than that in the control condition (93.4±3.0 %)(p =.002). Normalized sample entropy of force fluctuations in the BFR condition (95.1±2.5%) was smaller than that in the NR condition (104.3±2.9 %)(p =.026), in support of hypoxia-related decline in the complexity of force fluctuations. But, normalized root mean square (RMS) of force fluctuations was not significantly different between the two experimental conditions (p >.05). In addition, normalized RMS and mean frequency of the surface EMG did not differ between the BFR and NR conditions (p >.05). The force and EMG variables were contrasted under the condition of a significant lower SmO2 during the contraction of the BFR condition (average SmO2_BFR: 58.6%±4.7%) as compared with the NR condition (average SmO2_BFR: 84.2 %±5.5%)(p < .05) Conclusions. Force steadiness and muscle activities for repetitive low-load static contraction appears not to be vastly affected by acute effect of partial arterial occlusion, despite that blood flow restriction reduces blood oxygen in the working muscle. Nevertheless, force generation strategy underlying BFR is implicitly altered, in view of hypoxia-related reductions in MVC and force fluctuation complexity.

1-B-32 Movement preparation time determines the precision of movement preparation

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All our movements have a certain degree of variability, which is due to noise in the planning as well as execution of the movement, among others. It is well-known that decreasing the movement execution time increases the variability, but how will decreasing planning time affect variability? A recent study found that the accuracy of a movement is unrelated to its reaction time, suggesting that movement preparation and initiation are independent processes (Haith, Pakpoor, & Krakauer, 2016). If so, it can be

hypothesized that the reaction time is unconnected to the planning variability. On the contrary, in macaques it is known that variability in preparatory activity declines after target onset and shapes movement variability. From this perceptive, shorter reaction times could also be associated with more movement planning variability. To test between these hypotheses we had subjects perform speeded reaching movements to four unpredictable target locations. Reaction time was manipulated by using two different stimuli: a visual target or a visual target accompanied by a non-startling, non-informative auditory beep. To characterize variability we measured the standard deviation of the heading angle across trials during each time point of the movement. The beeped trials showed reduced reaction times compared to non-beeped trials (RT difference = 23 ms). Furthermore, movements with shorter reaction times were more variable during the first phase (first 100 ms) of the movement than movements with longer reaction times, although movement time, peak velocity and endpoint accuracy were very similar. These results are consistent with the simple principle that time-dependent variability of a movement trajectory is dependent on 1) the initial variability that is determined by the movement preparation time, and 2) feedback-driven decay in variability after the onset of the movement. We conclude that the precision of movement preparation is determined by movement preparation time.

1-B-33 Characterizing age-related changes in supplementary motor area primary motor cortex connectivity

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Cortico-cortical connectivity between motor areas is important for motor control. The supplementary motor area (SMA) is densely connected with the primary motor cortex (M1); these two regions are important for bilateral motor control. Connectivity within the cortical motor network declines with advancing age, therefore, age-related changes in SMA--M1 connectivity might underlie age-related decline in bilateral motor control. First, we examined the reliability of facilitatory interactions between SMA--M1 measured using transcranial magnetic stimulation (TMS): we hypothesized good test re-test reliability for SMA--M1 facilitation. Second, we measured SMA--M1 facilitation in younger and older adults, and investigated associations between SMA-M1 facilitation and bilateral motor control: we hypothesized less SMA--M1 facilitation in older than younger adults, and positive associations between SMA--M1 facilitation and bilateral motor control. Dual-coil TMS was used to measure SMA--M1 facilitation (and preSMA--M1 as a control): a conditioning TMS pulse to SMA preceded a test TMS pulse to M1 by 7 ms. The Purdue Pegboard and four square step test were used to measure bilateral motor control of upper and lower limbs, respectively. An intra-class correlation coefficient of 0.74 showed good test re-test reliability of SMA--M1 facilitation. SMA--M1 facilitation was reduced in older compared to younger adults, and SMA--M1 facilitation was positively associated with task performance. Findings suggest that SMA--M1 facilitation can be reliably measured with TMS, and that reduced SMA--M1 facilitation with age might play a role in age-related decline in bilateral movement control.

1-B-34 Remote activation of the ventral midbrain using tDCS of prefrontal cortex enhances online performance of a motor sequence skill

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Remote activation of ventral midbrain by transcranial direct current stimulation (tDCS) of prefrontal cortex was recently reported to enhance prefrontal-midbrain connectivity and increase attractiveness ratings. It was proposed that an increase in midbrain dopamine resulted from anodal tDCS of frontal cortex which in turn contributed to the modified behavior. Both consolidation and long-term retention following practice of sequential motor skills is enhanced possibly through reward-related dopaminergic signaling to M1. The primary objective of the present work was to determine if the application of anodal tDCS at ventral medial prefrontal cortex (VMPFC) during practice of a motor sequence task would facilitate encoding, consolidation and/or long-term retention of the trained skill. The working hypothesis was that non-invasive stimulation at VMPFC influences remote ventral midbrain region in a manner similar to reward. Spontaneous eye blink rate (EBR) has been reported and used in the present work as a non-invasive indirect marker of central dopamine function such that higher EBR is associated with higher dopamine function. For all participants, EBR was first assessed prior to practice of a 12-element motor sequence executed with the non-dominant hand. For the duration of practice, individuals were exposed to either 2 mA anodal tDCS at VMPFC or sham stimulation. At the conclusion of practice, EBR was again assessed. Performance of the trained was evaluated prior to training, immediately after training was concluded and then again after an additional 6-hr, 24-hr, and 168-hr. An increase in mean EBR was observed for individuals administered velum stimulation at VMPFC during training suggesting heightened dopamine function whereas a decrease over the same interval was observed for the sham condition. While all participants displayed improved skill across practice, training in the presence of stimulation at VMPFC led to greater gains across training. Consolidation across the initial 6-hr after practice was similar for the real and sham conditions as was long-term retention after 24-hr. The change in EBR across training was positively correlated with offline gain 6-hr post practice. These data highlight a positive impact of anodal stimulation at VMPFC for the initial encoding of motor memories.

1-B-35 Spinal stretch reflexes support efficient reaching

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It is widely assumed that the spinal circuits generating the stretch reflex in upper limb muscles only act to regulate the length of the stretched muscle. Recently, however, we showed that there is a spinal circuit that integrates feedback from the elbow and wrist, understands how this multi-joint feedback maps on to the hand's position in the external world, and generates a spinal stretch reflex in elbow muscles that is appropriately tuned to keep the hand stable at its location in space. Here we tested whether this putative spinal circuit also has the capability to help move the hand to a goal-location while reaching. In our first experiment participants grasped the handle of a robotic exoskeleton and reached towards a goal-location that required 10 degrees of elbow extension. At movement onset on roughly half of the trials the robot mechanically flexed the participant's elbow - stretching the triceps - and simultaneously flexed or extended the participant's wrist. These perturbations displaced the participant's hand away from the goal-location, but critically, the perturbation that yielded the largest hand displacement relative to the goal-location did so with the least amount of elbow flexion (and vice versa). We found that the triceps' spinal stretch reflex was tuned to the hand's displacement away from the goal-location, and thus the amount of elbow extension needed to complete the reach, and not by the amount the triceps was stretched. In our second experiment participants completed a block of trials by grasping the robot handle with their thumb pointing upwards and in another block of trials with their thumb pointing downwards. Across both blocks, participants reached towards a goal-location that required 10 degrees of elbow extension and the robot mechanically flexed their elbow and simultaneously flexed or extended their wrist at movement onset. Critically, the different grasp orientations diametrically altered how the same wrist rotation moved the hand relative to the goal-location. For example, in one grasp orientation, flexing the wrist moved the hand away from the goal-location, whereas in other orientation, flexing the wrist moved the hand towards the goal-location. We found that the triceps' spinal stretch reflex was always tuned to the hand's displacement from the goal-location rather than how much the triceps was stretched. In fact, changing the grasp orientation diametrically altered the pattern of the triceps' spinal stretch reflex and did so in a way that was appropriate for amount of elbow extension needed to complete the reach. Taken together, these results show that there is a there is a spinal circuit that integrates feedback from the elbow and wrist to support efficient reaching. These results, in conjunction with our previous findings, indicate that spinal circuits do not simply regulate the length of the muscle, but can also supports efficient hand control in a variety of contexts.

1-B-36 Goal utility varies as a function of movement strategy

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When faced with multiple potential goals, individuals choose their actions to maximize task success (Wong and Haith 2017). Indeed, previous work has demonstrated that in the presence of goal uncertainty, reach direction is influenced by the relative likelihoods or rewards associated with the available options (Chapman et al. 2010, 2015; Hudson et al. 2007). However, performance is dominated first and foremost by a choice between two distinct strategies for resolving goal uncertainty: guessing prior to movement onset and reaching directly to one of the targets, or delaying the decision by reaching partway between the targets until more information becomes available. The information used to choose a reaching strategy may not be the same as that used to subsequently determine a reach direction. For example, if one opts to delay and produce an intermediate movement until the correct target is revealed, it is likely less important to weigh the relative values of the two targets prior to movement onset. Thus we sought to examine whether the choice of strategy (i.e., making direct or intermediate reaches) influences how individuals weigh goal likelihood and reward value in determining reach direction. We asked individuals to complete a go-before-you-know task in which they were presented with two potential targets that were associated with differing reward values and likelihoods of being correct. Individuals were aware of the target likelihoods and reward values, but were required to begin reaching before the correct target was revealed. We found that in this task, reach direction was determined according to the relative utility (i.e., a weighted product of likelihood and reward value) of the two targets. Critically, however, the relative weighting of likelihood and reward information differed depending on whether a reach was direct or intermediate. That is, the bias in reach direction for direct reaches was less strongly influenced by reward values compared to the bias for intermediate reaches. Thus while individuals compared the relative utilities of the two potential goals to inform their movement decisions, this computation depended on the particular strategy chosen to resolve goal uncertainty (guessing versus delaying). Importantly, these findings stand in contrast to the idea that intermediate movements reflect a low-level interference between competing motor plans (Cisek 2007; Gallivan et al. 2015, 2018), as in that case one would expect reach-direction biases due to likelihood and reward to be similar for direct and intermediate reaches. Instead, this suggests that individuals rely on a hierarchical decision-making process to maximize task success.

1-B-37 Motor cortical control of muscle tone: evidence from the pelvic floor in humans

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Muscle activity is controlled by a series of efferent centers in spinal cord, brainstem, and motor cortex. These centers are typically viewed in a hierarchical fashion, with a continuum of functions ranging from more basic in spinal circuitry to more complex in motor cortical circuitry. To assess the validity of this conceptual model, we examined the degree to which motor cortex can influence a very basic motor function in humans - the maintenance of pelvic floor muscle tone during supine resting. We began with a series of experiments that used pelvic floor electromyography (EMG), task-based functional magnetic resonance imaging (fMRI), and transcranial magnetic stimulation (TMS) to provide a detailed map of the motor cortical representation of pelvic floor muscles in humans. These experiments provided novel evidence that the pelvic floor representation is highly distributed in supplementary motor area (SMA) and primary motor cortex (M1). We then used resting-state fMRI (rs-fMRI) to map the whole-brain functional connectivity of the SMA and M1 portions of the pelvic floor muscle representation, and showed that SMA expresses preferential connectivity with brain centers known to be involved in sensory processing for continence control. We finally performed a causal experiment to determine if we can temporarily perturb pelvic floor muscle tone with repetitive TMS (rTMS) targeting SMA, both upregulating SMA activity with high-frequency rTMS (HF-rTMS) and downregulating SMA activity with low-frequency rTMS (LF-rTMS). In this experiment, we performed rs-fMRI before and after rTMS to assess changes in SMA activity. We found that HF-rTMS increased SMA activity and decreased pelvic floor muscle tone; we found that LF-rTMS decreased SMA activity and increased pelvic floor muscle tone. We interpreted the opposite effect of rTMS on brain and muscle activity as evidence for an important inhibitory influence of the motor cortex on pelvic floor muscle tone, and we confirmed the existence of this inhibitory influence using paired-pulse TMS. We discuss our findings in the context of recent clinical evidence of profound disturbances to SMA in multiple disorders of pelvic floor muscle tone, including chronic pelvic pain and incontinence. We explain our findings by arguing that allocation of motor functions to different efferent centers can not be done based on an assumed complexity of that function, but rather the degree to which that function requires direct input from particular cortical centers. Since evolutionary and societal pressures demand the conscious monitoring of waste storage in the bladder and bowel, control of pelvic floor muscle tone may provide an excellent model system of how basic motor functions are integrated into motor cortical networks.

1-B-38 Linear summation of spinally-induced forearm force field in macaque monkeys

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Pioneering works by Bizzi and his colleagues (mussa-ivaldi, 1992) indicated that the co-stimulation of two intraspinal sites results in a force field which is a simple linear summation of the responses evoked from stimulation of each site alone. These force field has been regarded as computational "primitives" that could be used by the central nervous system for generating a variety of motor behavior, and indeed, a number of different human movement and activity of multiple muscles involved has been characterized based on this idea (i.e. muscle synergy). However, the linear summation of force fields generated by ISMS of the cord has yet to be studied in the monkey, and as such it is not known if the primate spinal cord still follows the same principle for movement control. Toward this end, three macaque monkeys were chronically implanted at the C5-7 level with floating microelectrode arrays. EMG recording electrodes were implanted in the left shoulder (N=3) and arm muscles (N=5-6). Under atropine-medetomidine anesthesia, the monkey was placed in a supine position and the arm moved throughout its normal range of motion lateral to the body on a 4 or 8cm grid. A 200µs bipolar stimulation train was applied at 40Hz for 500ms simultaneously to a pair of electrode sites. Different force fields were evoked which, in some cases, contained an equilibrium point or line where the force output was zero with restorative forces being generated at other positions, while others were uniformly directed as would be the case for direct recruitment of motor pools or passing motor fibers. We found that most cases of co-stimulation showed high similarity to a simple linear combination of the two stimulations (83% of pairs) similar to results in the frog and rodent. Unexpectedly, however, the amplitude of evoked force field evoked to co-stimulation was often highly facilitated than that expected from linear sum of individual field. Size of this facilitation was correlated with the intraspinal depth of stimulating electrode pair: A pair stimulating superficial area within the spinal cord produced stronger facilitation, while deeper electrodes produced forces closer to linear. These effects of non-linear facilitation and depth dependency were also reproduced when examining muscle activation using EMG, but their facilitation effects were tended to be smaller in proximal muscles. In conclusion, a linear summation of two spinal force field evoked by co-stimulation of primate cervical spinal cord suggest that the CNS may control volitional, forearm movement by combining "primitives" that are probably located in the spinal cord (see also Takei et al. 2017). In addition, they could take advantage of non-linear facilitation property, which could be specific for the spinal module in primate cervical cord, for effective coordination of multiple muscles in the forearm.

C – Posture & Gait

1-C-39 Postural control with the error feedback in the elderly

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Background and aim: Balance training for the elderly is challenging, because of their association with declines in capacity of using visual cues. Error amplification (EA) feedback has been recently shown to be a promising approach to facilitate visuomotor skill. Therefore, the purpose of this study was to examine the effect of virtual amplification of execution errors to guide healthy elderly persons with visual feedback on an unsteady surface. Methods: Thirty-two healthy aged adults (65.5 ± 3.2 years) were instructed to maintain 60-s steady upright stance on a seesaw plate with visual feedback, by coupling plate movement with a target signal of actual error size (real error, RE) and twice of error size (EA) conditions. Three stance trials were collected with at least three minutes inter-trial interval. The order of experimental trials for two stance conditions was randomized. Stance performance and angular movement of seesaw were measured. Paired t statistic was used to compare the differences in postural dynamics between the RE and EA visual feedback. Results: The individual data were entered into statistical analyses for all participants (n=32). There was no significant difference in postural error between the EA and RE conditions ($p > 0.05$). Despite this insignificant difference, twenty participants still gained positive EA-related performance benefits (n=20). For those twenty participants, the results of paired t statistic showed significant differences in root mean square (RMS) and mean frequency (MF) of angular fluctuations of the seesaw movement between the RE and EA conditions ($p < 0.05$). The participants in the EA condition exhibited a lower RMS and higher MF in compared with the RE condition. Conclusion: Approximately two-thirds of the elderly could make use of visual EA (amplified error information) to advance posture control during the unsteady stance. The elderly with positive EA benefits display smaller posture fluctuations and more frequent attempts of postural adjustments during the seesaw stance. Corresponding author: Ing-Shiou Hwang, PT, PHD * I confirm that ethical consideration is given to my research. Keywords: Error, Visual feedback, Posture

1-C-40 Stick balancing while standing: an example of dual unstable task control

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Many activities of daily living require performing more than one task at once. A large literature is focused on performing cognitive and motor tasks while standing where control is usually described as Anticipatory Postural Adjustment (APA). Little attention has been devoted instead to dual task control when both tasks are unstable, for example the task of upright standing and the task of balancing a stick on the fingertip. We think that this dual task cannot be classified as an APA because the perturbation to upright standing induced by stick balancing is not predictable but a persistent balancing process. If we consider the need to perform tasks with upper limbs while standing upright, naïve subjects do not realize they are performing a dual motor task since postural balancing is mostly an automatic process. However, upright stance corresponds to the sophisticated task of stabilizing an inverted pendulum, given a delayed proprioceptive feedback. About the underlying control process, several studies showed that it is characterized by on-off intermittency able to overcome the feedback delay-induced instability on top of the intrinsic biomechanical instability. Recently, the same intermittent control strategy has been shown to apply to a cart inverted pendulum moved by a seated human subject. What it is still unexplored is the effect of putting these two paradigms together. Thus, in order to observe the baseline behavior, we first asked healthy participants to stay upright quietly on a force platform. Secondly, participants were asked to stabilize the stick with their upper limbs, while staying upright on a force platform, until they learned to perform the task for at least 30 seconds continuously. During the experiment the different components of the ground reaction force and the CoP were recorded. Kinematic data of the whole body and of the stick tool were collected using an optoelectronic system. This preliminary study reveals that upright standing coupled with another balancing task is modified respect to quiet standing. In particular we observe body sway enlargement and speed increase which might be related to the self-generated disturbance as well as to a synergistic effect, in support of the stick stabilization subtask: in order to facilitate stick balancing, upright standing control adapts to it, integrating the perturbations related to stick balancing control and trying to increase the range of motion of the tool. Understanding the effect of a second balancing task on upright stance may provide important information about how the central nervous system integrates two different control systems, essential also for specific neurological conditions. A typical example is Parkinson disease in which one of the main problems is the dual task interference because of the disruption of the motor functions of the basal ganglia, responsible for the control of learned and automatic movements.

1-C-41 Difference in gait adaptability in stroke patients due to symmetry of foot contact position: split-belt treadmill adaptation behavior

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[Introduction] Post-stroke survivors have an asymmetric gait caused by certain impairments that increase dependency on the non-paretic limb. The split-belt treadmill protocol involves two belts driven independently of each other. Many studies have aimed at improving the asymmetric gait in hemiplegic patients. However, the effect for split-belt is different in stroke patients. The reason for the different effect is unknown; hence, the split-belt cannot be used as a rehabilitation tool. The study aimed to investigate the differences in gait adaptation in stroke patients with respect to the relative positioning of the whole body and foot contact position of the leading leg. [Methods] Twenty-two chronic stroke patients with hemiparesis (age=67.0 ± 9.3 years) walked on a split-belt treadmill protocol. We investigated the changes in double support time, step length, and vertical angle between the line from the center of pressure (CoP) to the center of mass (CoM) and the vertical line from CoM (CoM-CoP angle) at heel strike using a motion capture system. All parameters were corrected for three periods, namely, in-belt velocity symmetry (tied-belt), immediately after belt velocity asymmetry (early-adapt), and six minutes after asymmetry (late-adapt). We classified the stroke as "responders" or "non-responders" by the CoM-CoP angle symmetry during the late-adapt. The symmetry of parameters from three periods was analyzed using analysis of variance with Bonferroni correction for post-hoc multiple comparisons. [Results] The maximum gait speed, FMA, TUG, and FIM were not significantly different between the responders and non-responders. The responders showed a significant difference in symmetrical index of step length between the early-adapt and tied-belt ($p<0.05$). During late-adapt, the symmetrical index showed no significant difference compared to tied-belt ($p=0.43$-0.53). Double support time also re-established symmetry via the split-belt condition in the responders. In contrast, the non-responders' step length and double support time were significantly different between the late-adapt and tied-belt. [Discussion] In the spatiotemporal parameters, step length and double support time re-established symmetry in the responders and asymmetry in the non-responders. Previous studies report that re-establishing symmetry in the interlimb parameters (step length and double support time) reflects gait adaptability. Our result showed that the adaptability differs depending on whether CoM-CoP angle symmetry is re-established. A study mentions that the interactions affecting foot placement, CoM, and CoP at the foot contact position are crucial in dynamic stability during walking. Our results suggested that only the responder could place the foot in an efficient position in dynamic stability predictively. This may be a reason for the differing split-belt treadmill effect among the stroke patients.

1-C-42 Are corrective muscle responses during a slip perturbation coordinated by the vestibular system?

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Slip-induced falls contribute to a significant number of injuries in the workplace and the community. Following slip initiation, the upper and lower extremities respond in a coordinated fashion to prevent falling. It is believed that the vestibular system may be responsible for initiating corrective reactions to slips as the semicircular canals and the utricle and saccule within the vestibule are sensitive to angular and linear accelerations of the head, respectively. If true, the timing of head acceleration during a slip event should correspond with the onset timing of corrective muscle responses. The purpose of this study was to compare the timing of head acceleration to the onset of upper and lower extremity muscle responses during a slip event. Ten healthy adults participated. Electromyographic activity of the left deltoid and right tibialis anterior were collected at 3,000 Hz using surface electrodes. Eleven motion capture cameras were used to collect kinematic data at 150 Hz. Participants were placed in a full-body harness attached to a low-friction trolley to prevent a fall in case the participant failed to regain balance. The participants walked along a 10-meter walkway at a speed of 1.45 m/s. Mineral oil was placed on the force platform between slip and non-slip trials (without the participant's knowledge) to induce a slip with the right foot. A minimum of 3 non-slip trials were collected prior to inducing the slip. EMG signals were band-passed filtered 10-500 Hz, and smoothed using root-mean square with a moving window of 50 ms. Onset of EMG activity was determined when the slip trial EMG activity levels exceeded baseline trial activity by 1 SD for at least 50 ms. Head acceleration was derived from a reflective marker placed on the forehead marker of each participant.. Onset of head acceleration was determined by when the head acceleration exceeded baseline trial activity by 2 SD. A one-way ANOVA was used to compare differences in the onset timing of the 2 muscles of interest and head acceleration. The ANOVA test was found to be significant. [$F(2, 27) = 67.53$, $p = 0.0001$)]. Post-hoc comparisons using Tukey HSD revealed no significant differences in onset timing of the left deltoid (mean: 63.8 ± 9.6 ms) and right tibialis anterior (mean: 61.6 ± 8.1 ms). However, the onset timing of both muscles were significantly earlier than the head acceleration (mean: 239 ± 66.7 ms). Corrective neuromuscular responses of the upper and lower extremities preceded the onset of head acceleration. As such it is unlikely that the vestibular system is responsible for initiating corrective responses during a slip event. The onset muscle timings associated with slip initiation (approximately 60 ms) suggests that the spinal cord may be initiating the compensatory responses to a slip perturbation. This study suggests that the vestibular system is not likely responsible for initiating corrective neuromuscular responses to a slip perturbation.

1-C-43 DeepLabCut: a tool for fast, robust, and efficient 3D pose estimation

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Quantifying behavior is crucial for many applications in neuroscience and motor control. While cameras provides easy, noninvasive methods for the observation of animal behavior in diverse settings, the extraction of particular aspects of a behavior for further analysis can be highly time consuming. Recently, we presented an efficient method for markerless pose estimation based on transfer learning with deep neural networks that achieves excellent results with minimal training data. We demonstrated the versatility of this Python package, called DeepLabCut, by tracking various body parts in multiple species across a broad collection of behaviors [1]. Current experiments produce vast amounts of video data, which pose challenges for both storage and analysis. Here we improve the inference speed of DeepLabCut, and show that poses can be inferred at up to 1200 frames per second (FPS). For instance, 278 x 278 images can be processed at 225 FPS on a GTX 1080 Ti graphics card. Furthermore, we show that DeepLabCut is highly robust to standard video compression (ffmpeg). Compression rates of greater than 1,000 only decrease accuracy by about half a pixel (for 640 x 480 frame size). DeepLabCut's speed and robustness to compression can save both time and hardware expenses [2]. We will illustrate DeepLabCut's workflow and capabilities based on various datasets and further demonstrate the scope of DeepLabCut by tracking 3D poses of hunting cheetahs [3] and reaching dynamics. [1] Mathis et al. (2018) DeepLabCut: markerless pose estimation of user-defined body parts with deep learning - doi: https://doi.org/10.1038/s41593-018-0209-y [2] Mathis, Warren (2018) On the inference speed and video-compression robustness of DeepLabCut - doi: https://doi.org/10.1101/457242 [3] Nath*, Mathis* et al. (2018) Using DeepLabCut for 3D markerless pose estimation across species and behaviors - doi: https://doi.org/10.1101/476531

1-C-44 Long latency event-related desynchronization and synchronization of EEG beta-band in response to support-surface perturbations during quiet standing

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Supraspinal contributions to postural stabilization during human quiet standing have been investigated using various approaches, including characterizations of electromyograms (EMG) of postural muscles, neural oscillations using electroencephalogram (EEG), as well as postural movements expressed by the center of pressure (CoP). Such studies propose a role played by the cerebral cortex in postural control (e.g., Slobounov et al. 2005), suggesting that supraspinal control might be more complex than hypothesized traditionally. In particular, Loram et al. (2004) observed an anticipatory active control strategy, instead of a spinal stretch response, in the calf muscles during quiet stance first, and then relaxation in the restoration phase, which cannot be explained by the traditional stiffness control. Computationally, a novel hypothesis alternative to stiffness control is intermittent feedback control, which claims importance of the relaxation periods in the calf muscles during the restoration phase, referred to as the "off-control" period. In this study, we measured EEG, together with CoP and EMG, during quiet stance in 9 healthy young adults, in response to a small support-surface perturbation (200 ms; 4 m/s^2), to examine whether event-related potentials (ERPs) occur at onset of the relaxation phase of the calf muscles. After denoising EEG by artifact subspace reconstruction and independent component analysis, event-related spectral perturbations (ERSPs) were computed in the time frequency domain, for which each onset of the floor perturbation was used as the triggering event. We confirmed that powers at all frequencies (alpha: 8-13Hz; beta: 13-30Hz; gamma: >40Hz) increased immediately after the perturbation (N100 and P200 peaks of ERPs). Then, powers at alpha and beta bands decreased in the time-range of 0.5-1 second after the perturbation (event-related desynchronizations: ERD), at which the CoP and EMGs from all ankle muscles were almost relaxed. Interestingly, the beta-band power showed significant increases in the time-range of 1.0-3.0 seconds (event-related synchronizations: ERS), at which EMGs of the soleus (and the tibialis anterior) were completely relaxed, and EMG of the lateral gastrocnemius and the CoP were in the latest phase of the restoration process. The ERS of beta-band found in this study is likely to correspond to the one observed during decision-making in the Go/No-Go task (van Wijk et al. 2012). Therefore, our results propose a hypothesis suggesting that increased beta-band power in the latest phase of the postural response reflects active neural information processing to actively relax muscular force generation in postural stability, corresponding to the "off-control" timing of the intermittent control.

1-C-45 Sensorimotor adaptation to alteration of postural dynamics induced by a closed-loop perturbation system

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The human postural control system transforms sensory information into appropriate motor commands to stabilize the dynamically unstable standing posture (Lockhart & Ting, Nat Neurosci 2007). Conventionally, this process has been studied by imposing visual, proprioceptive, vestibular perturbations (Dietz, Physiol Rev 1992; Fitzpatrick & McCloskey, 1994). However, its flexible adaptation ability has not been fully investigated due to the lack of an appropriate methodology comparable to a robotic manipulandum in the upper limb movements. Here, we propose a novel method to alter postural dynamics. We applied electrical muscle stimulation (EMS) to tibialis anterior (TA) muscle (biphasic pulse train, duration 0.5 ms, 20Hz) to generate perturbation ankle joint torque. Notably, the TA is inactive during ordinary standing and the posture can be perturbed without interfering the activity of plantar-flexor muscles mainly involved in the postural control. We developed a system in which the EMS intensity and the resultant ankle joint torque can be flexibly modulated with the position and/or velocity of center of body mass (COM) measured by a laser displacement sensor (LK-500, Keyence, Japan). This closed-loop EMS system allows us to artificially alter postural dynamics. First, we confirmed that the intended perturbation torque can be generated by modulating EMS intensity according to the relationship between the EMS intensity and resultant torque obtained beforehand. Then, we examined how the postural control system adapted to control the posture with novel dynamics created by the closed-loop EMS system. Participants kept standing posture for 490 s under the presence of EMS that was modulated by position and velocity of COM. For example, in the presence of position dependent EMS, the forward shift of COM increased the dorsiflexion torque, which further induced the forward shift. The postural control system needed to adapt to such a new environment. Every 35 sec, a step torque (from 5 Nm to 8 Nm) was imposed to investigate how the step response of COM changed during the adaptation process (14 responses). As the adaptation to the position dependent torque progressed, the size of forward COM shift induced by the step torque became smaller, indicating the postural control system became more resistant to the forward perturbation. This adaptation pattern was similar to the pattern simulated by increasing the position gain in the PID controller model (Peterka, Biol Cybern 2000). The different adaptation pattern was observed when the velocity dependent torque was imposed, which was also reproduced by increasing the velocity gain in the PID control model. These results indicate that the postural control system adapts to the new dynamical environments by adjusting the control parameters specific to the imposed dynamics. Furthermore, the proposed closed-loop EMS system is a powerful tool to investigate the flexible adaptability of human postural control system.

1-C-46 To fall or not to fall: An initial passive phase that limits the time to recover and emphasizes the role of proprioceptive information

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In the present experiments, multiple balance perturbations were provided by unpredictable support-surface translations in various directions and velocities. The aim of this first study was to distinguish the passive and the active phases during the pre-impact period of a fall. It was hypothesized that it should be feasible if one uses a specific quantitative kinematic analysis to evaluate the dispersion of the body segments trajectories across trials. Moreover, a multi-joint kinematical model was created for each subject, based on a new 3-D minimally invasive stereoradiographic X-ray images to assess subject-specific geometry and inertial parameters. The simulations allowed discriminating between the contributions of the passive (inertia-induced properties) and the active (neuromuscular response) components during falls. Our data show that there is limited time to adjust the way one fall from a standing position. We showed that the pre-impact period is truncated of 200 ms. During the initial part of a fall, the observed trajectory results from the interaction between the destabilizing external force and the body: inertial properties intrinsic to joints, ligaments and musculotendinous system have then a major contribution, as suggested for the regulation of static upright stance. This passive phase is later followed by an active phase, which consists of a corrective response to the postural perturbation. We believe that during a fall from standing height, it takes about 300ms for postural responses to start correcting the body trajectory, while the impact is expected to occur around 700ms. It has been argued that this time is sufficient to change the way one falls and that this makes it possible to apply safer ways of falling, for example by using martial arts fall techniques. Also, our results imply visual and vestibular information are not congruent with the beginning of the on-going fall. This consequence is to be noted as subjects prepare to the impact on the basis of sensory information, which would be uniquely mainly of proprioceptive origin at the fall onset. One limitation of the present analysis is that no EMG was included so far but these data are the subject of a follow-up study.

D - Integrative Control of Movement

1-D-47 Visual feedback processing during a rapid sensorimotor decision task

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Sensorimotor decision-making under time pressure involves continuous integration of sensory information to dynamically plan and update a movement. Previous evidence suggests there are overlapping neural systems for perceptual decisions and for eye-hand coordination, but the behavioral consequences of this shared processing remain unclear. To address this issue, we developed a rapid reaching task that recruits the oculomotor system in both deciding the correct action and providing retinal and extraretinal signals to guide an appropriate hand motor command. We recorded limb and ocular kinematics as participants used a robotic manipulandum (KINARM Endpoint robot, BKIN Technologies) to perform right-hand reaching movements in a horizontal plane in response to visual targets on a virtual display. On each trial, a single target shape (circle or ellipse) appeared on either the right or left side of the visual workspace and remained in the same position (Static) or moved horizontally across the workspace at a constant Euclidean velocity (Moving). In the No-Decision condition, the target was always the same shape, and participants were instructed to hit the target as quickly and as accurately as possible. In the Decision condition, the shape of the target cued the participants to either hit the target or reach to a pre-specified location away from the target. We found that target motion and an added decision requirement during reaching each influenced speed-accuracy trade-offs for hand and eye movements. Participants exhibited higher hand movement accuracy and slower reaction times (RTs) for Static targets relative to Moving targets. The Decision condition resulted in both lower accuracy and slower RTs relative to the No-Decision condition for Static and Moving targets, reflecting a decision cost associated with processing target shape. Saccade latencies were faster but saccades were less accurate in the Decision condition for both Static and Moving targets, which suggests that when making a decision participants prioritized target identification over forming a specific motor plan early in the trial. Smooth pursuit gains (measured for the Moving target trials) were higher in the Decision condition, indicating that a more stable tracking of the target may be required for ongoing decision processing. Together, these results suggest that engaging the oculomotor system during rapid sensorimotor decision tasks affects how visual feedback is processed for the online control of limb movements.

1-D-48 Descending cortical pathways bidirectionally modulate forelimb tactile feedback in the cuneate nucleus

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A critical challenge for the mammalian motor system is managing the intricate coordination of dozens of muscles in the arms and hands to interact with the world. The impressive precision of forelimb behaviors suggests the existence of neural pathways dedicated to refining motor output. Coordinated movement depends on constant communication between feedforward neural circuits that produce movement and feedback systems that report sensory consequences. Fundamental to this interaction are mechanisms for controlling the influence that feedback signals have on motor pathways in a task-dependent manner, attenuating feedback signals when disruptive and augmenting them when advantageous. Peripheral feedback can be modulated during voluntary movement at many levels of sensory processing, including within the spinal cord, dorsal column nuclei, thalamus, and cortex. While the precise mechanisms underlying modulation of sensory feedback remain largely unknown, it has been proposed that descending cortical systems play a central role in adjusting the strength of sensory signals, thereby regulating their influence on ongoing motor output. We are exploring how sensory feedback is regulated at the level of the main cuneate, a brainstem nucleus that serves as a major conduit of ascending peripheral signals. Leveraging viral and genetic tools in mice, we find that direct sensory projections to the cuneate are primarily composed of tactile, as opposed to proprioceptive, afferents. Through a combination of slice electrophysiology and viral circuit connectivity studies, we identify descending pathways by which discrete cortical regions modulate the activity of cuneolemniscal neurons that convey tactile signals to the neocortex, via the thalamus. Specifically, we have identified two discrete circuits: one in which corticospinal collaterals directly increase cuneolemniscal excitability, and another in which a distinct set of corticofugal projections suppress the transmission of tactile feedback via feedforward inhibition of cuneolemniscal neurons. In ongoing experiments, we are exploring the behavioral implications of this descending modulation of tactile feedback gains for dexterous forelimb movement. Together, these findings identify distinct corticofugal pathways that exert bidirectional modulation of ascending tactile feedback, providing a potential circuit basis for filtering disruptive feedback while simultaneously enhancing the transmission of salient sensory signals during forelimb movement.

1-D-49 Influence of visual and tactile object recognition on motor planning in non-human primates

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One crucial point of sensorimotor transformation is to flexibly link information from different modalities to meaningful movements. The identification of objects and physical properties using different senses is particularly important when an object needs to be precisely grasped. Many brain areas are involved in the sensorimotor transformation process in control of hand grasping, ranging from object recognition to grasp preparation and execution. However, the interaction between these different cortical areas and whether grasp planning activity depends on the senses that were used to perceive an object has not been extensively studied. For this project, we recorded neural data from a rhesus macaque (Macaca mulatta) during a delayed-grasping task. In this task, the animal was instructed to lift different objects after they were perceived either visually or tactually beforehand, which allows us to gain insight into how these sensory modalities influence grasp planning. While the animals were performing this task, we recorded neuronal activity in four cortical areas (anterior intraparietal area AIP, premotor area F5, primary motor area M1, and the primary somatosensory area S1) relevant for grasp control. Preliminary analysis revealed differences in the activity of these brain areas between visual and tactile trials. We especially focused on the analysis of the preparatory period of this task, after the object was seen or touched but before it was grasped. Overall, we found stronger activity patterns during visual trials, compared to tactile trials. For M1 and S1, we were able to decode from activity during the beginning of the movement preparation epoch, whether the object was touched or seen, but not which object was handled. Interestingly, this changed the closer the analysis window was shifted towards grasp execution. During grasping, decoders built on M1 and S1 activity were able to predict the object quite well, but no longer whether it was seen or touched beforehand. In F5 however, the object and the condition can be decoded during early memory. The closer the analysis window is shifted to the actual grasp, the harder it becomes to decode the sensory condition, but the objects can be decoded well. This could hint towards a leading role of F5 for the planning of grasps, since F5 seems to hold information of the handled object from the start of the memory period, which cannot be decoded from M1 or S1. At the end of the memory period and during grasp execution, however, the handled object can be decoded from all four areas. These findings indicate different roles of AIP, F5, M1, and S1 for the planning and execution of grasping movements, and furthermore suggest distinct streams of visual and tactile information processing for the planning of grasping actions in these cortical areas.

1-D-50 Spinal cord stimulation modulates the sensory cortex during passive leg movements

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In an intact organism, locomotion and posture are controlled effortlessly and accurately with feedback from proprioceptive somatosensory pathways. Patients who suffer from degraded proprioception have severely impaired balance and dexterity. Such patients might use advanced brain-controlled motor prostheses in the future, but they will require sensory restoration to return to the performance levels of able-bodied people. Epidural spinal cord stimulation recruits proprioceptive primary afferent fibers. Therefore, spinal cord stimulation could, in theory, be used to provide sensory feedback to deafferented patients. However, the induction of illusory body experiences via electrical stimulation remains an elusive goal in the field of neuroprosthetics. Toward that goal, we are investigating the effects of spinal cord stimulation on the activity of neural ensembles in the primary somatosensory cortex during leg movement. We hypothesize that tailoring the stimulation to elicit a more "movement-like" evolution of the neural state (compared to control stimulation and actual movement) will result in the subjective experience of leg movement. In the behavioral paradigm, an intact non-human primate discriminates the magnitude of a passive leg movement caused by a robotic manipulandum in a two-alternative forced-choice scenario. We have recorded single unit action potentials from a microelectrode array implanted in its somatosensory cortex (area 2) during this behavior. We developed statistical models that reveal the baseline correlation between limb pose and neural activity. We then implanted the same animal with epidural spinal electrodes that target the proprioceptive afferent dorsal nerve roots. Inspired by the natural encoding scheme of primary muscle spindle afferents, we patterned the stimulation in space (laterally, over the dorsal root entry zone of flexor and extensor motor pools) and time (burst stimulation around the time of movement). We compare the effects of patterned stimulation to tonic stimulation over the midline. We show that epidural stimulation superimposes artificial information onto the ongoing neural activity that encodes true limb state. We quantified the somatosensory cortical integration of the natural and artificial afferent activity using standard machine learning techniques.

1-D-51 Tactile information in the fingertips modulates upper limb responses during manipulation of a slipping object

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Humans have the remarkable ability to hold, grasp and manipulate different kinds of objects in our hands. This is particularly important because when holding an object, several factors, such as movement or external forces, can cause the object to suddenly slip from your hand. This unexpected perturbation can elicit a compensatory response not only in the fingers but also hand and arm to prevent the object to fall. Previous work has shown coordinated feedback responses of the hand and shoulder muscles to account for an external perturbation in the arm1. However, little is known about how feedback responses of the arm arise from somatosensory feedback of an object slipping in your hand. Here, we built a device that can elicit slip perturbations in two directions on each of the fingers individually (in tangential direction). We coupled this device with a robotic exoskeleton (KINARM, BKIN Tech) that permits rotations of the shoulder and elbow joints to study whether somatosensory feedback of an object slip can elicit rapid feedback responses in the arm. The device was placed and fixated on top of the hand surface of the robot and thus was supported against gravity. Our setup allows us to decouple the tactile stimulation from the inertial forces usually involved in real-world scenarios. Fourteen participants performed three experiments in which they were instructed to perform postural tasks to study the arm feedback responses related to a) slip direction, b) speed and distance of the slip and c) combined mechanical torque plus slip perturbations (real-world scenario). Our results show that the slip direction led to distinct arm joint motion profiles. Participants were faster when they move in the same direction of the slip (mean onset time of 62 ms) compared to when they have to move in the opposite direction (mean onset time 148 ms). In addition, our results showed differential arm responses to speed but not to distance. Finally, the arm response to an external perturbation was potentiated if the participant received tactile stimulation showing increased muscle activity for the combined torque and slip perturbation compared to the torque alone. These results show modulation of the fast feedback response of upper limb muscles triggered by tactile information during complex object manipulation of a slipping object. 1. Crevecoeur F, Thonnard JL, Lefèvre P, Scott SH. Long-Latency Feedback Coordinates Upper-Limb and Hand Muscles during Object Manipulation Tasks. eNeuro 10;3(1), 2016

1-D-52 The effect of augmented low-frequency error feedback on visuomotor tracking for the elders

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OBJECTIVES: Error amplification (EA) feedback has been previously shown to improve quality of visuomotor tasks, However, EA feedback enlarges error information that may overload visuomotor system of the elderly, who suffer from age-related decline in detection and processing of fast execution errors. This study examined whether older adults could benefit from amplification of low-frequency errors during a force-tracking task, since those elderly do not effectively respond to fast oscillatory errors. METHODS: Ten healthy older adults (age = 64.7± 3.27 yrs, 3 males, 7 females) completed static isometric force at 20% of maximal voluntary contraction through index abduction under four various visual guidance, including real feedback (RF), low-frequency feedback without amplification (RF-LF), EA, and low-frequency EA (EA-LF). EA and EA-LF multiplied twice of full-spectrum execution errors and low-frequency execution errors under 0.4 Hz, respectively. RF-LF provided low-frequency execution errors under 0.4 Hz without error amplification. Root mean square (RMS), sample entropy (SampEn) and mean frequency (MF) of force fluctuations were featured. In addition, intramuscular coherence of the first dorsal interosseous muscle was characterized with 5-pin surface electromyography of small detection areas (diameter: 0.5 mm) following rectification. Two-way repeated measured ANOVA was used to examine the effects of low-pass filtering of error (low-frequency vs. full spectrum) and error amplification (EA vs. RF) on variables of force fluctuations and EMG. RESULTS: The results showed that RMS of force fluctuations was subject to effects of low-pass filtering ($p = .008$) rather than error amplification ($p = .624$). Both low-frequency feedback (RF-LF and EA-LF) led to larger RMS of force fluctuations than their counterparts (RF and EA). SampEn of force fluctuations was also dependent on effects of low-pass filtering ($p = .031$) rather than error amplification ($p = .248$). RF-LF and EA-LF exhibited smaller SampEn of force fluctuations than RF and EA did. MF of force fluctuations was a function of error amplification ($p = .013$) rather than low-pass filtering effect ($p = .092$). RF-LF and EA-LF exhibited larger MF of force fluctuations than RF and EA did. EMG-EMG coherence at 0-3 Hz was tuned to error amplification ($p = .036$) and low-pass filtering ($p = .006$). Low-frequency error feedback associated with larger coherence peak at 0-3 Hz, whereas RF and EA led to lower coherence peak at 0-3 Hz. No significant effect of low-pass filtering and error amplification was noted in other spectral ranges ($p > .05$). CONCLUSION: Contrary to expectations, visual feedback with EA did not improve force steadiness of the elderly. In particular, low-frequency error feedback with or without error amplification otherwise undermines the force steadiness in the older group, involving with modulation of low-frequency muscle oscillatory control at 0-3 Hz.

1-D-53 Compensatory responses and reflex mechanisms in postural tongue control

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Tongue is a fundamental organ in basic biological human functions, such as breathing, swallowing and speaking. Loss or deterioration of tongue functions and control seriously affect quality of life. And yet the neurophysiological mechanisms enabling fine tongue motor control have not been investigated thoroughly. Whereas many studies of postural limb control have documented the role of reflex mechanisms in rapid compensation for perturbations, it is still unclear whether such low-level control

mechanisms exist in the tongue. The study addressed this question by examining tongue responses to transient mechanical perturbations using a combination of behavioural observations and computational simulations with a biophysiological tongue model. In behavioural test, we tested eight native speakers of French. The task was to sustain the articulation of 3 isolated vowels (/i/, /e/, and /ɛ/), while voicing or whispering or silently. The movements of the tongue tip, tongue blade and tongue dorsum as well as those of the upper and lower lips and the jaw were recorded with an electromagnetic-articulometer, in synchrony with the acoustic signal. A robotic device was connected to the tongue blade via thin wires glued on the lateral borders of the tongue. During the task, step-wise pattern (1N during 1s) of transient mechanical force was applied to the tongue horizontally in the forward direction. The applied force induced sudden postural changes of the tongue during the speaking tasks. We found an immediate compensatory movement in response to the mechanical perturbation. Interestingly, the response was not induced along the horizontal axis to return its original position. Rather the movement operated in a diagonal direction to recover its original shape of the tongue counter by taking a shorter route. The spectral characteristics of the sound was also changed by the perturbation, but these changes tended to be reduced quickly in synchronization with the compensatory movements. The magnitude of the rapid compensatory response varied depending on the task and the posture of the tongue, suggesting the involvement of a reflex mechanism which gain can be tuned to preserve the tongue contour according to the requirement of the speech task. We simulated the force perturbation in the biophysiological tongue model, and successfully reproduced the observed compensatory responses by the inclusion of a reflex mechanism: passive mechanics alone did not generate the appropriate responses. The results provide evidence for the existence of compensatory mechanisms in the tongue, relying on tunable reflex. The tongue posture for vowels seems to be regulated in relation to the shape of the tongue contour, rather to a specific tongue position.

1-D-54 Dynamic modulation of brain activities during three-ball cascade juggling

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This study reports an EEG experiment during juggling movements captured by simultaneous recording of body movements and high-density EEG signals, and dynamic modulations in both the time and frequency domains associated with juggling events. The origin of jugging goes back to ancient Egypt, Greek, and China, and the academic investigation of juggling has attracted traditionally mathematicians and robotics engineers, and most recently neuroscientists. Although successful performance of juggling requires different levels of manual skills and eye-hand coordination that are not necessarily required in daily life, learning of basic juggling (e.g., three-ball cascade juggling) takes only hours to days. Recent MRI studies observed relatively rapid structural plasticity in cortical grey and white matters associated with juggling training on the time scale of weeks. However, fMRI constrains on body movements with low temporal resolution, so neural mechanisms of juggling skills on the sub-second order cannot be hitherto explored. EEG is only an option with high-temporal resolution but has not been frequently applied due to extensive movement-related artifacts. Here by exploiting recent advancements in measurement hardware and signal processing (collectively known as Mobile Brain/Body Imaging), we recorded EEG activities during juggling movements. Fourteen healthy amateur jugglers performed a three-ball cascade juggling task while their neural activities, body movements, and ball trajectories were monitored in synchrony with 205 EEG electrodes, a motion capture, and a video camera. The timings of catches and throws were defined, respectively, as the moments the ball contacted and left the hand which were determined by visually inspecting the frame images of video data. Independent component analysis extracted components associated with brain activities, followed by equivalent dipole fitting of those components localizing the corresponding cortical sources in the parietal, somatosensory and motor cortical areas. We found that time courses of some ICs in the parietal area were entrained with horizontal motions of the balls while others were entrained with vertical motions. ERPs of ICs in the sensorimotor areas were locked to the catching timings by the contralateral hands. Besides time courses, the powers of alpha and beta bands in parietal ICs and the powers of alpha, beta and gamma in sensorimotor ICs were modulated dynamically in synchrony with juggling phases. This study, for the first time, demonstrates dynamic modulations of both temporal and frequency EEG features of the order of milliseconds synchronized with juggling events and phases.

1-D-56 Beta activity in SMA signals cognitive demand in motor control

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Frontostriatal circuits are involved in cognitive control over movement. It has been proposed that this network is coupled in beta frequency oscillations (~13-35 Hz), potentially reflecting cognitive demand for motor control. In the present study, we aimed to characterize oscillatory beta activity in supplementary and primary motor cortical regions with respect to cognitive demand during performance. Therefore, 20 right-handed healthy adults were assessed with 64-channel EEG while performing a visuomotor task consisting on navigating as fast as possible on a digitizing tablet to reach a target circle shown on the screen with a pen. Pen to cursor mapping was either unperturbed (automatic condition) or inverted (controlled condition). All data were transformed to the time-frequency domain using wavelets and baseline corrected after source extraction with LCMV beamforming from Motor Cortex, Supplementary motor area (SMA) and presupplementary motor area (preSMA). Statistical analysis was conducted using Monte Carlo permutation and non-parametric Spearman's correlations. All p-values were false discovery rate corrected for multiple comparisons. Participants significantly increased reaction time, movement time and trajectory error during the controlled versus the automatic condition. A significant decrease in beta was found in all sources of interest (M1R, M1L, pre-SMA & SMA) aligned with the onset of the cue and movement initiation, which prolonged during movement. Only in the SMA, beta decrease was significantly higher in the automatic than in the controlled condition aligned to the cue onset. Furthermore, beta activity in the controlled condition was significantly greater in SMA than in M1 and preSMA. A negative correlation between high beta reactivity and trajectory error before and during movement onset indicated that more power in high beta oscillations was associated with less trajectory error. Moreover, a greater difference in high beta power between conditions was associated with increased trajectory error. Significantly higher beta activity in the SMA during controlled -compared to the automatic- condition may reflect inhibitory cortical signals during cognitive control of motor processes.

1-D-57 Trajectory deviation in the presence of distractors associated with positive and negative outcomes

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Past research has shown that visually searching for a salient target is slowed by the presence of a non-target item (distractor) that was previously associated with a monetary reward (e.g., Anderson et al., 2011). In addition reach trajectories veer towards the reward associated distractor suggesting the motor plan to the distractor is partially activated during the reaching movement (Moher et al., 2015). It is unclear however, how reach trajectories will be affected by distracting stimuli previously associated with a penalty. Such stimuli should receive preferential perceptual processing but intuitively the limb should avoid stimuli associated with negative outcomes. Therefore, any activation the action towards the penalty associated distractor should be suppressed. This experiment compared rapid reaching movements to a target in the presence of either a penalty or a reward associated distractor. To this end, there were two groups of participants, one that received reward for correct, fast answers and one that was penalized for slow or incorrect answers. Participants first performed a training phase, similar to Anderson et al., 2011, that consisted of searching for a red or green target among differently coloured non-targets. Participants then had report the identity of the line segment inside the target under a time constraint via key press. For the penalty group, for one of the target colours participants lost points for incorrect or slow identifications, whereas for the other target colour there was no penalties associated with any outcome. For the reward group, for one of the target colours participants gained points for fast, correct responses, whereas for the other target colour there was no reward associated with any outcome. For the testing phase participants were required to rapidly reach towards and touch a target in the presence of a distractor stimulus located to either the right or the left of the target. The distractor was either coloured in the previously associated monetary colour (penalty or reward distractor depending on group), the non-monetary colour from training (experienced distractor) or a colour not previously experienced during the training session (neutral distractor). Movement trajectories were measured using 3D motion capture to assess trajectory deviations. The trajectories revealed that reward and penalty associated stimuli produced different deviation patterns in relation to the experienced stimuli. Specifically, in the presence of rewarded distractors, participants' trajectories deviated towards the distractor but the deviation was smaller in the presence of the penalty distractor. The findings indicate that there are differences in the way participants plan actions in the presence of stimuli previously associated with rewards and penalties.

1-D-58 Maintaining arm control during self-triggered unpredictable unloading perturbations

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We often perform tasks during which we must break through some resistive force, but want to remain in control during this unpredictable transition; for example, when when an object we are pushing on transitions from static to dynamic friction and begins to move. We designed a task to replicate this situation in which participants pushed against a robotic manipulandum until they exceeded an unpredictable threshold, at which point the manipulandum moved freely. Participants were instructed to either stop the movement of the handle following this unloading perturbation, or to continue pressing. We found that participants were able to modulate their reflexes in response to this unpredictable and self-triggered unloading perturbation according to the instruction they were following, and that this reflex modulation could not be explained by the pre-perturbation muscle state. However, in a second task, when participants produced force during the pre-unloading phase in response to the robotic manipulandum to maintain a set hand position, they were unable to modulate their reflexes in the same task-dependent way. This occurred even though the forces they produced were matched to the first task and they had more time to prepare for the unloading phase. We suggest this disparity occurs because of different neural circuits involved in posture and movement, meaning that participants in the first task did not require additional time to switch from postural to movement control.

1-D-59 Active perception through muscle synergies: A force perception study

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Despite extensive investigations of the relation between action and perception, the mechanisms underlying their integration are still unclear. Non-linearity and redundancy of the musculoskeletal system, as well as noise and delays of sensory inputs, challenge sensorimotor integration processes. It has been proposed that to simplify these processes during perceptual decision making, the central nervous system (CNS) selects patterns of movements aimed at maximizing sampling of task-related sensory inputs, i.e., active sensing. Accordingly, active perception would rely on the coupling between movements and patterns of movement-generated sensory inflow. While previous studies investigated the action-perception loop focusing on the role of higher-level features of motor behavior (e.g., kinematic invariants, effort), the present study explored whether and to what extent lower-level organization of motor control contributes to active perception. Specifically, we tested the hypothesis that subjects' detection of force stimuli depends on the coordinated recruitment of groups of muscles, i.e., muscle synergies, engaged to counteract the same force. We asked subjects to judge the presence of an upward force (yes/no answer) applied on their forearm while maintaining the arm in a quasi-isometric posture against the force stimuli. We derived the psychometric curves describing subjects' probabilities of detection as a function of the external force. Using the EMG signals recorded from eight shoulder and elbow muscles, we developed two probabilistic models describing the modulation of EMG activity involved in the task. By comparing the curves of probabilities of each model with the psychometric curve we found that: 1) the probabilistic muscle-model taking into account the modulation of muscle co-activation patterns, i.e., muscle synergy model (MSM), explained about 70% of subjects' perceptual variance; and 2) the MSM probabilistic curve described probabilities of force detection significantly better than a model developed by linear combination of individual muscles activity, i.e., most contributive model (MCM). Our results extend previous findings on the influence of motor behavior on perceptual inference, by proposing that muscle synergies may mediate not only the coordination of activation across multiple muscles, but also perceptual inference.

1-D-60 Spatial attention reflects sensorimotor decision making in situations of target uncertainty

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Neurophysiological and behavioural evidence suggests that, the brain simultaneously represents multiple potential actions in situations of target uncertainty. According to this view, sensorimotor decisions reflect biased competition between alternative actions that are held active in parallel (Cisek &

Kalaska, 2010; Gallivan et al., 2018). Here, we exploited the tight coupling between motor preparation and spatial attention (Baldauf & Deubel, 2010) to track sensorimotor decisions in situations of target uncertainty by combining a delayed cueing paradigm with a covert spatial attention task. Two of twelve possible target locations were cued for a potential center-out reaching movement. After a delay, one of the two cued locations was designated as the final movement goal. A visual discrimination probe occurred at a random location and time during the trial. Prior final goal specification, discrimination performance was better at the two cued target locations than at other movement-irrelevant locations, indicating that potentially relevant targets had been selected by visuospatial attention. After final goal specification, discrimination performance further increased selectively at the movement goal. The time course of attentional sensitivity was related to reach onset, showing that attention was shifted to the reach goal prior to movement initiation. The sensitivity increase started earlier for fast than for slow reach initiation, indicating that faster decisions were preceded by earlier attentional selection. Together, our findings support the notion of a competition between simultaneously represented actions in situations of target uncertainty and demonstrate that the time course of visuospatial attention reflects decisional processes related to motor goal selection.

1-D-61 VTA is involved in both preparation and execution of motivated motor output

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In many countries, the local Olympic committee gives winners a monetary bonus. Monetary incentives facilitate primary motor cortex (M1) excitability and motor output (Thabit et al., 2011; Knutson et al., 2003; Mir et al., 2011). However, the linkage between reward and motor systems remains obscure, although previous rodent studies demonstrated that ventral tegmental area (VTA) directly projects to M1 (Kunori et al., 2014) and contributes to motor learning (Hosp & Luft, 2013). The purpose of this study was to investigate the hypothesis that VTA-M1 pathway is involved in human motivated motor output using functional MRI. Right-handed volunteers participated in a 3T MRI experiment. In the MRI scanner (Verio, SIEMENS Ltd.), participants performed both a simple and incentive grip-force task with their right hand. In the simple grip-force task, they were asked to respond toward a visual target stimulus following to a cue stimulus as quickly as possible. Then, the feedback message of "success" was displayed on the screen if the reaction time was faster than the median of practice session, whereas the feedback message of "failure" was displayed if not. Although the procedure of the incentive grip-force task was almost the same as the simple grip-force task, there were three types of cue stimuli corresponding to three conditions: high monetary gain (HG), low monetary gain (LG), and no monetary gain (NG). Performance measures were defined as reaction time and peak grip-force in each trial. For the behavioral performance, the amount of the potential monetary gains facilitated not only the reaction time but also the peak force, although the participants were only required to respond quick reaction to cue stimulus. Thus behavioral results could confirm that the incentive value facilitates human motor output as previous study did. For the fMRI data, the main effect of cues was found in cortical and subcortical motor areas: contralateral M1, supplementary motor area (SMA), bilateral caudate nucleus, putamen, and cerebellum. Reward-related cues (i.e., HG and LG conditions) facilitated M1, SMA, caudate nucleus, and VTA/substantia nigra pars compacta (SNc) activities along with the incentive values. Moreover, the degree of cue-related activation in VTA was positivity correlated with the trial-by-trial peak grip-force but not reaction time. At the movement phase, VTA was activated as well as cortical motor areas and caudate nucleus. The activations in VTA and caudate nucleus increased with the incentive value. Finally, successful feedbacks induced the activation in bilateral ventral striatum, whereas failure feedbacks activated insular and anterior cingulate cortex even. These findings show that VTA and M1 are involved in both preparation and execution of motivated motor outputs, suggesting that VTA-M1 direct pathway mediates the motor facilitation with motivation in humans.

E – Disorders of Motor Control

1-E-62 Insights from a brain computer interface user on intracortical control and feedback of robotic arms for object manipulation

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Brain-computer interfaces (BCIs) enable people with paralysis to use their brain activity to gain control over external devices to restore movement or communication ability. Over the last four years I have used an intracortical BCI to control a variety of robotic limbs, including a Luke arm from DeKa, the Modular Prosthetic Limb (MPL), the WAM Arm from Barrett Technology, the KUKA LBR assembly robot, and the Prensilia robotic hand. During this time I have been able to perform tasks that involve picking up and moving various objects with multiple devices. During my presentation I will overview what I believe to be the strengths and weaknesses of each device. In doing so I will also outline what I believe to be the minimum required features that a BCI controlled limb should have to be truly useful in multiple real-world situations i.e. at least two grasp dimensions and proper thermal regulation. In addition, I will discuss the different control strategies that I have used to control the BCI. The BCI that I have been using also has the ability to provide tactile feedback by stimulating microelectrodes implanted in my somatosensory cortex. I will discuss my experiences with receiving sensory feedback through the BCI. Even though the sensations I feel while doing tasks are not always very "natural," I will share my opinions on why I do better on certain tasks when I receive feedback than when I do without it. I believe that the primary reason sensory feedback can improve performance is because the brain expects to feel something when making contact with an object. For much of the time I used the BCI, I only had visual feedback. From where I sit, it is not always easy to see whether the hand has a good grasp on the object. However, after doing grasping tasks for a few days where I could see the robot hand visibly grasp an object, as well as feel the robot touch the object, my brain began to "expect" to feel the evoked sensation when grasping an object. Now it is that sensation, whatever it may be, that my brain expects when the hand makes contact with an object. This restored sensation increases my certainty that when I close the hand, I will have a stable grasp. Having that certainty allows me to begin moving the object without spending extra time and effort trying to make sure I won't drop it. After discussing my current experiences on control of robotic arms and sensory feedback, I will also provide thoughts on future research directions for improving BCI design and utility. These considerations may be helpful for doctors and engineers building the next generation of brain computer interfaces.

1-E-63 Force matching in post-stroke fatigue

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Sensory attenuation is a phenomenon whereby the perception (intensity) of afferent input caused by a self-generated movement is reduced. Sensory attenuation provides an account for how two physically identical sensory stimuli can be perceived differently. Post-Stroke Fatigue may be a result of reduced sensory attenuation. A commonly used method to assess and quantify sensory attenuation behaviorally is by using the force-matching task. We set out to assess whether sensory attenuation is reduced in high fatigue stroke patients using a modified version of the force-matching task. The study is being carried out in both healthy volunteers and stroke patients with varying severity of fatigue. Subjects performed a simple force-matching task in order to quantify sensory attenuation. The force transducer produced pre-determined force levels (1, 2, 3 and 20 Newtons) directly onto the index finger of their non-dominant hand for 3 seconds (target force). After the 3-second time window, subjects were instructed to simply remember the force they just experience on their finger and do nothing else for a further 3 seconds. Subjects were then given a cue to match the intensity of the force on the same finger by moving the force transducer using a lever with their dominant hand. Subjects had 5 seconds to produce the appropriate force and were instructed to hold it (match force) until they saw a stop signal on the monitor. If sensory attenuation is reduced in high fatigue stroke patients, we expect high fatigue patients to perform better on the task, they will be closer to matching the target force at the three low target force levels (1-3N) when compared to healthy subjects and low fatigue stroke patients.

1-E-65 Resting-state functional connectivity changes observed after five bouts of high-intensity cycling exercise paired with upper-limb motor practice in older adults

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Resting state functional magnetic resonance imaging (rs-fMRI) is a neuroimaging method that investigates how spatially distinct brain networks communicate while at rest. Aging is associated with both decreases (Ferreira and Busatto, 2013; Damoiseaux et al., 2008; Onoda et al., 2012; Wang et al., 2010) and increases (Hafkemeijer et al., 2013; Jacques et al., 2010) between resting state networks relative to young adults. Moreover, aberrant rs-fMRI activity in older adults is associated with motor and cognitive deficits (Mathys et al., 2014; Smagula et al., 2018). Exercise has been used as an intervention to potentially mitigate aging related resting state brain differences observed in older adults. However, how rs-fMRI brain network changes are related to multiple bouts of high-intensity exercise is currently unknown. Healthy older adults (M = 65.7 years old) underwent repeated bouts of high intensity exercise (n = 9) or a rest condition (n = 5) paired with an upper-arm motor learning task. Resting state fMRI changes were assessed pre- and post-intervention and compared between groups. We observed several significant differences between the two groups among sensorimotor and default mode networks (DMN). Specifically, seed-to-voxel and independent component analyses revealed decreases in the connectivity strength between the sensorimotor network and the frontal poles, and an increase between the sensorimotor network and the right precentral gyrus for the exercise group relative to the rest group. Whereas seed-to-voxel analysis revealed a decrease in connectivity between the hippocampus and cerebellum for the exercise group relative to the rest group. These results suggest that multiple bouts of of exercise may influence rs-fMRI across multiple networks including brain regions involved in executive and sensorimotor function and memory. Changes in these brain networks may relate to the protective effects of aerobic exercise on aging-related cognitive and motor decline.

1-E-66 Chronic stroke patients compensate loss of rotational joint work by increasing translational joint work during sit-to-stand motion

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[Background] Stroke is a typical condition that causes abnormalities in the neural control of movement. Among various habitual motions, sit-to-stand motion requires a large hip joint moment; therefore, it is difficult to perform because of motor paresis experienced by stroke patients. However, stroke patients who undergo long-term rehabilitation can perform the sit-to-stand motion while reducing their peak hip joint moment (Hanawa, 2018). We examined this compensation mechanism from the viewpoint of rotational and translational joint work, thereby contributing to the basic knowledge that helps predict the adaptive process of the nervous system from the resulting movement. [Methods] Ten chronic stroke patients (five years being the mean time since the stroke), and eight healthy adults performed the sit-to-stand motion. We used a camera motion capture system to measure the body kinematics. Subsequently, we use standard inverse dynamics approach to calculate the four kinetic parameters, as shown in the results. We compared each parameter by performing a t-test (Bonferroni correction) between the groups. [Results] In stroke patients, the peak hip joint extension moment and the rotational work about the hip joint were smaller than that of healthy adults (both were $p < 0.001$). However, the translational work about the hip joint was larger for stroke patients than healthy adults ($p < 0.001$). Therefore, the total work about the hip joint did not differ significantly between groups. [Conclusions] The hip joint extension moment plays an important role in lifting the thigh to carry the whole body forward for seat-off. Chronic stroke patients reduced the rotational work, which is the work that the hip joint moment directly rotated the joint itself. However, stroke patients increased the translational work, which is the work that the hip joint force (derived from the inertia and/or gravitational force from body segments) translated the joint center. This joint center translation, as well as joint rotation, carries the whole body forward. Our novel finding is that chronic stroke patients compensate for the loss of hip joint moment by increasing the hip joint force. Stroke patients might increase the hip joint force by modulating the inertia and/or gravitational force dependent on the velocity and/or posture of the trunk because the forward rotation of the trunk is responsible for most of the movements up to seat-off.

1-E-67 transcranial direct current stimulation for walking capabilities in Parkinson's Disease: A meta-analysis

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Parkinson's disease (PD) is a neurodegenerative disease potentially attributed to progressive degeneration of dopamine-producing neurons within the basal ganglia mainly affecting the motor cortex. The motor symptoms of PD include bradykinesia, resting tremor, and locomotion disturbance. Applying medications or surgical approach such as deep brain stimulation may be an efficient clinical option for improving rigidity and slowness of movement of patients with PD. However, these treatments have some limitations such as less effectiveness on disease progression and adverse effects (e.g.,

dyskinesia) and potential surgical risks. Transcranial direct current stimulation (tDCS), one of non-invasive brain stimulations, has been investigated for PD motor recovery. Despite insufficient findings regarding neurophysiological mechanisms underlying tDCS, this intervention is still attractive rehabilitation protocol because of its practical advantages such as economic efficiency, portability, and accessibility. Thus, the current meta-analysis investigated the beneficial effects of tDCS on walking abilities in individuals with PD. Eighteen total studies that reported short-term effects of tDCS on walking capabilities (e.g., gait speed and the time to complete certain locomotion tasks) in patients with PD qualified for this meta-analysis. A random-effects model meta-analysis on the 18 comparisons from the qualified studies regarding the short-term treatment effects of tDCS revealed a significant overall effect size (SMD = 0.359; SE = 0.105; 95% CI = 0.153-0.565; Z = 3.411; P = 0.001). Heterogeneity test results were: (a) Q-statistics = 26.524 and P-value = 0.065, (b) T2 = 0.067, and (c) I2 = 35.907%. These findings indicate that applying tDCS slightly improved gait functions in patients with PD with relatively low level of individual effect size variability across 18 comparisons. A moderator variable analysis on comparisons for tDCS targeting multiple brain regions versus for tDCS targeting single brain region showed two significant positive overall effect sizes: (a) six multiple targeted areas: SMD = 0.527; SE = 0.194; 95% CI = 0.146-0.908; Z = 2.711; P = 0.007 and (b) 12 single targeted area: SMD = 0.272; SE = 0.126; 95% CI = 0.026-0.518; Z = 2.165; P = 0.030. In summary, this meta-analysis revealed small positive treatment effects of tDCS on walking capabilities in patients with PD, and these improvements may increase when tDCS protocols targeted multiple regions of cerebral cortex.

1-E-68 Motor unit control properties in neuromuscular disorders

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Myopathic and neuropathic diseases result in characteristic alterations in motor unit action potential (MUAP) shapes and firing behavior [1-2]. However, the motor unit control properties that regulate force generation in neuromuscular diseases are still unclear, in part because conventional assessment using invasive needle electromyographic (EMG) recordings [1-2] restricts MUAP measurements to relatively few motor units and low-force contractions. In this work, we used a novel non-invasive surface EMG (sEMG) approach [3] that allows to obtain richer datasets of MUAP shapes and firing behavior of individual motor units at both low and high force levels to reveal distinguishable strategies of motor unit regulation for generating increasing force in the first dorsal interosseous (FDI) muscle of patients with selected myopathic and neuropathic diseases. Three male subjects (29, 36, 67 y.o.) with myopathy, all affected by type-I myotonic dystrophy; two male subjects (18, 60 y.o.) with neuropathy, one affected by Hirayama disease and one by amyotrophic lateral sclerosis; and three male healthy controls (30, 53, 68 y.o.) participated in the experiments. Subjects performed voluntary contractions of the FDI sustained for 10 s at a relatively low (10% maximal voluntary contraction, or MVC) and high (up to 80% MVC) force level. Four channels of sEMG signals were concurrently collected using a small 4-pin surface sensor and decomposed into the constituent MUAP shapes and firing times using a validated decomposition technology (dEMG system, Delsys Inc., Natick, USA) [3] that yielded on average 21±5, 20±7, and 9±6 individual motor unit firing trains in control, myopathic, and neuropathic subjects, respectively. In controls, increases in muscle force were associated with increases in motor unit firing rates and recruitment of progressively larger-MUAP amplitude motor units, in agreement with the Size Principle [4]. Myopathic subjects were also able to increase motor unit firing rates and recruit new motor units with higher-amplitude action potential shape in order to increase the level of exerted force, but the MUAP amplitudes of active motor units remained significantly reduced compared to controls. In contrast, altered modulation of MUAP recruitment was observed in neuropathic patients, with high MUAP amplitude motor units recruited at the lower force levels. These observations based on large populations of motor units at both low and high forces shed light on the alterations in motor unit control properties regulating muscle force production in patients affected by selected myopathic and neuropathic diseases. This work provides evidence that non-invasive measurements offers potential opportunities for further clinical research of neuromuscular disease. References: [1] Buchtal et al. Acta Med Scand Suppl 1952 [2] Preston and Shapiro Elsevier 2013 [3] Nawab et al. Clin Neurophysiol 2010 [4] De Luca et al. J Neurophysiol 2015 [5] Henneman Science 1957

1-E-69 ARCO: Cooperative arm rehabilitation after stroke

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Recent research has indicated that cooperative hand movements such as opening bottles, peeling carrots or slicing bread are controlled by a task-specific neural coupling mechanism. After stroke, this mechanism is often still partially intact leading to an increased influence of the non-lesioned hemisphere over the paretic arm. To be able to train these movements, a new device (ARCO) has been designed. The ARCO is a simple and lightweight device connecting two handles over a break-like mechanism allowing to be rotated against each other. Position and force sensors allow interaction with exergames. In this first pilot study, 8 chronic stroke patients trained with the ARCO for a total of 6 weeks, two in the clinic and 4 in their own homes. Clinical and neurophysiological assessments have been conducted before and after training. The participants also filled out a questionnaire regarding the device, the training and the subjective effect after the training. Increases in Fugl-Meyer Upper Limb Score, Box and Block Test and CASA (a new assessments for cooperative hand movements) and maximal voluntary force of wrist extensors were shown. Neurophysiological results showed a re-balancing of the inter-hemishperic disbalance. The concept of training cooperative hand movements in stroke patients seems to be very promising. One participant showed especially remarkable results. She started with 17 points in the Fugl-Meyer Score (with 0 points in the wrist category), 0 blocks in the Box and Block Test and 0 Nm in wrist extensor during the force assessment. After the ARCO training, she increased to 24 points in the Fugl Meyer score (4 in the wrist category), 2 blocks in the Box and Block test and 0.35Nm in wrist extensors. These results revealed a new feature of the ARCO: stroke patients with wrist function, that is too little to be measured or functional for any task, can train their wrists by stabilizing the ARCO while the other hand manipulates it. Thus, they can train the un-trainable. ARCO training might be a first step towards breaking the 70% proportional recovery rule.

1-E-70 Sex and APOE genetics affect the relationship between dementia risk and cognitive-motor integration performance

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Cognitive-motor integration (CMI) involves concurrent thought and action which requires the interaction of large networks in the brain. The objectives of our research are to 1) investigate the effect that dementia risk has on the ability to integrate rules into action, and 2) to examine the neural basis of

CMI impairment in individuals with dementia risk. Given evidence that early-stage dementia involves neural network dysfunction, we propose that problems with CMI can be used to detect dementia in its early stages. To this end, we recruited asymptomatic male and female participants both with and without dementia risk factors (family history and presence of APOE e4 allele). Participants were tested on four visuomotor tasks, one standard condition (vision and movement targets spatially coupled) and three cognitively-demanding non-standard conditions (vision and movement targets increasingly spatially decoupled). Multiple linear regression analyses revealed that having an e4 allele was a significant predictor of poorer CMI performance in two of the non-standard conditions (plane-change and plane-change + feedback reversal), while both sex and family history were significant predictors of worse performance in the third non-standard condition (feedback reversal). These data suggest that the CMI task may be detecting performance decrements in individuals genetically at-risk for dementia prior to clinical symptom presentation. Furthermore, the underlying brain networks that control thinking and moving at the same time may be different between men and women.

1-E-71 Visual feedback of object motion improves grip control but disrupts arm control in adults with ASC

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Among increasing evidence of motor difficulties in people with autism spectrum condition (ASC), several studies have indirectly suggested abnormal usage of visual feedback during reaching. In particular, two studies on force-field adaptation have suggested that people with ASC rely less on visual feedback for estimating [Marko et al., Brain, 2015] and representing [Haswell et al., Nat. Neurosci., 2009] the forces applied to the reaching hand. Another study revealed that they generalize prism adaptation to the other hand as if visual feedback of hand position was not provided during reaching [Masterton & Briederman, J Autism Dev Disord, 1983]. Here, in order to examine how adults with ASC process visual feedback for force estimation and arm movement control, we measured grip force pattern and hand movement trajectory while autistic and neuro-typical adults moved a virtual load attached to the grip with a damped spring. As a replication of our earlier finding, we found that neuro-typicals improved temporal control of grip force (i.e., improved synchrony with load force) but slowed down their hand motion (increase in movement cycle of the hand) when visual feedback of load position was provided. Our earlier study [Takamuku & Gomi, submitted] suggested that the former effect reflects force estimation from visual motion of the load based on inverse dynamics computation, whereas the latter effect is linked to slowing of hand motion caused by delayed visual feedback. Autistic participants showed similar trends. No significant effect of group was found for the improvement of grip timing. This suggested that inverse dynamics computation for motor control is intact in ASC, consistently with our earlier finding reporting typical perceptions based on the inverse computation [Takamuku et al., Autism Res, 2018]. On the other hand, increase in hand movement cycle was significantly greater in the ASC group. The increase correlated with AQ score in the NT group and the reciprocal social interaction score of ADOS in the ASC group. Furthermore, autism participants with abnormal eye contact had greater increase in hand movement cycle compared to those with normal eye contact. Taken together, our results suggest that the observed visuomotor processes for grip force control and arm movement control are independent, and that the latter is selectively atypical in adults with ASC.

F – Adaptation & Plasticity in Motor Control

1-F-72 Mechanical transparency guides the selection of internal models

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When approaching a novel tool or system to manipulate, humans appear naturally adept at inferring the dynamics of the physical system to attempt to predict its behavior. Fundamental assumptions about a system's mechanics are evidently derived from its visual features, which specify domain-specific knowledge, such as priors for laws of physics. These are potentially useful for generating an internal model of the visuomotor transformations involved in manipulating the observed system. Consistent with this, it has been shown that humans show different movement kinematics when controlling a tool, depending on whether the inner mechanics are visible (Mechanical Transparency) or not. Yet, no consensus has been reached over exactly how MT affects performance, as both deteriorations (Danziger & Mussa-Ivaldi, 2010) and improvements (Sülzenbrück & Heuer, 2012) have been observed. Critically, what remains unclear is what visual parameters are exploited to glean the dynamics of a physical system. To gain better insight into this ability, we systematically manipulated the visual properties of a stimulus to infer the subjects' internal model of its physical dynamics, such as its mass and moment of inertia. Participants saw a target object (a circular cursor) on a monitor. In a typical trial, a second object hit the target, simulating a certain force vector applied to the cursor's mass. The simulation stopped right upon collision. Participants were then asked to predict the motion trajectory of the cursor given the physical event that they just observed. Not surprisingly, when the target was viewed in isolation (noMT condition), observers predicted that its motion would conform to Newtonian laws of mechanics for point masses. On the contrary, when the cursor was connected to a physical system (MT condition), participants predicted that its motion would be affected by the constraints of the system, as though mechanical transparency specified a different physics prior for prediction (MT-induced prior). Interestingly, the shape of the MT-induced prior varied with the visual characteristics of the system, which we manipulated along two dimensions: We either added further complexity to the system's structure (i.e., the cursor was connected to a lever bar or to a two-link arm) or we parametrically varied the properties of the system's components without altering the global structure (i.e., changing length and mass of the links in a two-link arm). The precision of the MT-induced prior was significantly lower than noMT prior, and more susceptible to structural than parametric changes. The results confirm previous evidence that Mechanical Transparency affects how humans internally represent the functioning of tools, by exposing visual features that favor the selection of specific physics priors.

1-F-73 Sensory-prediction errors drive both motor adaptation and perceptual recalibration

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Visuomotor rotation tasks have served as a model paradigm to understand how the motor system adapts to changes in the body and the environment. A number of recent studies found that not only does the motor system adapts to these perturbations by modifying motor output (sensorimotor adaptation), but also results in changes to the perceived position of the limb (perceptual recalibration). Sensory-prediction errors are thought to underlie changes in the former, whereas simple mismatches between two sensory cues -- vision and proprioception -- change the latter. While elegant theoretical accounts have been put forth to explain how sensory cues are weighted and combined to bias perception through Bayesian integration, these accounts have not considered how perceptual mismatches are signaled in the first place. Indeed, previous research has shown that perceptual recalibration occurred after training on force field adaptation tasks, even though there is never any discrepancy between visual and proprioceptive observations. This finding thus suggest that the sensory-prediction error aspect of the training task may trigger both sensorimotor adaptation and perceptual recalibration. To test this, we used a modified visuomotor rotation task in which movements were constrained to a linear path using a stiff force channel. A persistent visual-proprioceptive mismatch was introduced when cursor feedback was clamped 30° from the direction of motion. We either suppressed sensory-prediction errors by displaying the target to align with the direction of the cursor, or enforced sensory-prediction errors by aligning the target position with the direction of the hand path. To assay perceptual recalibration, estimates of perceived limb position were obtained before and after training. We found that, while the magnitude of visual-proprioceptive mismatches were similar between conditions, removing sensory-prediction errors significantly impaired the shifts in the spatial location of the perceived hand position. However, because subjects actively pushed their hand out directly to a target while viewing a cursor headed directly 30° away, a potential alternative account could be that the proprioceptive shifts we observed are grounded in the mere experience of a visual task error, and not genuinely due to sensory-prediction errors. To test this possibility, a control group of subjects were passively moved through the same trajectories as the subjects who actively moved their hand and experienced task errors. We found that subjects in this passive-control condition showed no evidence of proprioceptive recalibration. These findings indicate that sensory-prediction errors appear to drive shifts in perceived limb position during visual-proprioceptive mismatches, and further emphasizes the idea that sensorimotor adaptation and perceptual recalibration are intimately linked.

1-F-74 The long-term shortfalls of implicit sensorimotor adaptation

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Learning in sensorimotor adaptation tasks has been historically viewed as a completely implicit learning phenomenon, this view was, in part, guided by the seminal findings regarding patient H.M. However, more recent work has discovered that this learning is supported by both explicit re-aiming strategies and implicit adaptation processes. An alarming finding from these recent studies is that implicit adaptation appears to be heavily constrained, calling into question its utility in long-term motor learning as well as the theoretical framework that has been built around canonical findings from sensorimotor adaptation paradigms. However, a potential caveat to these implications is that they have been based on results gleaned from single bouts of training. It is possible that the relative reliance on explicit re-aiming strategies to overcome the perturbation may give way to implicit adaptation processes with multiple bouts of training. In our first experiment, we set out to test this idea by dissociating the relative contributions of explicit re-aiming strategies and implicit adaptation as participants learned to overcome a visuomotor rotation over five consecutive days of training. While the relative contribution of explicit and implicit learning varied across individuals, implicit adaptation plateaued at a value far short of complete learning. In our second study, we sought to determine if these constraints on implicit adaptation extended to learning of a different sensorimotor adaptation task, mirror reversal. Given the apparent constraints of implicit adaptation, the mirror reversal task presents a unique challenge as, in order to be useful, learned corrections must be in the opposite direction of a visuomotor rotation. Over five consecutive days of training, we found that implicit adaptation was initially inappropriate for a mirror reversal - correcting as if it was a rotation. Surprisingly, it only became mildly suppressed with continued training but never reversed direction. These finding suggest that implicit adaptation processes, as have been previously studied in sensorimotor adaptation paradigms, should not be viewed as the putative implicit process supporting long-term motor skill learning.

1-F-75 Multiple motor memories depending on foveal and peripheral reaching

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In the motor planning of goal-directed arm reaching, the sensorimotor system represents the target location with the gaze-centered frame of reference. Many previous studies on visuomotor control have emphasized the impact of spatial coordination between gaze and reaching target on accuracy or systematic bias of reaching execution. While a recent neuroimaging study (Prado et al., 2005) showed separated neural activities between reaching in foveal and peripheral vision, it is still unclear how such eye-hand coordination is represented and is utilized for the visuomotor process. Recent theories of motor control emphasize the role of behavioral context in learning multiple motor skills that could interfere with each other. We here tested the hypothesis whether multiple motor memories are formed depending on different coordination between gaze and reaching. In the experiment, participants (n=6) performed reaching movements while looking at a fixation point. For each trial, locations of the target and the fixation point were independently selected from three possible locations. Nine possible combinations were categorized into two types of reaching: foveal reaching and peripheral reaching. Visuomotor rotation was applied to the hand cursor, and its rotation angle gradually increased from 0 to 30 deg throughout the training session (40 blocks of 12 trials). Importantly, the direction of rotation (CW or CCW) was randomly selected trial by trial, but uniquely specified by foveal or peripheral reaching. The result showed clear decrease in the initial direction error of reaching in each of foveal and peripheral conditions. When the rotation was removed after the training, we observed clear aftereffect in the direction opposite of each rotation. Error-decrease and aftereffects did not differ between both rotations, indicating that two opposing rotations can be simultaneously and equally adapted. Our data including trial-by-trial error on each participant were well fitted by a simple two-state model in which each state for foveal and peripheral reaching was independently updated using the error of each trial. The model fitting analysis with AIC suggests that peripheral reaching could be divided into "small peripheral" and "large peripheral". Additional experimental results showed that the adaptation gain for foveal reaching was fully transferred to that for peripheral reaching whereas the limited gain-transfer was observed from the peripheral reaching to the foveal reaching. Taken together, our data suggest the sensorimotor system would form and retrieve multiple memories of motor coordination that are separately linked with foveal and peripheral reaching mechanisms.

1-F-76 Neural correlates of sensorimotor adaptation in a spaceflight analogue environment

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During sensorimotor adaptation, individuals adjust their movements in response to mechanical or sensory perturbations. While aboard the International Space Station (ISS), astronauts must adapt to altered vestibular and somatosensory inputs from microgravity. Previously we employed a joystick adaptation task and found that patterns of neural activation vary throughout this task and with repeated exposures. However, it is unclear how altered sensory inputs on the ISS may impact the neural mechanisms associated with sensorimotor adaptation over time. Here, in a sample of eleven subjects, we investigate the impact of 30-days of 6º head down tilt bed rest combined with 0.5% CO2 (HDBR + CO2) on brain activity during sensorimotor adaptation as a spaceflight analogue. Functional MRI was acquired during two sessions pre-bed rest, two sessions during HDBR + CO2, and two sessions post HDBR + CO2. During scanning, subjects performed the adaptation task. They used a joystick to move a cursor to targets presented on a computer screen under veridical and 45º rotated cursor feedback. Preliminary whole brain neuroimaging analyses revealed pre-, during, and post- HDBR + CO2-related brain changes in all phases of the task. We found activity changes in right precentral gyrus and parahippocampal gyrus during baseline, left inferior temporal gyrus during early adaptation, right caudate and right hippocampus during late adaptation, and left middle frontal gyrus and right superior parietal lobe during de-adaptation. These findings provide insights into potential memory-related neural mechanisms that may undergo changes in response to spaceflight analogues. This work is supported by NASA grant #80NSSC17K0021.

1-F-77 Combining transcranial direct current stimulation and mirror therapy enhances upper limb motor control in chronic stroke survivors

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Improving upper limb control impaired by neurological disorders is critical in rehabilitation since the deficit can impact patients' activities of daily living and quality of life. Apart from conventional rehabilitation programs, mirror therapy (MT) has shown positive effects on motor recovery of the upper limb after stroke. To enhance the effects of MT, one promising approach is to combine MT with transcranial direct current stimulation (tDCS). In terms of the stimulation location, primary motor cortex (M1) has been the most targeted area due to its role in movement execution. However, M1 is often affected after stroke and applying stimulation over M1 may not yield sufficient neuroplasticity to improve motor performance. An alternative stimulation location is premotor cortex (PMC), based on its relation to motor planning and control. Here, we proposed two questions to examine the effect of tDCS combined with MT on motor performance in chronic stroke survivors: a) Can tDCS augment the effect of MT on motor performance after stroke, and b) Does tDCS over PMC lead to a greater improvement in motor performance than tDCS over M1? In this preliminary study, twelve chronic stroke survivors (11 M/1 F; age = 59.6±10.1 years; time since stroke = 3.9±3.7 years) were randomly assigned to one of the three intervention groups: 1) M1_MT: tDCS over ipsilesiopnal M1 followed by MT, 2) PMC_MT: tDCS over ipsilesiopnal PMC followed by MT, and 3) Sham_MT: sham tDCS followed by MT. All participants received intervention 90 minutes/day, 5 days/week, for 4 consecutive weeks. We chose reaching as a functional task to evaluate upper limb motor performance. Reaching movements were recorded before and after intervention using a 7-camera Vicon MX Motion Capture System at a sampling rate of 120 Hz. Kinematic data were calculated using Matlab. Outcome measures included reaction time, movement time, joint excursions and movement smoothness. Preliminary results revealed that all groups showed positive trends in shortening reaction time after intervention, suggests faster processing to activate related muscles. As for movement time of reaching task, PMC_MT group exhibited greater decrease, compared with other groups. Comparing the joint excursions patterns across groups, different shoulder-elbow control strategies were observed after treatment in each group. Additionally, all groups showed improvement in movement smoothness. As expected, our results suggest a positive effect of tDCS combined with MT in upper limb motor performance among chronic stroke survivors, and applying tDCS over PMC could lead to better improvement.

1-F-78 Critical Periods After Stroke Study (CPASS): A Phase II Trial

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Background: Better treatment of stroke, whether to reduce impairment or target the goals and preferences of individuals, can enable independence and increase participation. We are investigating the optimal time after stroke for intensive upper extremity motor training. There is evidence for timing effects in rehabilitation; motor training delivered at certain times may be more effective. It is hypothesized that the periods of greatest responsiveness after a stroke are analogous to the sensitive periods in normal human development. We expect that individuals receiving early intensive motor training will show greater upper extremity motor improvement measured at one year post stroke compared to individuals receiving therapy at later time points. Methods and Analysis: 80 participants will be adaptively randomized to receive an additional bolus of 20 hours of upper extremity therapy within 30 days post-stroke, 2 to 3 months post-stroke, 6 to 9 months post-stroke, or to a control group. The primary outcome is the Action Research Arm Test administered at one year. Blood will be drawn at up to 3 time points for biomarker studies. Results: We have enrolled two run-in subjects and randomized seventy-two participants to date; the study will be completed in 2019. Results from this study will help to plan a Phase III clinical trial. Conclusion: If sensitive periods exist in rehabilitation and can be identified after stroke, then current resources can be better targeted to promote recovery. Inclusion of biomarker determination opens up the possibility of understanding the biological mechanisms of recovery and supports future drug development.

1-F-79 The functional relevance of interhemispheric reorganization within the former sensory hand representation of unilateral amputees

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Introduction. Studies demonstrate that unilateral upper extremity amputation alters the cortical representation of the intact hand. Several fMRI studies report significant increases in both the contralateral and ipsilateral cortical sensorimotor hand territory when amputees move the intact hand. Whether similar interhemispheric reorganization is evident in response to sensory stimulation is uncertain, as is the potential functional significance of such changes. Method. To address these issues, we used fMRI to estimate responses to suprathreshold, cutaneous stimuli (8sec trains of compressed air at 3Hz) applied to the digit tips on the intact hands of 19 unilateral upper limb traumatic amputees (7 females, 10 below-elbow, mean age = 45 years, mean time since amputation 15 years, and 29 healthy controls (11 female, mean age = 44 years. These individuals were part of a larger group of 22 amputees (8 female, 11 below elbow, mean age = 47 years, mean time since amputation = 16 years), and 43 healthy adults (13 female, mean age = 47 years). The ability to localize touch in the absence of vision was assessed by delivering single-point stimuli with a suprathreshold monofilament to 16 locations on the digit tips and palm of the intact hand, and 10 locations on the volar surface of the intact forelimb. In below elbow amputees) the corresponding 10 locations on the volar surface of the residual forelimb were also tested. In addition, the Grating Orientation Test was used to evaluate tactile discrimination on the tips of the index fingers of all participants. Hypotheses. We reasoned that if chronic amputees exhibit interhemispheric reorganization in the sensory system, then cutaneous stimulation of the intact hand would be associated with increased activity within both the contralateral and the ipsilateral sensory hand territory. If such activity is functionally relevant, then amputees would differ from controls in their ability to localize and/or discriminate sensory stimuli applied to the hand. This could manifest as improved sensibility due to an increase in the number of cortical units coding intact hand stimulation, or to decreased performance resulting from the coactivation of units in both hand territories. Results. During stimulation of the intact digits, amputees displayed significantly greater responses within the ipsilateral hand territory that was formerly devoted to the now amputated hand. Nevertheless, we failed to detect any differences between amputees and controls in either sensory localization or discrimination ($p > .05$ in all cases). Correlations between fMRI responses in the former hand territory and performance on these sensory tasks were likewise n.s. Conclusion. Reorganization in the sensory representation of amputees' intact hands appears unrelated to the ability to touch localization or discrimination. These findings question the functional significance of deafferentiation-related cortical reorganization.

1-F-80 The motor engram as a dynamic change of the cortical network during early sequence learning: an fMRI study

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Practice improves performance of skilled movements, in terms of both speed and accuracy. Emphasis on speed improves performance, but learning can occur even without speed incentives. Thus, we hypothesized that the trace of brain changes brought about by motor training (i.e., motor engram) may be differently represented according to the training mode. To discriminate engrams formed by emphasis on speed or accuracy, we performed functional MRI on 58 normal volunteers, who performed a sequential finger-tapping task with the non-dominant left hand. Participants practiced alternately a tapping sequence as quickly as possible (maximum mode) or at a constant speed of 2 Hz, paced by a sequence-specifying visual cue (constant mode). To quantify the brain changes that characterize the engram at the network level, even when dormant, we applied the eigenvector centrality algorithm (EC) to the residual time-series after modeling out the task-related activity. We depicted the formation of the motor engram by characterizing the dormant state as the increase in EC of the resting epoch throughout the training course, and the activated state as the increment in EC during the task epoch relative to the alternated resting epoch. During maximum mode, the formation of the motor engram was found in the left anterior intraparietal sulcus (aIPS), connecting with the ventral inferior parietal lobule (IPL). During constant mode, a distinct engram was found in bilateral dorsal premotor cortex and right primary motor cortex (M1). Dormant EC values in these areas preferentially increased during specific speed mode. EC values in left aIPS increased during only maximum mode, whereas those in bilateral PMd increased during only constant mode. Furthermore, these dormant state ECs of left aIPS and right PMd were negatively correlated with the transition time during maximum mode and the reaction time during constant mode, respectively, suggesting that EC values are related with actual motor performances. A learning-related increment in task-related activity in the right M1 was observed in both modes. Using a novel method for representing both the dormant and active states of the motor engram, we successfully depicted an early-phase engram of sequential finger-tapping formed in an M1-centered parietal-premotor network. Within an M1-centered parietal-premotor network for motor engram, the left aIPS-IPL appears to represent the sensorimotor integration of precisely timed rapid finger movements, and the PMd and M1 the accuracy of their assignment.

1-F-81 Movement velocity is more susceptible than duration to implicit motor adaptation for movement distance

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When reaching for a cup of coffee, the motor system must determine a movement time and trajectory from an infinite number of repertoires. For instance, you can make a reaching movement towards an explicit target (e.g., a cup) with low velocity and long duration or with high velocity and short duration. This indicates that movement velocity (MV) and movement duration (MD) are redundant parameters, which would be determined by optimizing several cost functions (Haith et al., J Neurosci, 2012; Shadmehr et al., Curr Biol, 2016). Similarly, when a movement amplitude is altered by implicit motor adaptation, the motor system needs to solve the redundancy. Previous studies have just focused on how movement amplitude is altered to minimize a sensory prediction error (Krakauer et al., J Neurosci, 2000; Pearson et al., J Neurophysiol, 2010), while It is still unknown whether the motor system operates the same optimization during identical movements generated by implicit motor adaptation and directed towards an explicit target. To clarify it, in this explement, we investigated how the redundant parameters, namely MV and MD, are altered during implicit motor adaptation as those aiming an explicit target. Eight participants made self-paced reaching movements while holding a manipulandum to land a cursor on a target on the screen. The cursor was not visible during a movement, but only the final position was fed back. Consistent with the previous studies (Gordon et al., Exp Brain Res, 1994a, b), both of the MV and MD were systematically altered when the explicit target extents were varied from 6 to 14 cm. Then, while reaching towards the target located at 10 cm, the participants adapted to cursor shifting perturbations in which the cursor was gradually shifted up or down to 3 cm. Statistical analyses revealed that the participants implicitly but successfully altered their movement amplitude to approximately 7 or 13 cm. Surprisingly, although the MV was correspondingly altered with changes in the movement amplitude, the MD remained unchanged. The result illustrated that the resultant of MV and MD altered by implicit motor adaptation were clearly different from those directed towards explicit target extent, suggesting that the motor system may solve the redundancy for MV and MD differently between implicit motor adaptation and explicit movement control.

1-F-82 Enhancing somatosensory perception of pianists by a novel haptic training

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Somatosensory perception plays essential roles in skillful behaviors. Pianists are required to integrate somatosensory information derived from the fingertip into rapid correction and update of motor commands so that they can play various pianos with different mechanical properties. A previous study has shown that pianists have a superior spatial acuity of tactile perception of a fingertip than musically-untrained individuals (Ragert et al. 2004). However, a recent study demonstrated no difference in the proprioceptive perceptual ability between the pianists and non-musicians (Hosoda and Furuya. 2016). These findings raise two counteracting possibilities as to whether intensive training focusing on the proprioception improves that ability even in highly skilled individuals such as pianists, or yields no improvement due to a ceiling effect. It also remains unclear whether the somatosensory training facilitates fine motor control. Here, we examined these issues using a novel custom-made haptic training system. Twenty pianists were divided into two groups according to with or without haptic training. The subjects in the training group performed a haptic training so as to improve the proprioceptive ability of the right ring fingertip. Before and after the training (i.e. pre-session and post-session), three behavioral tasks were performed using the right ring finger; a weight discrimination task that assesses the proprioceptive perception threshold (PT), the fastest finger tapping task, and a repetitive keystroke task that measures how accurately subjects can produce a predetermined keystroke velocity. The control group took a rest for a period same as the training session. In the training group, both the PT of the weight discrimination and accuracy of low force production (i.e. 30% maximum keystroke velocity) improved following the training session. By contrast, neither the accuracy of high force production (i.e. 70% maximum keystroke velocity) nor the total number of strikes at the fastest tapping task changed through the training. In the control group, we found no significant differences in the PT, the accuracy of low and high force production during the paced keystrokes, and the total number of strikes at the fastest tapping between the pre- and post-sessions. Our results indicate that the present haptic training targeting the proprioceptive sensation can improve the proprioceptive PT of the fingertip even in highly trained pianists. The haptic training also enhanced the ability to accurately produce a target force during repetitive keystrokes. It is possible that enhancement of proprioceptive perception enabled pianists to perceive the keystroke velocity more accurately and thereby improved precision of force control during performance of successive keystrokes. It is likely that even highly trained individuals who commenced training in childhood have a potential of improving the haptic perception through intensive short-term training.

1-F-83 Effect of a viewpoint on long-term retention of motor memory

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Humans are capable of appropriate actions even when the popular viewpoint differs from their own viewpoints. Our previous research revealed that a motor memory was partially shared between different viewpoints. However, long-term retention of a motor memory depending on a particular viewpoint is not known. In this study, we investigated the effects of different viewpoint environments on the long-term retention of motor memory. Fourteen healthy right-handed volunteers participated in this study. They were required to manipulate a robotic device through grasping to move a visual cursor. They performed a delayed reaching task in which the cursor was moved along a straight line from a starting position to a target position. A target appeared in one of four equally spaced positions with equal probabilities of occurrence. This reaching task was carried out from either a frontal or a right-sided viewpoint. The two viewpoint environments were set by switching between two web cameras' images, which were projected to the participants through a head mounted display. This experiment was composed of five blocks. The first (from the frontal/right-sided viewpoint) and the second (from the right-sided/frontal viewpoint) blocks included 20 trials for each viewpoint and were set as the baseline (null force field). The third block (the frontal/right-sided viewpoint) included 120 trials and had a clockwise velocity-dependent force field. This block was set as the learning block. The fourth (the right-sided/frontal viewpoint) and fifth (the frontal/right-sided viewpoint) blocks included 20 trials for each viewpoint and were set as the washout data (null force field) to verify the presence of an after-effect and to cause the participants to forget the memories that they had learned. Six participants started from the frontal viewpoint, and eight participants started from the right-sided viewpoint. The same experience was repeated one year later to evaluate the long-term retention of motor memory. The results showed that motor memory that the participants learned for the force-field environment at the frontal viewpoint showed saving, which indicated that relearning had a more rapid rate for retention than the initial learning, whereas that from the right-sided viewpoint did not show saving. This result suggests that long-term retention of motor memory differs depending on the viewpoint of learning. Moreover, the motor memory from the frontal viewpoint could be retained for over one year. These results will provide new insights into the importance of viewpoints in the retention of motor memory.

1-F-84 Analyzing instrumental learning in blindsight monkeys with reinforcement learning model

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Blindsight is the residual visuo-motor ability without awareness after lesion of the primary visual cortex (V1). A variety of residual cognitive functions in blindsight has also been studied, however, reinforcement learning of motor actions remains to be investigated. Reinforcement learning is a fundamental learning system using one's own experience, in which novel actions are acquired and subsequently selected so that the rewards are maximized. In the reinforcement learning system, reward is not necessarily clothing, food or housing (primary reinforcer). Secondary reinforcers, which are associated with primary reward, can also induce reinforcement learning. In this study, we examined whether visual cues could effectively reinforce the acquisition of new responses in a motor-action selection task, when the reinforcing visual cues were presented in the lesion-affected visual fields of monkeys with unilateral lesions of primary visual cortex - a non-human primate model of blindsight. We designed a hidden target search task. In this task, the monkeys had to discover the location of the unseen target area (TA) by directing their eye-movements (gaze) on a monitor screen. If their gaze entered the TA and remained there >230 ms, a visual conditioning cue stimulus (CS) was presented at the edge of monitor and monkeys got reward after 2 seconds delay. Initially, search time and total length of trajectory of eye movement during the search in single trials were long. However, those were significantly reduced through repeated trials. This learning process was fitted well by a decaying exponential curve. To quantify the learning, we constructed a reinforcement learning model based on the one proposed by Chukoskie et al. (2013), which simulated the human's learning process to find a target which was drawn from a predefined distribution of possible targets on each trial. In our model, value of a particular location on the screen (V) increased with learning progress, and it well explained the process of action selection in both cases where the CS was presented in the intact and V1 lesion-affected field. These results showed that a visual CS presented to the affected visual filed was able effectively to reinforce the acquisition of a novel instrumental response. Finally, to evaluate the awareness of the visual CS in our experiments, we analyzed the pattern of eye movements after the CS had been presented. When the visual CS was presented in the intact visual field, the monkeys appeared to stop searching and their gaze tended to moved away from the TA. In contrast, when the CS was presented in the affected field, the monkeys continued searching in and around the TA, which suggested that the monkeys were less confident about presentation of the CS. We therefore conclude that the visual information about the CS can access the neural systems responsible for reinforcement learning even when the monkey is seemingly unaware of the presence of the reinforcing visual CS.

1-F-85 Peripersonal space and the experienced perturbation of a new force-field: story of a contraction

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In daily life, we are surrounded by objects we can interact with. To reach an object of interest with the hand, we have to judge whether the object is within our peripersonal space or not. How this judgment is made represents a compelling question. It has been suggested that such a seemingly perceptual task may imply a motor component. Indeed, experimental studies demonstrated an effect of sensorimotor adaptation to a biased visual feedback on both the proprioceptive estimate of the arm and the judgment of reachability (Henriques and Cressman, 2012; Bourgeois and Coello, 2012). The changes in motor behavior observed in adaptation paradigms are thought to be related to the updating of internal models which impacts in parallel both the motor commands and the prediction of their sensory consequences (Körding and Wolpert, 2004). Adaptation can be observed in the context of changes in the geometrical properties of the body (Redding and Wallace, 1996; Rossetti et al., 2008), or changes in the inertial, dynamic properties of the limb (Lackner and DiZio, 1994; Coello et al., 1996; Bourdin et al., 2001; Leclere et al., under review). However, the effect of adapting to new limb dynamics on the perception of reachability and the representation of peripersonal space has not been investigated so far. In this context, our aim was to assess the effect of sensorimotor adaptation to a new force field environment inducing change of limb dynamics on the representation of peripersonal space. We asked two groups of participants to sit on-axis of a rotating platform. Each group performed successively manual reaching tasks and perceptual tasks consisting in judging the reachability of visual targets. The experiment was divided in PRE-, PER- and POST-rotation periods. Participants completed the motor task during PRE-, PER- (adaptative phase) and POST-rotation periods, but the perceptual task only in PRE- and POST-rotation, that is just before and after the adaptative phase. To precisely assess the effect of sensory-motor adaptation on reachability judgement, we submitted both groups to different mechanical perturbations. Indeed, one group rotated clockwise and the other counter-clockwise, resulting in opposite motor perturbations and then to specific adaptive processes. Results showed that peripersonal space representation was systematically reduced whatever the direction of the mechanical perturbation. These findings suggest that adaptation to new limb dynamics clearly affects the peripersonal space representation. However, this "non-directional" effect could suggest that the change in peripersonal space representation is more related to the detection of an initial movement error during rotation rather than to the process of sensorimotor adaptation per se. We speculate that such error detection triggers a default, non-specific reduction of the representation of peripersonal space because of its defensive properties.

1-F-87 Starting to dissociate explicit and implicit learning in studies of speech auditory-motor adaptation

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Recent work on sensorimotor learning has dissociated explicit and implicit contributions. The explicit component involves intentional strategy use and is driven by target error. The implicit component involves the updating of an internal forward model without awareness of the learner and is driven by sensory prediction error. In studies of reaching in a perturbed visual environment (e.g. feedback rotated around the center of the workspace), it has been possible to estimate the explicit contribution by asking subjects to report intended aiming direction before each trial. The strength of the implicit contribution can then be estimated by subtracting this explicit aiming direction from the actual movement direction. An alternative approach has been to eliminate explicit contributions by constraining movement planning time. Sensorimotor adaptation also occurs in speech production (e.g. with shifts of vowel-specific resonance frequencies in the auditory feedback). For speech, however, it is not clear how to dissociate the contributions of explicit and implicit learning components, or even to determine if there indeed are contributions from both components: naïve subjects have no explicit knowledge of the mapping between speech articulator positions and resonance frequencies in the auditory feedback, and efforts to ask subjects about intended auditory "aiming" have been unsuccessful. Approaches such as constraining planning duration or examining interference from a second task could be considered, but would negatively impact speech execution or leave open alternative interpretations. As an additional complication, the perceptual boundaries between auditory speech targets have been reported to change over the course of learning. We report an initial attempt at determining the existence of an explicit component in speech auditory-motor learning while also examining changes in auditory targets. Typical adults and adults who stutter (a population with limited adaptation) produced words in baseline, perturbation, and post-perturbation phases. The perturbation consisted of shifting the first resonance frequency of the produced words "bed" and "pet" such they perceptually moved toward "bad" and "pat." After each trial, subjects used a scale on a touch-screen monitor to indicate how much they had intentionally changed their speech. Every 10 trials, they used a similar scale to listen to unaltered and altered versions of their own production of the target word and to select the best match for what the word "should sound like" (estimating the current target). Stuttering adults showed substantially less learning than nonstuttering adults. Neither group showed a systematic target shift in parallel with learning. With very few individual exceptions, neither group reported any intentional (i.e. explicit) adjustments in their speech. Speech auditory-motor adaptation may be an entirely implicit learning process, but improved experimental paradigms should be explored.

1-F-88 Motor learning with four types of robot controls

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Robot-aided rehabilitation after stroke has been expected to facilitate self-rehabilitation, reducing therapists' effort. Although previous studies have proposed various control methods for robot-aided motor learning, they have not directly compared their effects on the motor performance, which makes difficult for therapists to select suitable control methods in practical use. To address this issue, we investigated the effect of four distinct robot control methods on motor learning using a two degrees-of-freedom parallel robot. As a target movement, we made a counter-clockwise spiral trajectory. In the experiments, participants held a stylus attached to the end effector of the robot in a power grip to draw the spiral as accurately as possible in terms of a specified path and time course. We used four robot control methods: target constraint, force assistance with path constraint, path constraint, and null constraint. In the target constraint condition, the robot governed movement of the stylus. In the force assistance with path constraint condition, the robot pushed the stylus on the running direction. While the stylus movement was not restricted and participants could move it in the running direction, a virtual wall prevented the stylus from deviating the path. In the path constraint condition, the virtual wall existed but participants had to move the stylus entirely by their force. In the null constraint condition, no robotic constraints and force assistance existed. Sixty participants were assigned to one of the four groups. The learning schedule consists of five evaluation phases and four practice phases. The two types of phases were alternately conducted. An evaluation phase and practice phase had 3 trials and 25 trials, respectively. In the evaluation phases, all participants performed the task with the null constraint without visual feedback of the stylus trajectory. In the practice phases, participants performed the task under their control condition and received visual feedback of the trajectory after each trial. The errors of the null constraint and path constraint groups were statistically smaller than those of the force assistance with path constraint and target constraint groups at the evaluation phases 3 and 4. While the null constraint and path constraint groups showed a significant decrease of the error in the evaluation phases 4 from the baseline, the path constraint and target constraint groups did not. These results imply that the robot assistance in the running direction might not the best way in motor learning. Furthermore, the path constraint, which provided learning effects comparable to that of the null constraint, could be the first choice in the robot-aided rehabilitation if participants can move their arm by their own effort.

1-F-89 Perceptual learning induced by active movements with ambiguous visual stimuli

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Somatosensory and visual changes have been observed to occur together in contexts such force-field learning, visuomotor adaptation, and prism adaptation. Motor adaptation elicits lasting and concurrent changes to motor, visual, and somatosensory networks, supported by the presence of reciprocal neuroanatomical pathways between cortical motor and somatosensory areas, but how movement influences perception remains relatively unclear. In the literature on visual processing of motion, a plaid pattern moving through an aperture is a well-known paradigm whose interpretation is ambiguous. Plaid

stimuli are a checkered display formed by two superimposed drifting square-wave gratings in transparent regime, which move in different directions, separated by a defined angle. By varying either grating's features (spatial frequency, drifting speed, contrast, depth, luminance) or plaid properties (drifting speed, presentation time), it is possible to modulate the perceptual ambiguity of this stimulus: it can be perceived as a single pattern moving coherently in one direction (this perception is named integration or coherent motion), or as two overlapping gratings, which slide over each other in different directions (this is called segmentation or transparent motion). We hypothesized that the visual perceptual uncertainty caused by moving plaids may be influenced by the active interaction between the observer and the stimulus. Moreover, during this interaction the ambiguous visual feedback of plaid motion may bias proprioception. Here, we present an experimental procedure involving active motor training and both visual and proprioceptive tests, which are repeated before and after the training to identify any changes in subjects' perception. The perceptual uncertainty of the plaid stimuli during motor training is modulated by varying the luminance level of each grating. During training, subjects grasp the handle of the robot to actively drive the motion of a plaid stimulus during a reaching task. Preliminary results show that the active interaction between the observer and the stimulus can induce both visual and proprioceptive changes, which can be interpreted as a perceptual skill learning.

1-F-90 The effects of reward on movement chunking

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The expectation of receiving reward has been shown to improve both the speed and accuracy of saccadic eye and simple reaching movements reflecting a decision whereby reward discounts the cost of effort. Movement chunking, the concatenation of action units into temporally stable action sequences, is believed to be based on a similar trade-off between computational complexity and future efficiency, with recent findings suggesting a dopamine-dependent component. In the present study we aimed to investigate whether reward facilitates spatial chunking of sequential reaching movements. Participants were randomly allocated to a reward and non-reward condition (both N=15) and over the course of 2 testing days were asked to produce 8 consecutive reaching movements to hit a series of targets. Rewarded trials were cued using an auditory and visual stimulus and participants received monetary reward depending on their movement time (MT). Missing a target resulted in a failed trial which had to be repeated, hence forcing them to produce highly accurate movements. Participants in the rewarded condition produced faster MTs over the course of the experiment ($p = 0.027$) and were significantly faster than the non-rewarded group at the end of training on Day 2 ($p = 0.021$). Similarly, the chunking index (CI), operationalised as differences in peak velocities compared to minimum velocities at via points, improved significantly over time ($p = 0.0032$) and in comparison to the non-rewarded group on Day 2 ($p = 0.012$). Importantly, in Post-Training assessments in which reward was not provided for either group, participants in the rewarded group produced slower MTs when compared to their previous performance during training. However, they produced similar CIs which were significantly higher than the ones produced in the non-rewarded group ($p = 0.028$). This suggests the formation of a temporally stable change in motor output whose expression becomes reward independent over time. Finally, the significant difference in CI levels between groups persisted in additional Post-Training assessments during which reward was provided for both groups (0.032).In contrast, the differences in MT became non-significant. These results highlight that MTs can be invigorated by reward and seem to follow an 'on-off-principal' depending on the availability of reward. In contrast, the expression of spatial chunks seems to become reward independent with training. Their formation, however, is a training-dependent process which can be facilitated with reward, thereby complementing recent research findings demonstrating the involvement of the basal ganglia dopamine pathway in chunking formation. Taken together, our findings suggest that reward improves reaching performance via two mechanisms; (1) an invigoration effect which is training-independent and follows an 'on-off-principal' and (2) a learning effect which is training-dependent and temporally stable even in the absence of reward availability.

1-F-91 Robotic assistance increases the user's feedback gain

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In physical rehabilitation, providing robotic rehabilitation is known to cause a patient to 'slack' or relax and let the robot do the task. This is problematic as the patient's voluntary muscular activity is known to be a critical factor to restoring motor function after stroke. Studies so far have quantified slacking by measuring the reduction in the patient's muscular activity (or force) before and after providing robotic assistance. However, such comparisons have a confound where the patient may simply be relaxing because the robot has brought them closer to their objective. For example, a robotic assistant during a reaching task necessarily brings the patient's hand closer to the target, which reduces the patient's effort required to fulfil the task. Thus, relaxation in the presence of robotic assistance is not a sufficient measure of slacking. Here, we propose that the patient's feedback gain provides a measure of their involvement in the task, and if their feedback gain decreases during robotic assistance, then the patient is slacking. Subjects were asked to complete a 15 second tracking task using their arm in an isometric condition. The forces applied by the subject were used to control a virtual cursor to chase a randomly moving target. On some trials, a robotic assistant helped the virtual cursor to track the target. Different types of assistance were tested, some that helped reduce positional errors and others that assisted velocity errors. The tracking error, mean force and the feedback gain (position, velocity) were calculated every trial. Although the force decreased with some assistants, the subject's feedback gain increased in response to all robotic assistants. Thus, previous studies that observed slacking may have measured the effect of the assistance only, rather than measuring the change in the patient's control during the task.

1-F-92 Directional tuning of stretch reflexes after implicit and explicit visuomotor adaptation

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Motor adaptation can be driven by explicit and implicit processes. These different processes have been associated with distinct neural substrates, with frontal regions more important for explicit learning and cerebellar regions more involved in implicit learning (see McDougle et al., 2016 for a review). Recently, it has been shown that the rapid stimulus-locked visuomotor response (SLR) is modulated by implicit, but not by explicit, motor adaptation (Gu et al., 2019). Here we investigate how these two types of motor adaptation affect the muscle stretch reflex, elicited by mechanical perturbations applied to the joint. While previous work has shown that the reflex gain is modulated by (force field) adaptation (Ahmadi-Pajouh et al., 2012; Kimura et al., 2006), it is yet unknown how, and in which coordinate system, implicit and explicit motor adaptation influence the directional tuning of the shoulder (pectoralis major, PEC) stretch reflex, elicited after the onset of the SLR. To investigate this question, participants performed a visuomotor adaptation experiment in which they were exposed to an abrupt (eliciting more explicit) and a gradual (eliciting more implicit) learning schedule on separate days. In every trial, a stretch reflex was elicited by a perturbation force in the pulling direction of the PEC, which also served as the go cue to start a movement to a target. By using twelve possible target locations, we can measure a tuning curve of the stretch reflex (Pruszynski et al., 2008) before and after adaptation. We hypothesize that if, just as for the SLR, only the implicit part of learning is transferred to the reflex circuitry, the shift of the tuning curve will be modulated by the learning schedule, with a larger shift for the gradual learning schedule. Preliminary results show that the tuning curve indeed shifts in the direction to compensate for the visuomotor rotation, but only from the R3 time window (75-105 ms post-perturbation) onwards. This shift in tuning is present both after learning with an abrupt and with a gradual learning schedule. More data are currently collected to dissociate the implicit and explicit contributions. Concluding, both abrupt and gradual motor adaptation influences the tuning of the shoulder stretch reflex to compensate for a visuomotor rotation expected for an upcoming movement. References 1. McDougle et al., 2016. TiCS, 20(7), 535-544. 2. Gu et al., 2019. J Neurophysiol, 121, 85-95. 3. Kimura et al., 2006. J Neurosci, 26(36), 9272-9281. 4. Ahmadi-Pajouh et al., 2012. J Neurosci, 32(28), 9537-9545. 5. Pruszynski et al., 2008. J Neurophysiol, 100, 224-238.

1-F-94 Impact of reinforcement on action selection, initiation and execution during motor skill learning

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The ability to learn motor skills is a fundamental feature of human behavior, which relies both on sensory and on reinforcement feedbacks (i.e., reward and punishment, Galea et al. 2015, Nat Neurosci). How such reinforcements lead to improved performance during motor skill learning remains an open question. In fact, skill learning can result from improvements at several levels of control, including action selection, initiation or execution. Here, we tested the impact of reinforcement on these different levels during motor skill learning. After 2 short practice blocks, subjects performed 10 blocks (360 trials in total) of a modified version of a force-tracking task (Steel et al., 2016, Sci Rep). Each trial started with a cursor appearing at the bottom of the screen and subjects were asked to squeeze a pinch-grip sensor to bring the cursor at the center of a fixed target and maintain it there for the rest of the trial. To reach the target, subjects had to exert a force (TargetForce) corresponding to 10 % of the individual maximal voluntary contraction. On most trials, the cursor disappeared shortly after the beginning of the trial. Hence, subjects had to learn to approximate the TargetForce in the absence of visual cursor. A trial was classified as successful if the mean of the difference between the actual force and the TargetForce was under an individualized threshold. At the end of each trial, subjects received a reinforcement feedback based on their performance (i.e., Success or Failure). In this task, success depended on force control at the level of action selection (i.e., ForceSel; the closer the mean of the selected force was to TargetForce, the higher the chances of success), at the level of initiation (i.e., the faster the onset [ForceStart] and the steeper the rate [ForceRate] of force production, the better) and execution (i.e., ForceExe; the lower the force variability during the tonic phase, the better). Moreover, we analyzed the evolution of the different force variables at the three levels of control, as well as the impact of reinforcement (i.e., Success or Failure) on performance in the next trial across training. As expected, the proportion of successful trials increased over training, indicating that subjects learned the motor skill. Moreover, we found that skill learning occurred at the level of action initiation (earlier ForceStart and steeper ForceRate) and execution (reduced ForceExe) but not at the level of action selection (no change in ForceSel). Interestingly, subjects improved at all levels of control in trials following a Failure, while they exhibited the opposite pattern following a Success. However, importantly, this effect of reinforcement changed over the course of learning. In fact, the beneficial effect of Failure increased across training while the detrimental effect of Success decreased. It remains to be determined whether these effects would vary with a reinforcement involving an actual monetary loss or gain.

1-F-95 Triggering the switching between motor control strategies in complex unstable tasks

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Many complex activities of daily living show some unstable component that the brain has to deal with. Manipulating a compliant object, controlling the upright human posture, collaborating physically with another agent, are all examples of tasks that humans need to face with every day. In these situations, the intrinsic task instability can be modeled as a divergent force-field that moves the state of the system away from an unstable equilibrium. Exploiting the dynamical characteristics of the environment and the biomechanical properties of the human body, the central nervous system (CNS) is able to develop strategies to accomplish the tasks. From a motor control point of view, there are two extreme stabilization mechanisms that require to integrate multi-joint coordination aspects: 1) stiffness stabilization strategy (SSS), aiming at asymptotic stability, where the visco-elastic muscle properties are exploited by learning optimal co-activation patterns that allow to achieve a sufficient level of joint stiffness for compensating the intrinsic instability; 2) positional stabilization strategy (PSS), a low-stiffness strategy, aiming at bounded stability, where feedback corrective movements are produced in an intermittent manner. Here we propose an experimental paradigm where both PSS and SSS could be adopted to investigate stabilization strategies, generalization, strategy-switching and dyadic cooperation. In particular we focus on a the following question: to which extent modifications of the environment's dynamical properties can guide the preference for one strategy with respect to the other? Healthy participants, experts in both PSS and SSS, performed a stabilization experiment in which they faced different task dynamics. The subjects used a Virtual Underactuated Bimanual Tool, simulated by means of a bimanual planar robot. The tool, consists of two elastic linkages, connected to a virtual point mass, immersed in an unstable force-field. In order to understand how sensitive is the actual behavior of the subjects to variations of the system parameters, five different sets of tool parameters were chosen to induce a subject to choose a specific strategy for stabilizing the end-point of the virtual tool field in different positions of the workspace. Data demonstrated that the choice of a more or less intermittent strategy for the stabilization of unstable tasks can be strongly influenced by the environment's dynamics. Indeed, the difference between the performances of the expert subjects when using different strategies is not negligible in particular set configurations, leading us to define strategy preference metrics.

G – Theoretical & Computational Motor Control

1-G-96 Brain electrical activity in response to delayed visual feedback after motor execution

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In most interfacing systems based on visual feedbacks, e.g., personal computers, tablet PC, and smart phones, time delays between command inputs and feedbacks are generally inevitable. The ideal systems should provide non-delayed visual feedbacks as the users might feel bad (unpleasant) to the delayed visual feedback. However, reducing the visual feedback delay generally requires a large amount of system resources, and thus might degrade the overall system performance. Thus, it is sometimes necessary to determine an optimal visual feedback delay that balances the users' subjective preference and the system resource occupation. In a previous study, a survey result was presented, but the brain activity in response to the delayed visual feedback after motor execution was not investigated. The goal of this study was to investigate the changes of brain electrical activity in response to the delayed visual feedback after motor execution using quantitative EEG analyses. Twenty-five healthy subjects participated in our experiments, and they were asked to move a computer mouse horizontally at a constant speed. The mouse movements were fed back to the participants as the movements of a mouse cursor on the computer monitor. The time delay between the command input and the visual feedback was randomly selected from nine different time delay values (0, 30, 60, 90, 120, 150, 180, 210, and 240 ms except basic system delay of 78 ms). After each trial, we asked the participants whether they recognized the time delays. EEGs were also recorded from 19 electrodes, which were attached to the scalp according to the international 10-20 system. This procedure was repeated 10 times for each time delay condition (90 trials in total). After applying filtering and baseline correction, the EEG data were epoched into 2-s segments with 50 % overlapping. The spectral power of each 2-s segment was obtained using FFT, and the results were averaged across trials for each time delay and each electrode. Then, the spectral powers of each time delay condition and electrodes were accumulated over 6 frequency bands; delta (1-3 Hz), theta (4-7 Hz), alpha (8-12 Hz), low beta (13-21 Hz), high beta (22-30 Hz), and gamma (31-50 Hz). To compare the difference in spectral power with respect to time delays, repeated measures analysis of variance (RM-ANOVA) was applied. Finally, electrodes and frequency bands showing significant difference with respect to time delays were selected. The frontal-alpha power was tightly correlated with the survey results, which seems to reflect the sense of agency. The decrement of frontal-theta and occipital, temporal-alpha power (ERD) with respect to the time delay increment might reflect the increment of unpleasantness of the participants in response to the visual feedback delay. It is expected that EEG can be used as a tool to monitor user's preference to visual feedbacks as well as the sense of agency during a motor-related tasks with visual feedbacks.

1-G-97 Decoding of kinematic information using functional specificity of primary motor cortical neurons

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Neural decoding technologies that estimate upper-limb movements pursue to mimic the kinematic or kinetic control of vertebrates. The consistent patterns of the primary motor cortical neurons (M1) play a critical role in the development of an intracortical brain-machine interface (BMI). However, conventional decoding algorithms seldomly consider characterizing the functions of individual M1 neurons that contain informative kinematic covariates with synergic muscle activities during upper-limb movements. In this study, we propose a decoding algorithm using latent motor commands extracted from canonical correlations between M1 neuronal ensemble and kinematic states. To extract the latent motor commands from M1 neurons, we first defined extractable kinematic variables for each neuron with a precise tuning model. Then, we conducted a canonical correlation analysis between these variables and M1 neuronal activities to identify latent canonical variables. We assume that the latent motor commands represented by the canonical variables contain specific information transferred from M1 to upper-limb muscles, which are potentially correlated with kinematic states such as movement velocity. To estimate the kinematic states from the latent motor commands, we utilized the long short-term memory (LSTM) model to approximate an unknown, presumably non-linear function, which would describe the relationship between movement velocity and the latent motor commands. As a control model, we used the LSTM model in the same way as the traditional, directly decoding original neuronal firing rates to velocity. Assessment with testing data showed that our new algorithm performed better (> 9.66 %) than the control LSTM model. Our results have demonstrated an improvement in decoding performance as we took functional specificity of M1 neurons into consideration, which will allow for an effective design for high-performing BMIs.

1-G-98 Finding 1-Dimensional substructures in set of kinematic time series in a cyclic motor task

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Recently using graph based data analysis is a popular approach when large datasets are collected and processed. In motor control this may be novel and here we apply it for a cyclic motor task. 18 able-bodied participants performed arm cranking exercises on an arm cycle ergometer (MEYRA, Germany). They rotated the crank of the ergometer with a cadence of 60 rpm. From each participant, data from twenty-four 30 seconds trials were collected by a ZEBRIS ultrasound based motion analyzer. The 3D coordinates of 8 markers were recorded (100Hz), 6 on the arm, 1 on the ergometer's handle and 1 reference marker. Surface EMGs were recorded (900Hz) from the biceps, triceps, delta anterior, delta posterior of both arms. For each trial, the time series of 24 coordinates (3 per markers from one arm) and 8 EMG time series gave the input to the graph based dimension reduction algorithm. We computed pairwise correlation coefficients of the 32 time series. Thus we got 32x31/2=496 numbers and defined a 32 by 32 symmetric matrix C. The i-th element of the j-th row of C is the correlation coefficient of the i-th and j-th time series. Then we computed the determinants of all the 2 by 2 submatrices of C. We arranged the resulted values into a 496 by 496 symmetric matrix D. This gave the adjacency matrix of a graph G. If the entry in the i-th row and j-th column of D is close to 0, then nodes i and j are adjacent in G. A clique in this graph identifies a subset of the time series that can be substituted by one reference time series as they differ only in a scalar multiplier, thus they form a 1D structure. Our algorithm finds such 1D structures. We point out that principal component analysis may find the data set having a relatively high dimension. In the same time the new method may detect a number of 1-dimensional subsets in the data. A union of various 1-dimensional subsets can easily prevent the whole data set having an overall low dimension. We had large matrices and run the clique searching algorithm on G for all trials. We note that the computational time is strongly increasing with the number of time series. The most common clique, found in 96% of the trials, was a 4-clique. This corresponded to the time series (upward-downward movements) of 4 markers: 3 on the participant's hand and 1 on the ergometer's handle. These spatial points moved up-down in phase, in 96 % of the trials. For the forward-backward movements of these points this rate was 30%. In the lateral direction their movement weren't in phase and didn't correspond to a clique. The latter was found for EMG time series of the studied muscles as well. Comparing the right and left arms the same results were found when identifying 1D subsets. These results were not surprising in arm cranking. Though, our algorithm identified those time series, which changed in phase and thus offered a research tool for studying other motor tasks and many time series, to find (maybe hybrid) kinematic and muscle synergies.

1-G-99 Redundant visual error information processing by motor adaptation system according to divisive normalization mechanism

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Maintaining accurate movements is accomplished by the ability of the motor system to constantly correct the movement according to sensory prediction error. Previous studies have demonstrated that this ability is adversely affected by the visual feedback uncertainty (Burge et al., 2008; Wei & Kording, 2010). Although the reduction of motor adaptation rate with the uncertainty was explained by the idea of Kalman filter, the neuronal mechanisms have been largely unknown. Notably, the visual feedback uncertainty was provided by multiple cursors (dots) (Wei & Kording 2010). Thus, clarifying how the motor adaptation system processes multiple visual error information could lead to mechanistic understanding of influence of visual feedback uncertainty on motor adaptation. Here, we tried to elucidate the way of processing by a mechanism of divisive normalization (Carandini & Heeger 2011). Participants tried to move a cursor toward a front target with their unseen hand. In the visual perturbation trial, the hand movement was constrained with a force channel, while a single cursor or double cursors deviated in various directions from the forward direction (single cursor condition: ±30, ±22.5, ±15, ±7.5, 0 deg; double cursor condition: combination of two of ±30, ±15, and 0 deg) (Kasuga et al. 2013). In the subsequent trial, the force channel was also used to measure the lateral force as an index of motor adaptation (i.e., aftereffect). This probe trial was followed by 2 null trials to washout the possible adaptation effect. The patterns of dependence of aftereffect on perturbation(s) were complicated. First, when the perturbation directions for double cursor condition were opposite (e.g., ±15 deg), the aftereffect was suppressed. Second, the aftereffect to double cursors (e.g., 15 and 30 deg) was not merely the summation of aftereffects induced by each of double cursors. Third, the aftereffect to double cursors (e.g., 0 and 15 deg) was different from the aftereffect to the averaged perturbation (7.5 deg). Such a complicated pattern was observed in our previous study proposing that visual and proprioceptive errors were integrated by a divisive normalization mechanism (Hayashi et al. 2019). Similarly, the present results were explained by our computational model assuming that neuronal elements encode visual error with their own receptive field and the output was normalized by the summation of outputs. The additional experiment indicated that this model also explained the aftereffects when three cursors were simultaneously displayed. Notably, this model predicts that, as the variance of multiple cursor directions increased with the mean remained constant, the aftereffect can become smaller. Thus, the present study clarified the way of redundant visual error information processing in the motor adaptation system and how this mechanism could explain the adverse effect of visual information uncertainty on motor adaptation.

1-G-100 Classical conditioning effects in human visuomotor adaptation

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Approaches to the study of cerebellar-driven motor learning vary widely across species. One of the more common cerebellar learning tasks in studies of laboratory animals is Pavlovian delay eyeblink conditioning, where a conditioned stimulus (CS; e.g., a tone or a light flash) is paired with an unconditioned stimulus (US; e.g., a puff of air to the cornea) to drive a conditioned response (CR; e.g., a blink in response to the CS). Eyeblink conditioning research has led to a rich understanding of how computations in the cerebellum link sensory cues, error signals, and well-timed motor responses. In humans, cerebellar-dependent learning is often studied with visuomotor adaptation tasks, where perturbations of sensory feedback, such as visuomotor rotations, are used to examine an implicit adaptive response, such as a change in reaching direction. Such studies have led to a detailed control theory-based framework of cerebellar adaptation that invokes internal models and state estimates. These two learning processes - eyeblink conditioning and implicit sensorimotor adaptation - have been studied in relative isolation, despite their putative dependence on the cerebellum. Here, we present preliminary evidence for Pavlovian-like effects in human visuomotor adaptation. We used a recently-developed error-clamp paradigm that isolates the implicit visuomotor adaptation process. We deterministically paired visuomotor errors (15˚ clamp, conditioned trials) with a sensory cue (e.g., an auditory tone) that was presented just before and throughout movements, and intermixed those trials with zero-error outcomes (0˚ clamps, extinction trials) that were associated with a separate sensory cue (e.g., a visual flash). Trial-by-trial reaching behavior showed significant effects of the presented sensory cue, with signs of positive adaptation on the conditioned trials and negative adaptation on the extinction trials. This result suggests that at least some proportion of the adaptive response can become linked to an arbitrary conditioning cue. We also hypothesize that the movement goal itself could be framed as a salient conditioning stimulus, consistent with theories of plan-based adaptation. This study acts as a first step toward linking visuomotor adaptation and classical conditioning, and suggests that the former could be viewed through the lens of the latter.

1-G-101 Real-time BMI control for virtual navigation based on rhythmic neural activity

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Brain-machine interfaces (BMIs) for 2D cursor control have become increasingly high-performance and are presently being evaluated in human clinical trials. There is also significant clinical need for locomotor BMIs, yet there exist fewer studies in this domain. We recently characterized rhythmic neural activity in motor cortex while monkeys cycled a hand-pedal forward and backward to navigate a virtual environment (Russo et al. 2018). Such activity is robust and structured, and thus a potentially good substrate for BMI control of locomotion. Yet during cycling, neural activity lacks the conveniently simple statistical relationships with hand kinematics leveraged by traditional BMIs (i.e., direction 'tuning'). For example, the dominant neural signals are surprisingly similar during forward and backward cycling. This situation highlights the need for decode algorithms that leverage robust responses without assuming straightforward relationships with kinematics. We trained a monkey to perform the cycling task under closed-loop BMI control, based on decoded spiking activity from 192 electrodes chronically implanted in motor and premotor cortex. We developed a decode algorithm that leverages three aspects of spiking activity projected into a state space. First, neural activity translates from one part of state space to another just before movement onset, and translates back around movement offset. We used this translation to determine when the monkey was cycling. Second, steady-state cycling was accompanied by elliptical state-space trajectories that were similar for forward and backward cycling in the dominant principal components. Nevertheless, when more dimensions were considered, forward and backward trajectories occupied subspaces with a significant angle between them. Cycling direction could thus be discriminated by comparing angular momentum in those two subspaces. Third, at movement onset, neural trajectories transiently diverge during forward versus backward cycling. This allowed us to infer cycling direction early, before the steady-state ellipses became established. The monkey achieved a success rate of 95%±1% in brain control over 20 sessions. This compared favorably with performance in arm control: 98%±1% over 8 sessions. Success rate was high even for the first few days of exposure to the algorithm - no period of learning or adaptation was necessary. Indeed, it was our impression that monkeys were largely unaware of the transition to brain control. These results demonstrate that decode algorithms can successfully decode kinematics, by leveraging robust regularities of the data, even in the absence of the simple statistical relationships exploited by traditional algorithms. This holds the potential to expand the class of movements amenable to prosthetic decode.

1-G-102 A neuromorphic implementation of afferented muscles demonstrates that only phase-advanced gamma drive of particular amplitudes allows fast voluntary cyclical movements

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Given the difficulty in recording from the fusimotor system, it is not known how fusimotor drive is modulated to produce voluntary movement in humans. From a control-theoretic perspective, this means we do not know how the gains in the feedback loops are dynamically modulated to enhance the production of voluntary movement. We extended our published neuromorphic system simulating innervated muscles[1,2] to allow cyclical voluntary alpha drive. This system consists of populations of alpha-motoneurons with feedback from spindle Ia and II afferent signals. This system runs in real-time on Field-Programmable Gate Array (FPGA) chips and is coupled to robotic and cadaveric hands, subjecting our model of afferented muscles to the ultimate test of physical implementation. The system has been validated in our previous work to successfully reproduce the dynamic and static phases of stretch reflex responses. For an antagonist pair of muscles rotating a single planar mechanical joint, we applied voluntary alpha-motoneuron drive to both muscles as out of phase, non-overlapping, half-wave rectified sinusoidal inputs taking either one (1 Hz) or two seconds (0.5 Hz) to complete one full back-and-forth oscillatory movement about the joint. To determine the effect of fusimotor drive on the resulting sinusoidal movement of the joint, we applied similarly shaped inputs of the same frequency to the (static and dynamic) gamma-motoneuron drives at different phases and of different amplitudes with respect to the alpha drive. When the 1 Hz input drives are applied, we see that only when fusimotor drive is phase-advanced by an average of 22 degrees for specific amplitudes is the movement amplitude enhanced, compared to the baseline case when gamma drives are set to zero. But for the lower velocities at the 0.5 Hz input drives, we see that there is little effect of fusimotor drive modulation on movement amplitude; likely due to the more minor role stretch reflexes play. This suggests that, when stretch reflexes are relevant for faster movements, it is phase advanced (as opposed to strictly synchronized) gamma drive that best enhances voluntary movement. -- [1] Niu CM, Jalaleddini K, Sohn WJ, Rocamora J, Sanger TD, Valero-Cuevas FJ. Neuromorphic meets Neuromechanics PART I: The Methodology and Implementation. 2017. Journal of Neural Engineering, 14(2). [2] Jalaleddini K, Niu CM, Chakravarthi Raja S, Sohn WJ, Loeb GE, Sanger TD, Valero-Cuevas FJ. Neuromorphic meets Neuromechanics PART II: The Role of Fusimotor Drive. 2017. Journal of Neural Engineering, 14(2)1.

LB - Late Breaking Abstracts

1-LB-103 Association between muscle coordination and kinetics of trunk and leg in knee osteoarthritis

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[Background and aim] Knee osteoarthritis (knee OA) is a chronic disorder resulting in deterioration of the knee joint. Many studies have tried to clarify the characteristics of disease progression caused by mechanical stress (external knee torque and muscle co-contraction) around the knee joint. However, no study has considered the effect of proximal muscle (i.e. trunk and hip muscle) coordination on knee muscle activity. We hypothesized that knee OA would lead to altered behavior of the proximal joint (hip and trunk) in order to reduce mechanical stress upon the knee. The purpose of this study was to clarify the effects of muscle coordination include the proximal joint muscles during gait in knee OA through muscle synergy analysis. [Methods] Ten healthy elderly subjects and ten patients with knee OA volunteered for this study. Subjects walked on a treadmill at 3 km/h for one minute. Electromyography (EMG) was recorded from 14 muscles in the hip, knee, and ankle on the OA affected side and from the lower back muscles on both sides. To determine muscle synergies, EMG were assessed by means of non-negative matrix factorization. To compare the muscle coordination of each subject, four muscle synergies were assumed. A Wilcoxon rank sum test was used to compare the EMG of each muscle in the synergy that was activated in the early stance phase between the healthy elderly and knee OA groups. The peak external joint torque in the sagittal and frontal plane during the early stance were also compared. [Results] No significant difference was observed for the coordination of muscles around the knee during gait between the healthy elderly and knee OA groups. However, paravertebral muscle (PVM) and opposite PVM (oppPVM) activity was significantly increased among knee OA compared to healthy elderly ($p<0.05$). According to kinetic data, there were no differences between the waist and knee torque at the sagittal and frontal plane. [Discussion] There was no significant difference in the knee torque between the healthy elderly and knee OA groups. Therefore, there was no alteration in muscle coordination for muscles around knee joint. On the other hand, the PVM and oppPVM showed the increased muscle synergy in the knee OA patients compared to healthy elderly. During normal gait, the PVM is usually active at the timing of contralateral heel strike. Our results showed higher activation of the PVM with the oppPVM at the ipsilateral heel contact. Regarding the waist torque, no difference has been identified between the two groups, largely because the waist torque showed greater variation between individuals. Therefore, both sides of the PVM may need to be active to control trunk movement. In summary, no significant difference in muscle coordination around the knee joint was observed; however, the PVM and oppPVM were overactive in knee OA patients. This may indicate that knee OA leads to altered behavior of the proximal joint to reduce mechanical knee stress.

1-LB-104 Role of parietal cortex involved in postural control during forelimb reaching in the cat

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Voluntary movements accompany optimized postural control that precedes the goal-directed action. Such a feed-forward postural control, so-called anticipatory postural adjustment (APA), predicts and prevents equilibrium disturbances associated with movement performance from taking place. Previous studies in primates and cats demonstrated the importance of the parietal cortex in the control of forelimb reaching movements. However, little information is available how it contributes to postural control. Here we tried to understand the role of parietal cortex in the achievement of APA associating with forelimb reaching in the cat. Specifically, we examined how APA was altered in response to reaching to the different target positions, and how the APA altered after inactivation of parietal cortex. Two cats were trained to maintain standing posture on force transducers beneath each limb so that they perform forelimb reaching task. Ground reactive force, which was exerted in each limb, was measured (10 kHz) to calculate center of vertical pressure (CVP). A chamber was attached to the cat's skull so that muscimol, a GABA-A receptor agonist, was microinjected (10ug/2ul per site) into the parietal cortex (5 area and S1). Cat's movements were monitored by video-tracking systems (60f/s) from the top and side. Following parameters were measured; 1) CVP positions before starting movement (700 ms prior to paw lift), and those at paw-lift and target-reach, 2) movement time of forelimb reaching (duration between paw-lift and target-reach), 3) with or without gaze to the target before movements. When the target was moved from default positions to either left or right and either forward or backward, CVP positions at paw-lift and target-reach were altered as functions of the target positions. There was no difference in the CVP positions between tasks with and without attention. We note that each cat had the preferred target's direction and distance with the smallest difference in CVP positions between paw-lift and target-reach, indicating that postural adjustment for target-reach is achieved in advance at the instance of paw-lift so that postural disturbance during forelimb movement can be minimized. When muscimol was injected into the parietal cortices, CVP positions of paw-lift and target-reach was not altered but their distribution range became smaller compared to control condition. However, frequency of tasks with gaze and movement time were increased. Therefore, cats may achieve APA at the expense of movement time in addition to mobilizing the attention process when parietal cortical activity is insufficient. Our tentative conclusion is that the parietal cortex contributes to the integration of temporospatial information and attention so that accurate APA which is optimal to the purposeful action can be achieved.

1-LB-105 Spontaneous Emergence of Leader-Follower Relationship in Different Physically-jointed Interactive Conditions

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Leader-Follower (LF) relation spontaneously emerges when humans work together to achieve a common goal in a collaborative manner, in spite of not having a priori role assignment. Although this relation has been mostly described for social interactions, the extent to which LF relation also occurs

during physical interactions has not been systematically studied. To address this gap, we investigated factors that might underlie the emergence of LF relation during human-human physical interaction. Dyads used a two-armed manipulandum to grasp both ends of a virtual bar using their right hand and move it into the target cooperatively while maintaining a horizontal orientation of the bar. To investigate the effect of stiffness and the stability of the bar on LF relation emergence, 2 bar models with 2 stiffness parameters were tested. The first bar model had a rotational pivot at the center whereas the other had it at the far end. Each model was tested in high and low stiffness conditions. All dyads experienced 4 conditions in blocks with intervals in between. Task terminated with 40 successful trials or a maximum of 250 trials. If dyads could drag the bar to the target within the time limit and the maximum angular displacement of the bar throughout the movement remained within the maximum allowed angle, it was counted as a successful trial. Subjects were not informed that they were interacting with another human subject. We hypothesized the formation of LF roles to be necessary in experimental conditions where the action of one agent is more likely to affect the bar's orientation (high stiffness and center pivot). On the contrary, when the action of one agent does not affect the bar's orientation (low stiffness and far end pivot), LF relation would not be relevant as the task can be more easily attained. Surprisingly, our results were opposite from our expectations. In difficult conditions, dyads' force trends measured at the manipulandum handle were more synchronized than that in easy ones. Conversely, the force trends in easy conditions revealed one participant's leadership in performing the movement toward the target. Moreover, dyads could learn to adapt to any condition. However, interaction strategies learned under easy conditions were not easily transferable to difficult ones. In contrast, dyads could immediately establish an appropriate interaction strategy when performing the easy conditions after having learned the difficult ones. Some dyads realized that they were working together. Answers to a questionnaire on the interaction strategies after the experiment revealed that each subject in a pair selected different strategies. Our study revealed important factors driving the emergence of LF relations in dyads. The identification of principles underlying cooperation through a physical interaction task has the potential to improve our understanding of human-human interactions.

1-LB-106 Muscle synergy analysis of forearm muscles in macaque monkey after cross-tendon transfer surgery

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Tendon transfer surgery is used as a clinical treatment for substituting the lost function of muscles. Patient adapts to use the transferred muscles gradually, but the underlying neural mechanism of adaptation is still unclear. To address this issue, we first analyzed the grasping behavior of the monkey before and after the cross-tendon transfer. Grasping performance of the monkey recovered almost perfectly within two months after the surgery. In this study, we investigated the recovery process through the analysis of muscle activities during the performance. One macaque monkey participated in our experiment. We trained this monkey for two "grasping to pull" tasks: pull with short and long stroke, respectively. Next, we implanted wires for recording EMGs (electromyograms) to finger and forearm muscles (n=12). Then, we performed cross-tendon transfer surgery in the following procedures. 1: the tendons of flexor-digitorum-superficials (FDS, a flexor muscle of the finger) and extensor-digitorum-communis (EDC, an extensor muscle of the finger) were amputated, 2: the end-point of these two tendons (muscles) were exchanged with passing through the space between ulnar and radial bones, and

3: the transferred tendons were reconnected. From the measured EMGs before and after the tendon transfer, we analyzed the adaptation mechanism of the neural system. To estimate the neural mechanism of adaptation from the EMGs, we assessed muscle synergies before and after surgery. Muscle synergy is a coordination structure of multiple muscles and the muscle synergy is supposed to reflect the neural structure in the motor control. The structure of muscle synergy were estimated from measured EMGs using non-negative matrix factorization (NNMF). We extracted four muscle synergies and their temporal coefficient. We found the spatial structure of muscle synergies did not change by the tendon transfer and recovery. However, the temporal coefficient changed after the tendon transfer such that the synergy for extension and the synergy for flexion exchanged. Subsequently, these two synergies gradually returned to the original patterns in accordance with the recovery of motion. These results suggest that the temporal command from the neural system changed by the tendon transfer and returned with recovery, while maintaining the synergy structure.

Poster Session 2

A – Control of Eye & Head Movement

2-A-1 Topographic representation of saccade vector in frontal eye field of common marmoset

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Frontal eye field (FEF) is an important cortical area controlling saccadic eye movements. However, because this area is deep in the rostral bank of arcuate sulcus in macaques, which makes it difficult to access, whether it contains a continuous topographic representation of saccade vector remains undetermined. In the current study, we took advantage of the almost-flat cortical surface of common marmosets and systematically mapped the FEF with electrical microstimulations. We applied electrical microstimulations with tungsten electrodes in potential cortical areas identified by the atlas during the gap period, when marmosets performing gap saccade task to control the initial eye position and baseline state of eye fixation. The stimulations were applied with biphasic current at 300 Hz for 30 trains. We varied the stimulation amplitude in some cases but most of our stimulations were kept at 0.05 mA to ensure enough power to evoke saccades while minimizing the brain damage. We also systematically varied the initial fixation locations to identify whether the evoked saccades were vectors-based or toward a single endpoint. We successfully evoked saccades in area 8 and 45 according to the atlas. When the stimulation sites moved from medial to lateral, we observed a systematic decrease in amplitude and changing of direction from upper to lower visual field of the evoked saccades. The evoked saccades in these areas were vector-based. However, if the stimulation site was posterior to this region, the saccades became more toward a single endpoint. Taken together, we found a continuous topographic representation of saccade vectors in the marmoset FEF. Because several important cortical areas related to oculomotor systems are deep in the sulci of macaques, they are less understood. Using marmosets, we will be able to advance our knowledge on the organization of these areas and understand more about the primate oculomotor systems.

2-A-2 Neural mechanisms that allow cortical preparatory activity without inappropriate movement

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Many neurons in the motor cortex seem to be important for the generation of movement but still have firing rate modulation during motor preparation, at times when there is no movement. This raises the question: how does preparatory activity evolve without prematurely inducing movement? The smooth eye movement region of the frontal eye fields (FEFsem) is a vital node in the neural circuit responsible for generating smooth pursuit eye movements. During fixation, FEFsem neurons exhibit preparatory activity related to the expectation of impending visual motion and eye movement. We recorded the activity of 164 single units in the FEFsem of two awake behaving rhesus monkeys smoothly tracking moving targets during two different blocks of trials: a random 8-direction block and a single-direction block. Using data from the 8-direction block, we generated a linear model relating FEFsem population activity to eye velocity. Passing preparatory activity from the single-direction block into the linear model predicts eye movement that did not occur during fixation. Furthermore, principal component analysis reveals substantial overlap between preparatory- and movement-related dimensions. Our findings contrast with recent work on the arm movement system suggesting that preparatory activity in M1 and pMD resides in "output-null" dimensions, orthogonal to movement-related dimensions (Kaufman et al., Nat Neuro 2014, Elsayed et al., Nat Commun, 2016). We can understand the operation of FEFsem in the context of previous conclusions that the output from FEFsem controls the strength or "gain" of the transmission to the oculomotor machinery of the visual motion signals that drive pursuit initiation (Tanaka and Lisberger, Nature 2001). We propose that the use of FEFsem output as a gain signal allows preparatory activity to progress without causing movement: gain can be dialed up, but without the movement-driving visual-motion signal, movement does not occur. To test the gain hypothesis, we presented 50 ms pulses of visual motion at random times during fixations leading up to target motions that initiate pursuit. We find that eye speed responses to the perturbations are enhanced during preparation in close correlation with the progression of FEFsem preparatory activity; because the motion pulses were always the same, we interpret this as modulation of visual-motor gain. We conclude that FEFsem enhances visual-motor gain in anticipation of a behaviorally-relevant visual motion and that the use of FEFsem as a gain controller allows preparation to occur without premature movement.

2-A-3 Predicted tracking error triggers catch-up saccades during smooth pursuit

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For primates, visual tracking of moving stimuli requires the synergy between saccades and smooth pursuit eye movements. The decision to trigger a catch-up saccade during pursuit influences the quality of the visual input. This decision is a trade-off between tolerating a certain position error when no saccade is triggered or a transient loss of vision during the saccade due to saccadic suppression. Although catch-up saccades have been extensively investigated, there is still a lack of understanding as to how the trigger decision is made by the brain. de Brouwer et al (2002) demonstrated that catch-up saccades were less likely to occur when the expected time to foveate a target using pursuit alone is between 40 and 180ms into the future, referred to as the smooth zone. However, this descriptive result lacks a mechanistic explanation for how the trigger decision is made. More recently, we proposed a decision model (Coutinho et al., 2018) that relies on a probabilistic estimation of predicted position error (PEpred) during visual tracking. To test the model predictions, we investigated how human participants used predicted position error, retinal slip, and the uncertainty in those estimates to make trigger decisions. We found a significant effect of PEpred magnitude on latency and occurrence of catch-up saccades. To test the role of uncertainty, we blurred the moving target which resulted in larger and more variable saccade latencies and more smooth pursuit trials, consistent with model predictions. As predicted by our model, large PEpred (>10deg) led to short latency saccades regardless of the level of uncertainty. Conversely, when PEpred was small (<10deg) uncertainty significantly modulated the saccade trigger decision. Our model also predicted increased signal dependent noise as retinal slip increases, which resulted in more variable and longer latency saccades. In conclusion, the data supports our hypothesized role of PEpred in deciding when to trigger a catch-up saccade during smooth pursuit while taking into account uncertainty.

2-A-4 Initial movement planning under uncertainty about task goal intends to prepare a desired state for the execution of possible secondary-movements

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Humans are often required to launch a reaching movement before knowing the final target among multiple potential targets. Several studies have investigated how humans plan their movements under such situation using go-before-you-know paradigms and revealed that humans launch their reaches toward a weighted average direction between given potential targets. One of the hypotheses for such behavior is that humans represent intentionally an averaging of the distinct motor plans that have been prepared for each potential motor goal. However, such intermediate behavior is abated when the strategic values of intermediate movements decrease by reducing the time available to make online corrective movements, by increasing the spatial separation between potential targets, or by penalizing the intermediate movements. Therefore, another possible hypothesis is that the intermediate initial movements are generated as the result of the flexible planning process that selects a single motor plan to optimize performance or to reduce costs related to movements execution. Here, to clarify the role of initial movements, we investigated the planning of initial movements under the situation where the distances from a start position to each potential target were different. In our task, participants were required to launch their movements toward two potential targets 15 cm or 20 cm away from the start position. The target-separation angle between two potential targets was 5°, 10°, 15°, 20° or 25°. The correct target was presented, and the other target disappeared only after the cursor away 1 cm from the start position. If the former hypothesis was adopted, the intermediate initial movements can be observed in this target setting. If the latter hypothesis was adopted, participants are expected to initiate their movements on a curvature path toward the shorter target to reduce the intervention costs for possible following movements, taking minimum intervention principle into account. Initial reach direction (the vector from the start position to the cursor 100 ms after movement onset) as the index of initial movement features indicated that the initial movements frequently directed toward a shorter target, rather than the intermediate direction between the potential targets. Additionally, curved trajectories toward a midline of the potential targets were observed before correcting their movements according to the final target location when initiating their movements toward the shorter target. These results showed that the participants generated the initial motor plans that could reach both potential targets with fewer intervention costs, rather than intermediate initial movements. These findings support the idea that the initial movements reflect minimizing costs depending on task demands, suggesting that the planning of initial movements intends to prepare the desired state for expected following movements.

2-A-5 Identification of the frontal eye fields in the common marmoset using microstimulation

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Studies in old world macaque monkeys have demonstrated that the frontal eye fields (FEF) play an important role in the control of saccadic eye movements and visual attention. The macaque FEF, however, lies deep in the anterior bank of the arcuate sulcus, making it inaccessible to laminar-specific electrophysiological recordings and 2-photon imaging both of which are needed to reveal the functional microcircuitry of this area. The common marmoset (Callithrix jacchus) with its largely lissencephalic cortex is a promising nonhuman primate model for exploring FEF microcircuitry but the precise location of the FEF in marmosets and its functional properties remain largely unknown. Here we implanted a 96-channel Utah microelectrode array (1mm electrode length, 400 µm pitch), in the left frontal cortex of an adult male marmoset, targeting the border of area 8aD with area 6DR. We selected this area on the basis of resting-state fMRI, which revealed strong functional connectivity with the superior colliculus. Individual electrodes were stimulated with 100 ms biphasic pulse trains (300 Hz, 0.2 ms pulse duration, 50-200 µA) while the monkey was head-restrained and freely viewing a video clip. We observed skeletomotor and oculomotor responses at many array sites. At posterior sites, hindlimb movements were elicited at more medial sites and forelimb movements were elicited at more lateral sites. Back, shoulder and ear movements were evoked at more anterior sites. Eyelid movements and blinks were elicited at the most lateral sites. Saccadic eye movements were evoked at anterior sites, often overlapping those at which hand, neck, or shoulder movements were observed. The majority of saccades were directed to the contralateral hemifield, though some ipsilateral saccades were also observed. At dorsal sites, evoked saccades had a long onset latency (M = 100-120ms) and tended to converge at single locations in craniocentric space. At the most anterior sites, saccades were evoked at shorter latencies (M = 40-50ms). Contralateral saccades were reliably elicited when the initial eye position was in the ipsilateral hemifield but microstimulation often failed to elicit saccades when gaze position was initially in the contralateral hemifield. Amplitude mapping was observed at these sites. Larger amplitude saccades (>18degrees) were elicited at more medial sites and smaller amplitude saccades (<5degrees) at more lateral sites. This pattern of results demonstrates a similarity of organization between the premotor cortex and FEF in marmosets and macaques. Our finding that microstimulation often evoked neck, shoulder, and hand movements together with saccades suggests that the marmoset FEF may be less effector-specific than the macaque FEF. Taken together, our data suggest that the common marmoset is both an appropriate and advantageous primate model for exploring FEF microcircuitry.

2-A-6 Does eccentric fixation alter head movement strategy for smooth pursuit?

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Age-related macular degeneration (AMD) can often lead to the loss of the fovea and the surrounding central visual field. This type of vision loss is extremely common (affecting nearly 7% of individuals over 40 in the United states alone, Klein et al. 2011) and can present particular challenges for oculomotor tasks that rely on the high-acuity foveal retina. For certain tasks, individuals develop a new, eccentric fixational area - the preferred retinal locus (PRL). We have previously shown that smooth pursuit is impaired in individuals with macular degeneration, and the degree of impairment depends on the direction of target motion relative to the location of the damaged retina (scotoma) and the fixational PRL (Shanidze et al. 2016). One might consider that it is the lack of the fovea that causes deficit in smooth pursuit performance. However, we have also shown that scotoma size and PRL location do not directly contribute to variations in smooth pursuit gain (Shanidze et al. 2017). Another consideration could be that individuals' eccentric fixation leads to an eccentric eye position that might impede smooth pursuit in the standard head-fixed experiment, especially for target directions along fovea-PRL axis (Stahl 2001). Thus, head movements could become particularly important for successful pursuit in this population. In this experiment we examined head movement strategies in 7 individuals with AMD (75-95, 4M) and compared them to 4 age-matched controls (72-76, 1M). Participants pursued a ramp target that stepped from the center by 6° in one of 6 possible directions (4 cardinal, 2 oblique) and moved at 10°/s in the opposite direction, through the center. We found that there was variability in total head excursion in smooth pursuit in both groups. In the control group, 1 participant made large pursuit head movements, whereas the others relied almost entirely on eye movements. In the AMD group, 3 participants consistently relied on head movements across all target directions. However, for 2 others, the range of head movements was variable across directions, and 2 others relied solely on eye movements for pursuit. Overall, there was no significant difference between total smooth pursuit head movement across groups ($\mu AMD = 2.57$, $\mu Cont = 1.37$, $p>0.05$, 2-Way r.m. ANOVA). For both groups, there was more head movement in the horizontal than vertical direction ($\mu H = 2.74$, $\mu V = 1.06$, $p=0.03$). When we examined the relationship between PRL eccentricity and total head movement for all individuals who did exhibit smooth pursuit head movements, we found a slight negative relationship for the horizontal direction, however, these data were limited by the reduced sample size. Overall we find that individuals with AMD have similar head movement range during smooth pursuit as age-matched controls, despite known reduction in smooth pursuit eye velocity gain and often-eccentric eye position.

2-A-7 A novel method to measure 3D eye movements with Infra-Red video eye tracking

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The vestibular system provides ocular and postural compensation for movements in 3D space. Ocular stability in three dimensions is achieved by the Vestibule Ocular Refelx (VOR) controlling horizontal, vertical and torsional eye movements. Many vestibular disorders (e.g. vestibular neuritis, bppd, schwannoma's) severely impair the 3D kinematics of the vestibular ocular reflex (3D-VOR). A variety of tests are available to assess the quality of the 3D-VOR (head impulse test, Barany chair, VEMP). The most accurate technique to measure 3D eye movements is the search coil technique, which is more and more replaced by high-speed video oculography (VOG). Thusfar, attempts to reliably measure torsional eye movements with Infra-red eye tracker systems have had only limited success. With the increasing use of infra-red of video eye trackers in vestibular testing it is challenging not to limit measurements to horizontal and vertical VOR and thereby ignore the torsional component. Because torsion has a significant role in 3D ocular stability, we designed a modified scleral contact lens that allows to reliably measure horizontal, vertical and torsional eye movements using infra-red video eye tracking). The lens has a fixed pupil opening and a special imprint with markers on the outer rim. The design of the lens is such that it can be worn for hours without anesthesia while slip on the eye is neglectable. Here we present a number of tests with the lens in combination with an infra-red eye tracker ((binocular ESC system, 250Hz, EyeSeeTec, München, Germany) to show the performance of the lens. The fixed pupil of the lens has several advantages: 1- noise level is independent from light level resulting in the same low signal-to-noise- ratios in light and darkness. 2- Oscillatory artefacts typically seen in horizontal and vertical saccades with IR eye trackers are reduced due to the fixed pupil opening. 3- The markers on the outer rim enable IR camera systems that have marker detection software (such as the Eye See Cam) to measure torsional eye movements in addition to horizontal and vertical eye movements. The contact lens that we developed is useful in research and clinical environments to test vestibular (dys-)function, to test the effectiveness of vestibular implants, to test neurological damage (e.g. cycloversion and cyclovergence, concussion, neurodegeneration) and in a number of oculomotor disorders (e.g. see-saw nystagmus).

2-A-8 Vestibulo-ocular response suppression during voluntary eye closure in man and monkey

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The vestibulo-ocular reflex (VOR) stabilizes gaze by moving the eyes in the opposite direction of head motion. The relatively simple three neuron arc subserving the VOR ensures highly effective responses with limited loss of compensatory gain even in complete darkness, where corrective eye movements are no longer functionally relevant. The effect of eye closure on the VOR, however, has surprisingly received limited attention. Furthermore, the few studies examining the effect of eye closure have reported contrasting VOR behaviour: some authors described decreased/absent vestibular-evoked eye movements under this condition, while others described no change. Here, we present experiments performed in man and monkey investigating the mechanisms responsible for the modulatory effects of voluntary eye closure on the VOR. Human volunteers (N=26) and rhesus monkeys (N=2) were submitted to whole-body sinusoidal, step (horizontal) or pseudorandom (horizontal) rotations with eyes open and closed in darkness. Eye movements were recorded with scleral (human) or implanted (monkeys) search-coils. To test whether eye closure affected the VOR across all rotation directions, we first rotated subjects sinusoidally along the horizontal, vertical and torsional axes. We found that voluntary eye closure produced a systemic reduction in VOR gains in humans and monkeys to ~0.1-0.3 in all rotation directions, which contrasted the known directional dependence of the VOR with the eyes open (i.e. horizontal/vertical ~0.9-1.0 and torsional ~0.5). To test whether VOR attenuation is driven by sensory signals of lid closure, we taped one eye shut while human subjects kept the other eye open. Under these conditions we observed a moderate decrease in VOR gains to ~0.7 for the taped eye, and none for the untapped eye, suggesting that afferent feedback may play a minor role in attenuation for the closed eye. To test whether VOR attenuation is associated with the motor command to close the eyes, we taped both eyes shut while human subjects attempted to open their eyes against the tape. Although VOR gains decreased to ~0.45 in both eyes, they remained ~4 times larger when compared to conditions when subjects closed their eyes normally. This suggests that VOR engagement is partially related to the motor command to open the eyes. Finally, to examine the temporal characteristics of VOR attenuation associated with eyelid closure, we applied pseudorandom yaw rotations while subjects closed and opened either one or both eyes. When both eyes were closed, gains attenuated rapidly from ~0.8 to ~0.35 in both species, and in humans initiated 40-60 ms prior to eyelid motion. In humans this attenuation is specific to the natural closure of both eyes since voluntary closure of only one eye produced only a small decrease of VOR gains to ~0.7. Overall, our results show a rapid and robust attenuation of the VOR during voluntary eye closures related to the motor command to naturally close the eyelids.

B – Fundamentals of Motor Control

2-B-9 Learning compensation for different force fields and perturbation directions randomly applied during reaching

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Motor adaptation results from the acquisition of novel representations in the nervous system that allow improvement of control across a broad range of tasks. To date, there has been much emphasis on the acquisition of such patterns for predictable disturbances, and previous work highlighted that both prior ("feedforward") and feedback control mechanisms express the same knowledge of dynamical interactions that arise during movement. Based on this observation we sought to investigate whether learning could be achieved by updating feedback control during a movement, such that online corrections to unpredictable disturbances evoke gradually better online corrections and improve reaching performance. We instructed 18 healthy adults to perform reaching movements towards a visual target with a robotic handle (KINAMR, BKIN Technologies, Kingston). On a random subset of trials, we applied either a lateral force proportional to forward velocity (orthogonal force field), or a force proportional and orthogonal to hand speed (curl field) of clockwise or counter-clockwise directions. We found a reduction in path length across force field trials for both types of perturbations and directions, indicative of better compensation for the applied disturbance. An analysis of average surface activity from the main muscles involved in lateral corrections indicated that there was no systematic increase in co-activation. We found that the measured force at the handle became gradually better correlated with the commanded force, re-calculated offline based on the velocity profile of each trial. Furthermore, for each force field, this correlation reached values significantly larger than when the measured force was correlated with the commanded force of randomly picked surrogate trials. Together these observations indicate that online corrections were not based on the control of limb impedance through co-contraction, or based on a one-fit-all default feedback response. Instead, they were tuned to the specific force profile experienced within each perturbation trial. These observations are consistent with the idea that the nervous system performs very fast, possibly online, adaptation to environmental dynamics with flexible online learning rates across encountered disturbances.

2-B-10 Correlates of online changes in movement representations in 200ms

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Humans and animals use adaptive representations of movement dynamics, called internal models, which allow them to adapt motor commands to novel disturbances in the environment. To date this process has largely been described through learning curves characterizing changes in performance across movement repeats, yet recent evidence suggests that adaptive changes in reach representation may occur during a single movement. Here we sought to determine the latency of these rapid changes in movement representation based on electromyogram recordings. Healthy adults (n=18) performed standard reaching movement trials with a robotic handle randomly interleaved with force field trials (lateral force proportional to hand forward velocity) in unpredictable direction. First, we observed that the maximum hand displacement towards the direction of perturbation in a force field trial displayed very small improvement across trials, while the target overshoot was associated with a slower exponential decay. This result supports the presence of adaptive feedback control within each trial. Next, we identified in the main muscles involved in the motor corrections (shoulder flexors and extensors) a clear modulation explaining the reduction in target overshoot. Based on a sliding comparison of the difference between the first and last trials, we measured that the onset of the response tuned to the force field occurred on average at 210±15ms following reach onset (mean±SD). To further assess whether these corrections were tuned to the force field, we regressed the commanded force with the measured force and found highly significant improvements across trials. Moreover, the correlations became better than when measured force of a single trial was compared with commanded force of random trials. This is similar to what we have observed in a control experiment, when the force field is in a single predictable direction, indicating that the adjustments of feedback were tuned to the specific perturbation of each individual movement. These results confirm an online change in reach representation and provide an accurate measurement of the latency of adaptive control in the nervous system. The underlying process is a candidate mechanism for linking feedback control with motor learning.

2-B-11 Surrounding inhibition in the internal globus pallidus at task-relevant frequency to facilitate motor control during a cyclic drawing task

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Basal ganglia are known to be associated with control of voluntary movements. It has been proposed that pallidal neurons were selectively inhibited or disinhibited to shape focused output patterns during voluntary movements, namely, surround inhibition mechanism. We investigated local field potentials (LFPs) of the internal globus pallidus (GPi) in basal ganglia and motor thalamus (Vo and Vim) to examine how these subcortical structures were involved to regulate effective motor control and if we could observe surround inhibition mechanism in these structures. We hypothesized that selective inhibition in GPi at the task frequency would be exhibited during the movement, resulting in facilitation of thalamic activity at the task frequency. One patient (male, 18 years old) with idiopathic hemiplegic dystonia who previously underwent DBS implantation in his affected hemisphere, was implanted unilaterally on his 'non-affected' side with stereo-EEG electrodes in several brain areas including GPi, Vo and Vim. Following two days after the surgery, the subject was instructed to continuously draw 15 consecutive figures of eight on an iPad with his non-affected side, at a constant and predetermined speed (0.5Hz). The finger displacement was recorded to determine his predominant movement frequency. To analyze pallidal and thalamic LFPs, the power spectral density was computed using the Thomson's multitaper estimate, and active segments (periods during voluntary reaching) were compared against the resting condition. Approximately 95% of total power in the frequency domain of the movement trajectory was converged around the task-relevant frequency, confirming that the subject followed the predetermined speed. Regarding the pallidal and thalamic activities, no distinct peak frequency was observed in these activities at rest. Intriguingly, we observed selective inhibition/disinhibition in GPi during the motor task. In particular, the power spectral density of GPi showed two distinct peaks above and below the task frequency (5.4x, and 4.9x high relative to the resting condition, respectively), while the power at the task frequency remained lower (1.5x), which could be indicative of a surrounding inhibition phenomenon around the task dynamics. In contrast, thalamic activity peaked at the task-relevant frequency (4.4x), appearing to shape a "focused" thalamic motor output. Our preliminary results may indicate direct evidence of the proposed surround inhibition function of the basal ganglia. Moreover, the reciprocal relationship between pallidal and thalamic activities could also suggest the functional connection between two structures, as a center-surrounding organization, to suppress any competing motor patterns and to facilitate the desired motor program to execute an efficient motor output.

2-B-12 Widespread activation in human GPi and motor thalamus positively correlates with muscle activation during voluntary movement

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Traditional studies of basal ganglia and thalamic function have been limited to single microelectrode recordings in animals and anesthetized humans under the constraints of the operating room. Recent recordings from DBS electrodes implanted in awake patients with movement disorders such as Parkinson's disease have allowed researchers to find disease-related biomarkers in basal ganglia nuclei such as subthalamic nuclei (STN). However, in order to understand the interaction between the different subcortical structures that are involved in the motor loop, it is necessary to simultaneously record from multiple electrodes implanted in multiple brain areas. In this work, we present single unit recordings from depth multielectrode implanted in several brain areas, including GPi and STN in basal ganglia, and Vo, Vim, and VPL in the thalamus recorded from awake children with acquired dystonia, for whom neural activity can be associated with motor behavior. Two relevant observations arose from our analysis: 1) The vast majority of the detected neurons in basal ganglia and thalamus fire with median frequencies lower than 10Hz, which contrasts with typical reports of mean GPi discharge rates between 10 and 70Hz. 2) Increased widespread activity in GPi and motor thalamus that correlate with muscle activation during dystonic movement. Although low firing rates may be characteristic of secondary dystonia, because of the properties of the recording electrodes these results are likely an underestimate of the rates recorded using standard intraoperative microelectrodes, since GPi is known to fire at much higher rates at rest and with dystonic spasms. Despite discrepancies in the firing rates, the important observation from these simultaneous electrode recordings is the widespread activation in both GPi and motor thalamus, and the observation that both GPi and thalamus increase the firing rate during movement. This phenomenon does not necessarily agree with the classical rate mode, in which the inhibitory output of GPi would be expected to correlate inversely with thalamic activity. It is possible that this apparent paradox can be explained by a separate movement-related driving signal to the thalamus (most likely from cortex), or rebound excitation of the thalamus.

2-B-13 Robust control strategies in the presence of uncertain load environments

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Humans can control their actions in unpredictable environments, such as performing a tennis serve on a windy day. With environmental uncertainty there are conflicting reports as to whether the nervous system prepares for a worst-case scenario (e.g., the largest load) or minimizes prediction error (e.g., the mean load). Further, little is known on how the nervous system modulates feedback control as a function of environmental uncertainty. Here we use robust optimal feedback control (rOFC) as a framework to study human movement in uncertain environments. Critically, rOFC models can converge on a desired final state (stop in a target) by using enhanced feedback gains, even with inaccurate or noisy a priori estimates of environment dynamics. Similarly, in humans we expect enhanced feedback gains (e.g., greater long-latency response) when they experienced uncertain load environments. Participants were seated with their arm supported in the horizontal plane by an exoskeleton (KINARM) robot. On each trial, participants reached from a home position to a target. Once a participant's hand left the home position, the robot applied a step load (primarily an elbow extensor torque) that displaced the hand perpendicular to the intended movement. In the constant condition, participants experienced three blocks of trials where the load magnitude was either 3N, 5N or 7N. In the random condition, the load magnitude (3N, 5N or 7N) was drawn from a uniform distribution. Conditions were counterbalanced. As indexes of predictive control, we examined average brachioradialis muscle activity prior to load onset (-200 to 0 ms) and the maximum perpendicular deviation of the hand relative to the straight line connecting the home position and target. As indexes of feedback control, we examined average brachioradialis activity following load onset in the short- (20 to 45 ms) and long-latency (45 to 105 ms) epochs. The rOFC model did well to predict hand trajectories. Participant hand trajectories and maximum perpendicular deviations were most similar between the random and constant conditions when the load was 5N. That is, participants overcompensated for the 3N load and undercompensated for the 7N load in the random condition. Further, in the random condition we found that the brachioradialis activity prior to load onset was aligned with resisting a constant 5N load. These data suggest that participants minimized prediction error by compensating for the mean load (5N) of the uniform distribution. As expected, we found enhanced feedback control in the random condition. Specifically, we found greater brachioradialis activity in the long-latency epoch in the random condition relative to the constant condition ($p = 0.025$). No significant differences were found between conditions in the short-latency epoch. Our data suggest that the nervous system minimizes prediction error, while also enhancing feedback gains to make the arm more robust to uncertain load environments.

2-B-14 The effect of reward and punishment on upper limb motor control

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Performing motor actions requires fluency in selecting the right action and consistency in accurately executing the chosen action, both of which are highly susceptible to reward. However, to this stage the effect of reward has only been studied independently for each component, and mainly in saccadic control rather than limb motor control such as arm reaching. In a study dissociating selection and execution components of reaching movements, we show that reward improves both components concomitantly without interference by shifting their speed-accuracy function, consistent with observations in saccadic control. We then compared this effect to punishment and show that a similar shift in speed-accuracy functions is observed for the selection component with contingent punishment, while the execution component exhibits this shift even in non-contingent trials. Analysis of autocorrelation suggests that control over accuracy constraints may happen via joint impedance regulation, which we test in a follow-up experiment. Participants reached at a single target, and were then immediately exposed to a small fixed-length perturbation to measure the resistance against the robot handle. Results show that in rewarded trials, participants showed a clear upregulation of arm stiffness. Overall, this set of studies extend previous findings regarding the effect of reward on saccadic control to limb motor control, and provides further mechanistic information as to how the shift in speed-accuracy function with reward takes place. Finally, we addressed what brain regions may be involved in reward processing for motor control. To this end, we selectively disrupted the supplementary motor area and ventromedial prefrontal cortex using theta-burst transcranial magnetic stimulation, to determine their respective involvement in the reward-based effects observed.

2-B-15 The inhibition of voluntary muscle relaxations depends on similar mechanisms to the inhibition of muscle contractions

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Successful control of the body requires rapid initiation and cancellation of voluntary action. Actions usually result from muscle contraction, but are also often caused by a combination of gravity and voluntary muscle relaxation. Such voluntary relaxations have been found to be preceded by increased activity in prefrontal and motor regions of the brain, suggesting they result from a motor plan. It is not known if these motor plans can be cancelled once initiated, how long such inhibition may take, and whether such inhibition is achieved via similar mechanisms to the inhibition of actions caused by muscle contractions. We conducted three experiments using the Stop Signal Task in humans to address these questions. In all experiments participants performed actions in response to visual go stimuli and attempted to rapidly cancel the actions when an auditory stop signal was presented after a variable delay (30% of trials). In experiment 1 (n = 13) we compared the inhibition of elbow extensions caused by relaxations of the biceps muscle to elbow extensions caused by activations of the triceps muscle. In experiment 2 (n = 12) we compared inhibition of elbow extensions caused by relaxation of the biceps to inhibition of flexions of the elbow caused by activation of the biceps. Finally, in experiment 3 (n = 14) we compared the inhibition of increases and decreases of force caused by activation and relaxation of the first dorsal interosseous muscle. Across experiments we found that: 1) muscle relaxations could be cancelled once initiated, 2) Across movement types the probability of successfully cancelling an action decreased as a function of increasing stop signal delay, 3) Stop signal reaction times (SSRT) did not differ between muscle relaxation and contraction conditions and were positively correlated for the two movement types across participants, 4) Electromyography (EMG) showed that movement inhibition was preceded by transient changes in muscle activity, 5) These EMG changes were different depending on the type of movement being cancelled. Our results suggest that muscle relaxation is inhibited in a similar manner to muscle contractions and that cancelling muscle relaxations can be understood as a race in the brain between a stop and a go process. The inhibition of action may depend on an effector-independent pathway that cuts excitatory input to the motor cortex. Inhibition signals may also trigger task-specific increases in muscle activity, which serve to prevent gravitationally assisted movements.

2-B-16 Urgency tunes center-surround inhibition in the motor system during action selection

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Action selection involves a tight balance between the competing demands of decision speed and accuracy. Recent work suggests that this balance is regulated by a context-dependent urgency signal, operating as a gain modulator of task-related activity: when decision between reaching movements are made under time pressure, activity in motor areas involved in arm movements is amplified. An open question relates to the generalization of this gain modulation in the motor system. Here, we investigated the impact of urgency on the excitability of different task-related and task-unrelated motor representations in humans by applying transcranial magnetic stimulation (TMS) over the primary motor cortex. Subjects performed a modified version of the tokens task (Cisek et al., 2009, J Neurosci). In each trial, 15 tokens jumped one-by-one every 200 ms from a central circle to one of two lateral target circles; participants had to guess which of those two targets would ultimately receive the majority of the tokens, and to report their decision on a keyboard with either the left or right index finger. Importantly, the reward provided for correct choices was proportional to the number of tokens remaining in the central circle at the time of the response. Hence, because this number decreased as time elapsed during the trial, the urge to act grew accordingly. More critically, we manipulated the overall level of urgency by providing a different penalty for incorrect responses in two separate block types. The use of a low penalty encouraged the subjects to make hasty choices, thus ensuring a high urgency in a category of blocks, called UrgencyHigh. Other blocks were associated with a low urgency (called UrgencyLow) as they involved a higher penalty, promoting accurate choices at the cost of speed. We exploited TMS to elicit motor evoked potentials (MEPs) at different times during the token jumps, in muscles that were either involved in the task (i.e. an index finger "task-related" muscle) or in surrounding muscles that were not involved (i.e. thumb and pinky "task-unrelated" muscles). MEP amplitudes obtained from these muscles provided us with a muscle-specific assay of corticospinal excitability at the time of stimulation in UrgencyHigh and UrgencyLow blocks. MEP amplitudes in task-related muscles became larger over time when elicited in a selected muscle. In contrast, MEPs obtained from task-unrelated muscles showed a progressive decrease in their amplitude. Interestingly both of these effects were stronger in the UrgencyHigh than in the UrgencyLow blocks. That is, higher urgency concomitantly increased facilitation of selected task-related muscles and suppression of surrounding task-unrelated muscles, a mechanism reminiscent of center-surround inhibition.

2-B-17 A multi-domain task battery reveals functional boundaries in the human cerebellum

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Thirty years of research have provided compelling evidence that the human cerebellum is engaged in a wide array of motor and cognitive tasks. However, the full extent of the functional organization of the cerebellum has not been mapped. Furthermore, given the homogenous cytoarchitecture of the cerebellar cortex, it is not clear whether it can be divided into discrete functional regions, or whether functional specialization simply varies in a smooth manner across the cerebellar cortex. Here we used functional magnetic resonance imaging (fMRI) to characterize the spatial distribution of cerebellar fMRI activity, which is mostly determined by mossy fiber inputs, across a large variety of tasks. During fMRI scanning, 24 participants performed a multi-domain task battery (MTDB) with 47 unique tasks conditions, spanning a broad range of motor and cognitive processes (e.g., attention, memory, social cognition). The task battery was subdivided into two task sets, each of which was scanned in two separate sessions, yielding a total of 5.5hrs of fMRI data per participant. The heterogeneous patterns of task activation were then used to derive a functional parcellation. We also evaluated the strength of each identified functional boundary, by asking how well it could predict changes in the functional specialization in a completely new set of tasks. We found that the MDTB parcellation successfully predicted functional boundaries in the human cerebellum for novel task sets, and that it did so better than existing parcellations based on task-free (resting state) data. Anatomically defined lobular boundaries, still the dominant way of subdividing the cerebellum into functional regions of interest, did not coincide with functional boundaries. These results argue for a change in reporting and analysis of cerebellar activity. The rich task set also allowed us to characterize the task-activity profiles in each region in terms of the underlying motor and cognitive features. Even though our task set did not include tightly-controlled conditions for studying hand or eye movements, the variation of these movements across the different conditions allowed us to clearly identify regions related to left and right hand movements, as well as saccadic eye movements in the cerebellum. Interestingly, the BOLD signal in these regions did not only vary with the number of movements, but also with the attentional and control demands related to the tasks. Activity in a diverse set of regions in lobules VII were mostly

explained by features that describe cognitive processes, such as divided attention, understanding a narrative, social cognition, working memory, semantic retrieval, and episodic memory. An extensive part of the inferior motor representation (lobules VIII) was activated during action observation. Overall, the new multi-task parcellation offers an important tool for future studies that test domain-general hypotheses of cerebellar function.

2-B-18 Sensory context interferes with volitional modulation of single neurons

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Primary motor cortex (M1) drives intentional movement, as evidenced by operant conditioning experiments in which subjects are able to gain volitional control over the firing of even single neurons within M1 (Fetz, 1929; Fetz 2007; Clancy et al., 2014). However M1 also receives pronounced sensory inputs, some of which may be strong enough to drive cell activity (Hooks et al., 2013; Petrof et al., 2015). Indeed, studies have shown that M1 is involved in generating involuntary, as well as voluntary, motor responses (Evarts & Tanji, 1976; Scott, 2004; Shemmell, An & Perreault, 2009). To what extent do non-volitional sources influence the firing of neurons within M1, and how does this affect our ability to voluntarily control the activity of these neurons? We trained Rhesus macaques in a single-cell brain-computer interface task, where they controlled the 1D movement of a cursor on a screen by modulating the activity of a single conditioned neuron. In this task, the subject's goal is to successively hit two opposed targets on the screen by repeatedly decreasing and increasing the conditioned neuron's firing rate. By keeping the neural requirements constant and allowing different aspects of the task's sensory feedback to be flexibly modified, such as the subject's posture or the orientation and location of the cursor's movement on the screen, this paradigm enables us to dissociate volitional from sensory drivers of activity. In doing so, this setup allows us to determine how these sensory features can influence the subject's ability to volitionally control neural firing in the context of a goal-directed motor task. Here we show that a subject's ability to volitionally control the activity of a single neuron in M1 can depend strongly on the sensory aspects of the task. In particular, we explored how the orientation of the 1D axis along which the cursor moves affects task performance. For each unit, we presented axis orientations around the circle at 45° intervals and found controllability was often affected substantially and in a repeatable way. Importantly, this performance dependence was not eradicated even after additional practice in an orientation that had proved challenging in the past. Extending this to other aspects of task feedback, we found that axis location within the screen did not have a noticeable impact on controllability. However, arm posture had a moderate effect that varied from neuron to neuron: for some neurons the change in posture accentuated the difference in performance from one orientation to another, for other units the postural change had an additive effect on controllability. Together, these observations suggest that sensory context interferes with volitional modulation of single M1 neurons.

2-B-19 Errors in motor control correspond to increased mental workload during an object manipulation task

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In order to successfully interact with objects, our brain must predict the outcome of motor acts based on a copy of the motor command - often termed an efference copy. One of the ways these predictive models are updated is through reactive adjustments based on sensory feedback during movement. In this circumstance, to adjust an ongoing movement and recover from deviations in prediction, the motor system requires an error signal of a short latency. Recently, we demonstrated that error related negativity (ERN) corresponds with errors in an object manipulation task; the ERN component is associated with a brain system for detecting errors and engaging in corrective behavior. Additionally, we showed that those trials associated with increased ERN had significant errors in prediction (as reflected by an increase in load phase duration), and corrective responses to motor control errors (systematic increases or decreases in load force and grip force). We hypothesized that in circumstances in which errors in motor control occur, as evidenced by increased ERN amplitude, additional cognitive resources may be required to correct these errors. Therefore, this study used electroencephalography and an object manipulation task to examine the effects of errors in motor control on mental workload--a physiological measure of mental demand imposed on the participant by the task they are completing. We examined electroencephalograms (EEG) and kinematic data from participants (N = 12) during an object manipulation task in which object weight was predictable or unpredictable, based on previous lifts. The epoch of interest when examining the EEG data was time locked to the initial corrections in lifting forces following a predictive error in motor control. A mental workload algorithm incorporating a frequency analysis of beta power / (alpha power + theta power) was calculated and used to discriminate type of lifting trial (erroneous vs. accurate) and then as a feature for the classification of cognitive state using a support vector machine to allow for trial-by-trial classification of mental workload. As predicted, there was a significant increase in ERN during trials in which object weight was unpredictable compared to predictable. Specifically, ERN corresponded to changes in load phase duration and maximum load force, indicating that correction in lifting kinematics were necessary. Further, as hypothesized, mental workload metrics were higher during trials in which errors were present, suggesting that the act of detecting and correcting errors required increased mental effort. This study demonstrates that errors in motor control have an impact on the level of mental workload experienced during an object lifting task. Importantly, these results suggest small errors in motor control may be a contributing factor to the generation of central fatigue in a number of disorders in which central fatigue and motor deficits co-occur, such as with stroke or multiple sclerosis.

2-B-20 Generalizability of a novel feedback controller is computationally demanding and sensitive to prior knowledge

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Recent experimental findings have shown fundamental differences between learning a new feedback controller de novo versus updating the mapping of an existing controller (Shmuelof et al., 2012; Telgen et al., 2014). Learning a novel controller appears to be dependent on decision-making processes (Chen et al., 2017), and may rely on reinforcement learning to learn an arbitrary stimulus-response mapping (Haith and Krakauer, 2013). To understand how a new controller is learned, we sought to bias learning toward either model-free or model-based processes by manipulating knowledge of the task demands. We modified a task developed by Fermin and colleagues (2010), in which subjects navigate a cursor across a virtual grid using a keyboard. The mapping between key-presses and movement of the cursor was arbitrary and unintuitive, which is thought to require learning de novo. We hypothesized that knowledge of the correct sequence would tip the balance between different learning processes, which would be revealed with a transfer test where subjects navigated to a novel set of start-end locations. We found that providing full knowledge of the required key-press sequence greatly speeded initial learning. However, on the transfer test, subjects who learned the sequence by trial and error far outperformed subjects given prior knowledge (i.e., key-press sequence). This suggests that the group given sufficient information to easily do the training task did not learn the full mapping. This is consistent with learning arising from a model-free process and echoes predictions made by the guidance hypothesis (Salmoni, et al. 1984). Control experiments confirmed that differences between groups were not attributable to variability in training, working memory, or explicit knowledge of the controller. Next, we sought to determine how well a newly learned controller could be used to plan out a set of future states (i.e., route between novel start-end locations) by removing continuous feedback of the cursor. When feedback was removed in the test phase, performance dramatically declined to at or just-above chance. This finding calls into question the ability to use a controller to plan future states; however, this ability may differ based on the complexity of the mapping and the degree of expertise. We conducted follow-up experiments and found that the complexity of the mapping and degree of learning interacted to determine how far in advance subjects could plan. What's more, we found that subjects' reaction times increased with the number of planned future states. This suggests that with extended practice a feedback controller can be co-opted to plan ahead, but it is computationally demanding. These experiments reveal that the knowledge a person has when learning a new controller determines their behavioral flexibility when conditions change and that planning with a controller may require extensive training, reflecting the common experience of mastering a new motor skill.

2-B-21 Spinal stimulus effects altered by voluntary muscle activity in monkeys

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Electrical stimulation to the spinal cord has been used as a clinical treatment to restore the motor deficit after spinal cord injury. Although spinal neural circuits receive convergent supraspinal and peripheral afferent information, and send signals to motoneurons for appropriate motor behavior, it remains unknown how electrical stimulation activates spinal neural circuits during voluntary movements. To reveal this issue, we investigated the effects of spinal electrical stimulation on muscle activity during a voluntary motor task. Two macaque monkeys were used in this study. A subdural 7-electrode sheet was placed over the C7-T2 spinal segments. Spinal stimuli were delivered while the monkeys were performing an isometric, eight-target wrist torque tracking task. The stimulus effects were identified by stimulus-triggered averages of electromyographic (EMG) activity in the 16 arm and hand muscles. Spinal stimuli from an electrode evoked the responses from elbow to digit muscles. In the intact monkeys, low-intensity spinal stimuli evoked facilitation or suppression effect in either muscle, but high-intensity spinal stimuli evoked facilitation effects in most muscles. On the other hand, in monkeys with spinal cord injury, spinal stimuli to the lesioned sites preferentially evoked facilitation effects in most muscles regardless of stimulus intensity. These results suggest that subdural spinal stimuli to the intact spinal cord mainly activates facilitatory and inhibitory spinal neurons via peripheral afferent fibers, but those to lesioned spinal cord directly activate residual spinal motoneurons or their axons. We also found that the magnitudes of evoked responses in the intact monkeys positively correlated with the magnitude of voluntary EMG activity, whereas those in the monkeys with spinal cord injury negatively correlated with the magnitude of voluntary EMG activity. These results reflect that the electrical stimulation to the lesioned spinal cord activates different neurons and axons from that to the intact spinal cord. In addition, muscle responses evoked by spinal stimuli changed depending on the movement directions. The preferred directions (PDs) of evoked responses in the intact monkeys were similar to the PDs of voluntary EMG activity, while the PDs of evoked responses in the monkeys with spinal cord injury exhibited the opposite to the PDs of voluntary EMG activity. These results suggest that activation of peripheral afferent fibers induces the PDs of stimulus effects in directions corresponding to the PDs of voluntary muscle activity. To elevate voluntary muscle activity by spinal stimuli, it is important to increasing the synaptic input to the motoneurons through peripheral afferent fibers.

2-B-22 Mapping motor unit networks of human movement - Forwarding new possibilities

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The complex network of motor units that regulate human movement remain relatively unexplored and undiscovered. Today most practices for interrogating the neuromuscular system focus on single-muscle, single-sensor recordings of individual motor unit firings that comprise the electromyographic (EMG) signal. Yet whether studied from single intramuscular electrodes or from more elaborate grids of 64+ monopolar electrodes, the impact of motor unit studies has been limited to relatively isolated muscle contractions performed in highly-constrained laboratory conditions with little translation to real-life function. Starting more than 10 years ago our team set out to overcome this limitation by rethinking the tools used by clinicians, scientists and engineers to probe the inner workings of the neuromuscular system. Through a series of scientific and technical evolutions, we recently achieved critical developments in noninvasive, high-fidelity sensors and pattern recognition algorithms for decomposing the surface electromyographic signal into constituent firings of individual motor units during functional tasks and voluntary movements of daily life. We tested the algorithms using sEMG signals recorded with the NeuroMAP? system (Delsys, Inc, Natick, MA) during four different applications: 1) in-clinic evaluations of neuromuscular disease; 2) rehabilitation assessments of spasticity and stroke; 3) investigations of upper-limb coordination for understanding multi-degree-of-freedom control; and 4) sports performance training during cycling. The algorithms identified a broad range of motor units above the 90% accuracy benchmark that provided a rich data source for empirically investigating the complex networks of motor units that coordinate functional movement. Across the 4 application areas tested, we observed: 1) motor unit metrics were able to successfully discriminate patient subgroups with neuropathy and myopathy; 2) motor unit firing rates demonstrated consistent decreases in temporal correlation across agonist/antagonist muscles in patients with spasticity; 3) investigations of upper-limb motor function revealed clear modulation in motor unit activation patterns across functional muscle synergies to coordinate complex multi-degree-of-freedom movements; and 4) metrics of gait training showed clear patterns of motor unit recruitment from networks of 6 muscles during cycling. These and other applications of NeuroMAP? technology are moving research beyond the current status quo to impact healthcare, shape assistive technologies and improve our understanding of the neuromuscular system through future research. Acknowledgement: This work was supported in part by two grants from the National Institute of Neurological Disorders and Stroke under award numbers R43NS093651 and R44NS077526 and by a grant from the Eunice Kennedy Shriver National Institute of Child Health and Human Development under award number R44HD094626 of the National Institutes of Health.

2-B-23 Action observation and execution differentially modulate basal ganglia-cortical activity in humans

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Introduction: To understand an observed action, without an overt execution, the observer is suggested to run similar motor plans for the production of the same movements; indicating a strong coupling between the neural representation of action observation and execution. Prior studies show activation of basal ganglia (BG), primary sensory, motor, and premotor cortex during contralateral body movements yet direct and concurrent electrophysiological recordings from these regions in humans are sparse. Deep brain stimulation (DBS) surgery in subjects with Parkinson disease (PD) provides unparalleled opportunities to record invasive neurophysiology directly from the BG. In this study, we aimed to characterize how movement execution and observation differentially modulate local and cross-regional electrophysiological activity within and between BG and sensorimotor cortex. Methods: We recorded LFP from globus palidus internus (GPi) concurrently with electrocorticography (ECoG) from ipsilateral sensorimotor cortices (using a temporally placed ECoG strip via the burr hole) in nine subjects with idiopathic PD. Recordings were acquired during DBS lead implantation surgery in the GPi while subjects were off stimulation and alternated between 30 second block of resting state and performing two tasks: 30 seconds of repetitive finger tapping and 30 seconds of observing the finger tapping while a human subject performed finger tapping (using a similar hand as the subject). We assessed changes in local spectral power at the GPi and sensorimotor cortices, along with pallidocortical coherence and cortical PAC. Results: We observed suppression of α-β (9-25 Hz) spectral power in contralateral GPi and across the sensorimotor cortex during both activities. This power suppression was significantly weaker in the motor cortex during the action observation compared to the execution ($P=0.02$). However pallidal spectral changes in α-β frequencies were not significantly different across two tasks ($P=0.3$). Uniquely during the action execution, there was a significant increase in the γ power (80-200 Hz) at the motor/premotor cortical areas ($P<0.05$). In addition, Pallidocortical coherence in β (13-30 Hz) frequencies and motor cortical β-γ PAC were significantly suppressed during action execution ($P<0.05$) and not the observation. Conclusions: Our results lend support on functional dissociation within the BG-cortical network during action observation and execution. Although spectral power changes in α-β in the BG is similar during execution and observation, suppression of BG-cortical functional connectivity is a feature of movement execution. In addition, increase in the cortical γ power and β-γ phase amplitude decoupling is only observed during the movement execution, in line with the theory that during movement execution the amplitude of γ signal is released from the constraint of β phase.

2-B-24 Neural representations of rapid unlearning of force planning following object rotation

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Feedforward motor planning for skilled grasping and lifting of objects is primarily based on previous experiences with the same object (sensorimotor memories) and visual cues of object properties. The acquisition of sensorimotor memories representing the dynamics needed for grasping and lifting an object is surprisingly swift compared to learning reaching dynamics for visuomotor or force field adaptation. Proficiency at minimizing the tilt of an object with an asymmetric center of mass (CoM) at lift onset occurs within 2-3 trials with little subsequent improvement by the 10th trial. Despite this swift learning, this sensorimotor memory does not transfer or generalize positively to the same object manipulated in a new orientation. This failed generalization occurs despite explicit awareness of the context change (seeing the object being rotated) and an intact knowledge of the CoM (correctly pointing to it). The behavioral literature is at odds over explaining the lack of positive generalization immediately following context shifts despite the recent object manipulation and sensorimotor learning. Some have attributed the error to a "negative transfer" effect (Bursztyn & Flanagan 2008) whereby subjects persist with, or attempt to use the same sensorimotor memory that was initially acquired, as shown by copying the motor behavior from the trial preceding the context change on the first trial in the new context. Others have attributed the error to a zero transfer ("blank slate") effect (Salimi et al. 2000) where subjects do not take into account or attempt to use the sensorimotor memory that was acquired prior to the context change. The present study tested the negative transfer hypothesis by investigating whether neural representations of newly acquired sensorimotor memories in a learned context are mimicked on the trial after a context shift. Cortical activity and movement kinematics were measured as 20 human subjects minimized tilt of a symmetrically shaped object with a hidden asymmetric CoM in blocked trials to the left and right. Without salient visual cues, subjects rely primarily on the sensorimotor memory of the object and its CoM. Representational similarity analyses of fMRI data examined neural representations prior to lift onset on trials before and after object rotation. In contrast to the negative transfer hypothesis, sensorimotor memory representations on error trials following a rotation were markedly different in their representational structure and statistically distinguishable from that during trials preceding the rotation in motor, parietal, somatosensory, and cerebellar regions. This suggests that subjects are not persisting with or accessing the previously learned sensorimotor memory. Instead, regions that encode the sensorimotor memory aspect of motor planning might reset or "efficiently forget" previously learned sensorimotor memories to prevent larger errors that would occur if copying the pre-rotation lift force strategy.

2-B-25 The influence of preceding muscle activity on force perception in ballistic contractions

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It has been demonstrated that the force perception (intention) doesn't always match to actual force production in ballistic contractions. Although there is a correlation between ballistic force and the muscle activity, motor unit activity is altered when ballistic contractions are superimposed on a sustained contraction. Therefore, the purpose of current study was to clarify the influence of preceding muscle activity on the relationship between force perception and force production in ballistic contractions. Healthy males who are right hand dominant participated in this study. The isometric flexion force at the elbow joint was measured using a customized dynamometer equipped with a load cell transducer. The participants were seated and adjusted to maintain their right arm abducted to approximately 90˚ and the elbow flexed to 90˚. The maximal voluntary contraction (MVC) was measured twice prior to an experimental task and the mean value of the two trials was determined as the MVC of each participant. We used a force-production task where the participants were verbally asked to produce isometric force at different percentages (40, 60 and 80%) of their MVC based on their force perception (perceived effort) without external feedback. Ballistic contractions were produced from either a resting state (resting condition) or superimposed a sustained contraction at approximately

20%MVC (active condition). The preceding muscle activity began 3-4 s prior to a ballistic contraction. Five trials were performed at each percentage (40, 60 and 80%) of their MVC. The participants were not given any external feedback about the actual force production through the experiment, which means that the force was produced based on their force perception. To evaluate the muscle activity during the force-production task, EMG activity was recorded by surface electrodes from the biceps brachii (agonist) and the lateral head of triceps (antagonist), and integrated EMG (iEMG) was calculated after full-wave rectification. The results showed that the magnitude of force production was larger under the active condition compared with the resting condition, even the same force perception. In contrast, iEMG of the agonist and antagonist showed no difference between two conditions, indicating that the muscle activity is consistent with the force perception. Therefore, these results suggest that the preceding contraction could alter the relationship between force perception and force production in ballistic contractions.

2-B-26 Emergence of spinomuscular and corticomuscular loops in dynamic vs. static phases of precision grip

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Volitional motor control typically involves dynamic movement and static maintenance of the state. While accumulated evidence shows the oculomotor control system accommodates separated circuitry dedicated for dynamic and static control, it is unknown whether such dedicated circuitry is implemented in the limb motor system for dexterous hand control. To explore the dedicated circuitry underlying limb control, we investigated neuronal interactions between spinal cord and forelimb muscles, as well as between motor cortex and the muscles, by examining coherence of local field potentials (LPFs) from the neural structures and electromyographic (EMG) signals of forelimb muscles. Recordings of the signals were carried out from four macaque monkeys, while the monkey was performing a precision grip task; a task consisting of dynamic grip and static hold phases separately. We found emergence of beta range coherent patterns between spinal cord LFPs and EMGs (spinomuscular coherence), as well as between LFPs of the motor cortex EMGs (corticomuscular coherence), each of which was pronounced in separate phases; spinomuscular coherence emerged almost exclusively in the grip (dynamic) phase, whereas corticomuscular coherence was evident in the hold (static) phase. Further analysis based on Granger causality and MVAR model revealed both of spinal and cortical beta range coherence were influenced by bidirectional interaction of afferent and efferent pathways, representing dedicated feedback loops. The characteristics of each feedback loop were common to those of short- and long latency reflexes that have been investigated in the pursuit of feedback control system. The spinomuscular coherence was specifically found in prime movers of forefinger flexion (FDI and FDPr), with interactions of hand flexors, whereas the corticomuscular coherence was observed in a broad range of intrinsic hand muscles, with rather broad interactions across forelimb muscles. The phase-specific emergence of distinct feedback loops, i.e., the spinally-mediated local feedback loop in the dynamic phase and trans-cortically mediated diverged feedback loop in the static phase, suggest that feedback controllers are utilized in the volitional control context to adapt phase specific requirements for limb motor system.

2-B-27 Bimanual training results in m1 excitability changes, while delay interval length after training influences response time in a visual perception task but not motor skill consolidation

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The current study examined whether training with a rhythmic bimanual task (90° relative phase) would produce prolonged post-training changes in motor cortex (M1) excitability that could be linked to action consolidation and visual discrimination processes that might emerge after a 30-min or 6-hr post-training delay. Research by Tunovic et al. (2014, Exp. 1) using transcranial magnetic stimulation (TMS) demonstrated that M1 excitability was below baseline at 6 min and above baseline at 21 mins after training with an explicit serial reaction time task (SRTT), while remaining above baseline for an implicit SRTT at both time points. In this study, TMS was used to probe left-hemisphere M1 excitability to develop a post-training excitability profile for the 90° bimanual task. Participants used index finger abduction/adduction motions to produce the 90° pattern and were trained for 10 mins with concurrent feedback. Motor evoked potentials (MEPs) from the right-hand first dorsal interosseous muscle (FDI) were measured at three time points: baseline (pre-training), and at 6 and 21 mins after training. Participants showed significant performance improvements with smaller error and variability in the 90° pattern for late compared to early training trials. After training, the MEPs of the FDI significantly increased at the 6 and 21 min time points compared to baseline. There were no differences between individuals assigned to the 30-min and 6-hr delay groups. This excitability profile is consistent with that seen in implicit SRTTs. After the 21 min TMS probe, individuals in the 30-min delay group were retested and the 6-hr individuals dismissed. A retest of the 90° pattern with concurrent feedback and a perceptual test of visually defined index finger motions representing 0°, 180°, 90° and 45° patterns were administered after the delay intervals. The interval did not influence coordination accuracy and stability with both the 30-min and 6-hr groups exhibiting consolidation in the form of off-line stabilization. Both groups identified the 90° visual displays as representing practiced finger motion on a majority of trials (74%) and significantly ($p < .05$) more often than any other pattern (40%). The 45° pattern (closest to 90°) was most often identified as not 90° (30%). The 6-hr delay group made significantly ($p < .01$) faster perceptual decisions (Mn = 2.36 secs) compared to the 30-min group (Mn = 3.28 secs). The difference between the groups was largest for the 90° pattern, 6-hr group 2.78 secs and 30-min group 4.58 secs ($p < .05$). In SRTTs, a longer interval between training and retesting often allows for more action consolidation. The use of concurrent feedback in the retest may well have neutralized that advantage for the 6-hr delay group in this task. However, the perceptual response time results suggest that the 6-hr group may have experienced greater consolidation that emerged through perception-action identification processes.

2-B-28 Facilitatory effects of ipsilateral, contralateral and bilateral upper-limb muscle contractions on corticospinal and spinal reflex excitabilities in lower-limb muscles

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Contraction of upper-limb muscles unilaterally can facilitate excitability of corticospinal tract and spinal reflex circuits in lower-limb muscles. Such mechanisms contribute to coordination of interlimb movements via inter-neuronal circuits within the central nervous system. However, it remains unclear whether unilateral and bilateral muscle contractions affect the excitability of these neural circuits to a different extent. Therefore, the purpose of this study was to systematically compare the effects of ipsilateral, contralateral, and bilateral upper-limb muscle contractions on the excitability of corticospinal and spinal reflex excitabilities in the lower-limb muscles. Fourteen healthy individuals (23-32 yr) participated in the following two experiments, which were performed on separate days, to investigate: (1) corticospinal excitability - single-pulse transcranial magnetic stimulation to the left primary motor cortex to measure motor-evoked potentials (MEP) from right tibialis anterior (TA) (Experiment 1); and (2) spinal reflex excitability - transcutaneous spinal cord stimulation (tSCS) to measure spinal reflexes in right TA, soleus (SOL), vastus medialis (VM), and biceps femoris (BF) muscles (Experiment 2). In both experiments, participants were asked to relax their lower-limb muscles, while they remained in the supine position. Measures were obtained during the following experimental conditions: (a) relaxation of the whole body (Baseline); (b) ipsilateral elbow flexion (Ipsi); (c) contralateral elbow flexion (Cont); and (d) bilateral elbows flexion (Bi). In the Ipsi, Cont and Bi conditions, participants were asked to match the isometric elbow flexion forces to a target level as fast as possible after an auditory cue, which was set to 30% of maximal effort of each arm and displayed on an oscilloscope. In each condition eight responses were evoked and the peak-to-peak amplitude of the MEP and tSCS responses was computed and averaged to evaluate excitability of corticospinal and spinal reflex circuits, respectively. In Experiment 1, MEP amplitudes in the TA muscle were significantly larger during Ipsi, Cont and Bi conditions, compared with the Baseline condition. However, there was no significant difference across the three conditions (i.e., Ipsi, Cont and Bi). Similarly, in Experiment 2, tSCS amplitudes in all muscles were larger in Ipsi, Cont and Bi conditions, compared with the Baseline, while there was no significant difference across the three conditions (i.e., Ipsi, Cont and Bi). Our results demonstrated systematically that ipsilateral, contralateral and bilateral elbow flexion has similar facilitatory effects on corticospinal and spinal circuits in lower-limb muscles. Lack of difference between unilateral and bilateral conditions may be attributed to interhemispheric facilitation and/or inhibition mechanisms, which depend on the remote effect contraction conditions.

2-B-29 Cooperative hand movements up-regulate bilateral input to the upper limb - an ipsilateral MEP study

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Bimanual tasks which engage the two hands in order to complete a common goal, such as opening a jar, may involve more bilaterally organised neural control than movements regulated by the crossed lateral corticospinal tract. Cooperative bimanual movements have been shown to increase ipsilateral afferent input to sensory cortex, as well as bilateral arm muscle reflex responses following unilateral nerve stimulation. The aim of this study was to investigate the role of ipsilateral motor pathways in the control of these movements. Paired-pulse transcranial magnetic stimulation (TMS) has been shown to increase ipsilateral motor evoked potentials (iMEPs). Sixteen right-handed adults received paired-pulse TMS on the left primary motor cortex while performing cooperative and non-cooperative movements. iMEPs were recorded from different arm muscles with focus on the left extensor carpi ulnaris (ECU) muscle. The number of iMEPs elicited in the ECU was significantly higher during cooperative than during non-cooperative movements. Root mean square over 20ms after iMEP onset was significantly higher during the cooperative tasks while pre-trigger activity was similar in all tasks. Nine participants were characterized as iMEP+, defined as showing an iMEP in the ECU in at least 20% of the trials in each movement condition. iMEP+ participants showed increases in both amplitude and area under the curve in cooperative task conditions only. These novel findings provide insight into the underlying neural regulation of bimanual movement and the role and significance of alternate motor pathways more generally.

2-B-30 Macaque ventral midbrain facilitates the output to forelimb muscles via the primary motor cortex

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The primary motor cortex (M1) is a major source of the corticospinal tract that regulates activity of spinal motoneurons and is directly involved in motor output. Several studies have reported that the M1 activity can be modulated by reward-related information in humans and monkeys, suggesting that the M1 activity may be under control of motivation to obtain reward. However, little is known about a neural substrate underlying this psychological effect on motor output. The ventral midbrain (VM) including the ventral tegmental area and the substantia nigra par compacta is recognized as an important brain area in the processing of motivational signals. We hypothesized that the VM might exert a modulatory action over the corticospinal pathway. To investigate the existence of such a descending projection arising from the VM to the spinal cord, rabies virus that permits retrograde transsynaptic transport was injected into the cervical spinal cord in macaque monkeys. We found that there was a disynaptic spinal projection from the VM, including the ventral tegmental area, the substania nigra, and the retrorubral field. To explore the functional significance of the disynaptic VM-spinal pathway as a modulator of motor output, electrical stimulation was delivered to the unilateral VM under sedation, and evoked responses were recorded from the ipsilateral M1 and contralateral forelimb muscles. The VM stimulation induced the field responses in the M1. Then, the responses in forelimb muscles occurred with a few milliseconds delay. These muscle responses were diminished during reversible inactivation of the M1. The present study is the first report demonstrating the existence of the VM-M1-spinal pathway in nonhuman primates. This pathway might be a candidate for the neural substrate underlying motivational control of motor output.

2-B-31 Planning of actions following predictive and non-predictive symbolic cues

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Predictive cues may help us to predict and plan an action relative to what will come next. Some cues such as arrows, contain directional information to orient the actor. Other cues, however, may contain no spatial information that directly orients the actor to the upcoming action. Non-directional predictive cues have been shown to reduce search times in visual search tasks but have not been explored in the planning and execution of actions. The first aim of this study is to determine whether participants can implicitly learn to associate symbolic cues with an upcoming action target location. The second aim is whether this association leads to automatic and transient activation or strategic activation of the action associated with the predicted target location. It was hypothesized that if this learned association was used strategically, participants' could pre-plan the action to the predicted target location and therefore

movements would deviate toward the predicted target location when reaching for the non-predicted location. High and low predictive symbolic cues preceded target appearance at long cue target onset asynchronies (1100-2000ms). The area between trajectories of participants' reaches were analyzed depending on whether they aimed to the predicted or the non-predicted side within each of the cue type conditions. For the highly predictive cue, participants' trajectories veered further away from the predicted target location when aiming to the non-predicted target in comparison with trajectories aiming to the predicted target location. The resulting movement was therefore more direct when reaching to the non-predicted side than to the predicted side. These results do not support the idea that participants strategically preplanned the movement to the predicted target location. Instead the results imply that the predicted response was likely automatically activated, then inhibited in the long intervening time between the cue and target, indicating that participants can associate an upcoming action with non-directional predictive cues. This finding is similar to the response to peripheral onset cues in inhibition of return type paradigms.

2-B-32 Optimal motor decision-making through competition with opponents

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Optimal decision-making is indispensable for ideal performance in sports and excellent motor control in everyday life. For example, selecting an appropriate trajectory for reaching a glass of water can lead to a low risk of spilling water, and likewise, deciding the best aiming location in a tennis match can increase the possibility of victory in a competition. Despite the importance of optimal decision-making, for over a decade, sub-optimal and overly risk-seeking behaviors have been reported in various motor decision tasks (Nagengast+, 2011, Proc B Soc B, Wu+, 2009, PNAS). Determining how to improve sub-optimal and risk-seeking decision-making behavior is crucial to enhance well-being in daily life and performance in sports. However, it remains unclear how motor decision-making can be optimized. A possible solution to achieve optimal decision-making is interactions with other people. It has been shown that the observation of other people's movements induces synchronization in one's movement speed during a competitive game (Naber+, 2013, PNAS) and facilitates movement adaptation (Mattar & Gribble, 2009, Neuron). Since risk-seeking behavior has been reported in motor tasks in which subjects perform alone, the presence of other people may influence sub-optimal motor decisions. Here, we investigated how humans alter their motor decision-making in a competitive game (a variant of 'chicken game'), which requires naturalistic interactions with other people. The game resembles situations in sports, such as a penalty kick in soccer, service in tennis or the strike zone in baseball. We had two main hypotheses. First, if the decision system imitates an opponent's movement, optimal decisions should be achieved when the opponent's decisions are also optimal. This hypothesis is based on evidence that the unintended imitation of movement speed or distance occurs in a competitive situation (Naber+, 2013, PNAS). Second, if the decision system adaptively changes the motor plan based on the opponent's movements, optimal decisions should be achieved when the opponent's decisions are sub-optimal. To test these hypotheses, we assessed subjects' behavior during competition with a virtual opponent who behaved either optimally or sub-optimally. First, we show that the direction of the sub-optimality of motor decisions is reversed from risk-seeking to risk-averse at the beginning of the competitive situation. Second, following this reversal of sub-optimality, we demonstrate that competition with sub-optimal risk-averse opponents promotes optimal risk-neutral decision-making. Finally, to explain these findings, we confirm that the subject's decisions are affected by the opponent's decisions in a non-linear function. These results suggest that interactions with others can alter motor decision strategies and that competition with a risk-averse opponent is the key to optimizing motor decision-making. The full version of our manuscript is available on bioRxiv.

2-B-33 Volitional control of motor unit firing behavior for improved human-machine interface

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Robotic and prosthetic devices have made strident gains in recent years, incorporating electromechanical components that are capable of closely approximating human movement. However, effective control of these devices has been hindered by fundamental limitations of human-machine interfaces that infer, but do not directly measure, how the human nervous system translates carefully regulated patterns of motor unit activation into output force and movement. To address this challenge, we developed a human-machine interface referred to as motor unit drive (MU Drive), that uses discrete increments of motor unit firing rates and recruitment to provide a more natural, proportionally varying control signal. Real-time pattern recognition algorithms were used to directly measure motor unit firings from surface electromyographic signals recorded from a single, dry, noninvasive, miniature sensor from muscles of the arm. The extracted firings were transformed into proportionally varying MU Drive control signals using empirically-based and mathematically calculated motor unit force twitches to approximate the biomechanical contributions of each motor unit to produce the intended movement. The MU Drive signal characteristics were evaluated and compared to conventional amplitude-based myoelectric signals (Root-Mean-Square and Mean-Absolute-Value) recorded from amputees (n=13) and control subjects (n=10) during intended and actual finger flexion/extension and forearm pronation/supination, respectively. Our test results demonstrated that MU Drive provides a more responsive control signal with more faithful replication of intended limb movement when compared to conventional amplitude-based metrics. Furthermore, MU Drive overcomes a critical trade-off inherent to typical amplitude-based myoelectric signals: namely that the variability in the signal amplitude can only be reduced through increased filtering at the expense of the delay and subsequent signal responsiveness. MU Drive overcomes this trade-off between performance and latency by leveraging the natural biomechanical filtering properties of muscle fibers to map increases and decreases in motor unit activation directly to a smooth, proportionally varying signal that approximates the physiological changes in joint position within a 25 ms delay in processing time. The established proof-of-concept demonstrates significant advantages of MU Drive over traditional myoelectric control methods. This work provides a foundation for MU Drive controllers that can be developed in the future to leverage multiple muscles to enable simultaneous multi-degree-of-freedom limb control. The technology holds promise for improving functional use of prosthetics by achieving control that better reflects the user intent. It may also provide an innovative alternative for advancing the control of robotics, and other assistive devices.
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2-B-34 Decoding muscle activity using electrocorticographic signals in freely behaving marmosets

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Significant progress has been made in the development of Brain-Machine Interfaces (BMIs) over the past two decades. This progress relies heavily on the development of new methodology in the field of neural decoding, in which neuronal activities are translated into signals that can be used to control external devices such as limb prostheses or computers. However, the application of these technologies may be limited to patients in static conditions, as these developments have been largely based on studies of animals (e.g., non-human primates) in constrained movement conditions. The ultimate goal of BMI technology is to enable individuals to move their bodies naturally or control external devices without physical constraints. Here, we demonstrate accurate decoding of muscle activity from electrocorticogram (ECoG) signals in unrestrained, freely behaving monkeys. We recorded ECoG signals from the sensorimotor cortex as well as electromyogram signals from multiple muscles in the upper arm while monkeys performed two types of movements with no physical restraints. As in previous reports using restrained monkeys, we confirmed that muscle activity during a lever pulling task (forced forelimb movement) was accurately predicted from simultaneously recorded ECoG data. More importantly, we demonstrated that accurate prediction of muscle activity from ECoG data was possible in monkeys during free movement within the cage (natural whole-body movement). We found that high-gamma activity in the primary motor cortex primarily contributed to the prediction of muscle activity during natural whole-body movement as well as forced forelimb movement. In contrast, the contribution of high-gamma activity in the premotor and primary somatosensory cortices was significantly larger during natural whole-body movement. Thus, activity in a larger area of the sensorimotor cortex was needed to predict muscle activity during natural whole-body movement. Furthermore, decoding models obtained from forced forelimb movement could not be generalized to natural whole-body movement, which suggests that decoders should be built individually and according to different behavior types. These results contribute to the future application of BMI systems in unrestrained individuals.

2-B-35 Towards a neural population-level understanding of the effects of methylphenidate (Ritalin) in motor cortex of reaching monkeys

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A fundamental goal of motor neuroscience has been to understand how patterns of activity in the motor cortex drive behavior. One successful strategy has been a "perturbation" approach, in which neural activity and/or behavior is disrupted using tools such as electrical or optogenetic stimulation, task-related (e.g., mechanical or stimulus) perturbations, or pharmacological manipulation. Many of these studies to date have focused on the effects of pharmacological inactivation (e.g. with muscimol) of particular cortical regions, and/or other local manipulation of particular neurotransmitter systems with iontophoretic application of specific drugs. However, research regarding the relationship between cortical activity and behavior has not rigorously addressed the effects of commonly used cognition-altering drugs. Recently, there has been a lot of interest in studying how populations of neurons implement behaviorally relevant computations. While the effects of common behavior-altering drugs have been well studied in humans, it has been challenging to uncover how they influence and shape population neural activity. Here we take a first step towards this goal by studying the effects of methylphenidate (MPH), a commonly prescribed (and abused) stimulant which inhibits catecholamine reuptake, on motor control in rhesus macaques. This approach provides both a precise behavioral assay and the opportunity to study the correlates of the behavior in populations of single neurons. We administered either oral MPH or vehicle alone (frosting or crushed cookie) as a control to two adult male macaques (U and P) 10-15 min prior to the start of a center-out delayed reaching task, and measured two classic motor variables: reach speed and reaction time. We tested the effects of two different doses in each animal. Preliminary results show significantly faster peak reach speeds during MPH treatment at individually optimized doses (U: 6 mg/kg, P: 1.3 mg/kg) compared to control sessions in both animals ($p < 0.01$ for both U and P). Reaction times were significantly reduced in U only ($p < 0.05$). These results show some dose dependence, with significantly reduced peak reach speeds in P ($p < 0.05$) at a higher MPH dose (3 mg/kg), and attenuated effects on both RT and peak speed in U at a lower dose (4.5 mg/kg). Concomitant to the behavioral measurements, we recorded motor cortical neural activity (in U through 3 Utah electrode arrays in premotor and primary motor cortex, and in P through V-probes in premotor cortex). Given that we observe significant behavioral effects of MPH, this presents an opportunity to study the population-level effects of the drug in motor cortex. We plan to study the effects of MPH on previously described neural population correlates of reaction time and speed. To our knowledge, this will constitute one of the first investigations of the effects of MPH on neural population activity and dynamics.

2-B-36 Explaining the neural activity distribution associated with discrete movement sequences: Evidence for parallel functional systems

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To explore the effects of practice we scanned participants with fMRI while they were performing four-key unfamiliar and familiar sequences, and compared the associated activities relative to simple control sequences. On the basis of a recent cognitive model of sequential motor behavior (C-SMB), we propose that the observed neural activity would be associated with three functional networks that can operate in parallel and that allow (a) responding to stimuli in a reaction mode, (b) sequence execution using spatial sequence representations in a central-symbolic mode, and (c) sequence execution using motor chunk representations in a chunking mode. On the basis of this model and findings in the literature, we predicted which neural areas would be active during execution of the unfamiliar and familiar keying sequences. The observed neural activities were largely in line with our predictions, and allowed functions to be attributed to the active brain areas that fit the three above functional systems. The results corroborate C-SMB's assumption that at advanced skill levels the systems executing motor chunks and translating key-specific stimuli are racing to trigger individual responses. They further support recent behavioral indications that spatial sequence representations continue to be used.

2-B-37 Motor-cortical activity during bilateral and unilateral lower-limb force control

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Unilateral performance of maximum voluntary contraction and reaction time tasks is typically superior compared to bilateral performance. This phenomenon is known as bilateral deficit. However, bilateral deficit in lower-limb force control is not well understood. Therefore, the objectives of our study were to investigate: (1) force control ability and (2) corticospinal excitability during bilateral and unilateral force-matching tasks of ankle dorsiflexion. Two studies were conducted. In experiment 1, fifteen healthy young adults performed isometric ankle dorsiflexion force control during: (a) Ballistic task - target appeared for 1 sec; and (b) Tonic task - target appeared for 5 sec. In both tasks, participants were instructed to match the target force level (10% of maximal effort) as quickly and precisely as possible in two conditions: (a) with their right foot only (unilateral); and (b) both feet simultaneously (bilateral). Performance was evaluated using force error, force steadiness, amount of muscle activity of the tibialis anterior (TA) muscle, and reaction time. In experiment 2, thirteen healthy young adults performed the same tasks as in experiment 1. During the tasks, motor evoked potentials (MEP) from the TA muscle of the right leg were elicited by transcranial magnetic stimulation (TMS) in four different phases: (i) pre-contraction; (ii) ascending contraction; (iii) plateau; and (iv) rest. MEPs at the plateau phase were only evoked during the Tonic task. Peak-to-peak amplitudes of MEPs were used to compare the corticospinal excitability between bilateral and unilateral tasks. As a result, in experiment 1, bilateral performance had significantly larger error and less force steadiness compared to unilateral condition, only during the Tonic task. No significant difference in the amount of muscle activity was found. In experiment 2, although there were no significant differences in MEP amplitude between the Ballistic and Tonic tasks in all phases, larger facilitation of MEPs in the pre-contraction phase was observed during unilateral condition compared to bilateral condition. The present study demonstrated that bilateral deficit occurred during the lower-limb force-matching tasks. Bilateral force control with homologous legs, specifically in tasks demanding feedback control (i.e., Tonic task), might affect performance. However, our results showed no task-specific activation of motor pathway during both Ballistic and Tonic tasks. Furthermore, our findings suggest that anticipatory control is modulated prior to the force generation in order to initiate precise and quick force execution, especially during unilateral performance. Increased corticospinal excitability during preparation phase is possibly due to interhemispheric inhibition, which is relevant to better performance in the unilateral motor-tasking.

2-B-38 Interactions between short-latency afferent inhibition and cerebellar stimulation in the human motor cortex

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Transcranial magnetic stimulation (TMS) allows for the testing of various inhibitory processes within the human motor cortex (M1). Previous studies utilizing TMS have shown that applying stimulation over the cerebellum as a conditioning stimulus 5 ms prior to stimulating M1 reduces corticospinal output, a phenomenon known as cerebellar-brain inhibition (CBI). A similar effect on corticospinal excitability is achieved when somatosensory input via electrical stimulation of a peripheral nerve is administered ~20-25 ms prior to TMS over M1 (termed short-latency afferent inhibition, SAI). In a series of experiments, we were interested in understanding how CBI and SAI interact with one another in order to better understand the underlying physiology of these mechanisms. While studies have suggested that cerebellar activity may influence the arrival of late sensory inputs to M1 (i.e. around 23-25 ms), this idea has not been previously investigated by directly assessing the connections between the cerebellum and this cortical circuit. To do this, we utilized paired- and triple-pulse paradigms on 15 healthy volunteers in order to assess how cerebellar stimulation influences SAI at different inter-stimulus intervals (20-25 ms). CBI and SAI were assessed for the abductor pollicis brevis (APB) muscle in healthy participants by measuring inhibition of a test motor-evoked potential conditioned by a magnetic pulse applied over the right cerebellar hemisphere at 70% of maximum stimulator output or an electrical pulse applied to the median nerve with an intensity just above motor threshold (0.2 mV APB M-wave), respectively. Here, we found that the presence of CBI specifically reduced the effects of SAI for the arrival of late sensory inputs (23-25ms) while not affecting earlier inputs (20-23ms), supporting a role for the cerebellum in mediating afferent input to M1. In a follow-up study (n=12), we examined the sensitivity of SAI to changes in cerebellar excitability produced by direct current stimulation of the cerebellum (tDCSCb; anodal 2ma). SAI was measured at both early (N20+2) and late (N20+4) intervals during the application of either anodal or sham tDCSCb. We found that anodal tDCSCb significantly reduced SAI for the N20+4 interval, but not for the N20+2 interval. This result demonstrates that there is a time-specific influence of cerebellar activity on sensory processing. Taken together, these findings suggest that the cerebellum or interconnected structures along the cerebellar-thalamic-tract are capable of both gating and dynamically modulating sensory information to M1.

C – Posture & Gait

2-C-39 Corticospinal excitability modulation during a precision locomotor task in humans

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INTRODUCTION. Animal studies have shown that the primary motor cortex (M1) is involved during complex gait tasks such as ladder walking and obstacle avoidance. While M1 has been shown to contribute to normal walking in humans, only one study looked at additional contribution of the corticospinal system to more complex walking (stepping onto coloured spots) using transcranial magnetic stimulation (TMS). It reported significant but limited effects, which might be explained by the fact that the task only required small lateral adjustments in the locomotor pattern. The first aim of the current study was therefore to measure if a more complex precision walking task (requiring step length adjustments) would lead to a larger modulation in corticospinal excitability in humans. The second aim was to measure if such a modulation was related to the task's difficulty. METHODS. Sixteen young healthy participants walked on a treadmill at a speed of 1.0 m/s while facing a large screen during 2 tasks (counterbalanced order): regular walking (the 'simple' condition) and stepping onto virtual targets projected on a screen (the 'complex' condition). During the complex condition, 3 target distances were presented in random order (80, 100 and 120% of individual step length). Real time foot position was also projected onto the screen in the form of small spheres and participants had to adjust their step length to hit the targets with the spheres. At the end of the task, success score (% of targets hit) was calculated. To assess corticospinal excitability, motor evoked potentials (MEPs) were recorded from the left tibialis anterior muscle in each condition during walking (25 MEPs/condition). MEPs sizes (area under the rectified MEP) were compared across conditions. RESULTS. MEPs size was larger during the complex task (vs. the simple one) in all participants (mean increase of 93 +/- 72%; $p<0.01$). The group success scores were 75.5, 93.2 and 97.1 for the targets located at 80, 100 and 120% of step length respectively (post hoc analyses indicated difference between 80-100% and 80-120%; $p<0.0005$), but no differences in MEPs sizes was found between the 3 target distances ($p>0.05$). There was also no correlation between the MEP facilitation and global success score (for each participant) ($r= 0.43$; $p=0.11$). It was also observed that performance in the complex task improved over time (from 79.7% to 92.6 % target hits) associated with a decrease in MEPs size ($p<0.05$), but the last 10 MEPs of the complex condition

remained significantly above MEPs during simple walk ($p<0.05$). CONCLUSION. As hypothesized, corticospinal excitability was increased during the precision gait task. There was no additional MEPs modulation related to the difficulty of each target or success score. This precision locomotor task is now being tested in individuals with an incomplete spinal cord injury to quantify its potential effect during gait rehabilitation.

2-C-40 Association of cortical inhibition with gait and balance

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Approximately 30% of individuals age 65 and older and over 40% of individuals age 80 and older fall each year, leading to disability, limited mobility, and death. However, it is unclear what neural mechanisms might contribute to why some older adults are more likely to fall than others. Our past work revealed an association between brain inhibitory function and bimanual coordination. Here, we test whether concentration of cortical GABA, the brain's primary inhibitory neurotransmitter, contributes to individual differences in lower limb coordination and impairments with aging that could increase one's risk of falling. Specifically, we determine whether cortical GABA levels contribute to gait and balance performance in healthy young and older adults. We test this hypothesis using GABA-edited Magnetic Resonance Spectroscopy (MRS) to quantify in vivo cortical GABA levels in frontal cortex and in the lower limb region of sensorimotor cortex. We test whether this metric of cortical inhibition explains individual differences in postural sway and in spatiotemporal parameters and phase coordination during overground walking. Preliminary results indicate that, among young adults, frontal and sensorimotor cortex GABA is associated with postural sway, double support time, and phase coordination. Forthcoming analyses will include a sample of older adults to examine age differences in cortical GABA and whether age interacts with the relationship between GABA and motor performance. Findings from this work could implicate the GABAergic system as a specific neural target for future interventions. Given the substantial prevalence of falls and fall-related injuries among healthy older adults, there is a critical need to understand the underlying neural factors of individual differences in gait and balance behaviors.

2-C-41 Facilitation of spinal reflexes in the lower-limb muscles during action observation combined with motor imagery of walking

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BACKGROUND & AIM: Action observation (AO) and motor imagery (MI) of walking are used in gait rehabilitation. Several studies have examined the neural effects of AO and MI. For example, it has been shown that AO combined with MI (AO+MI) increases spinal reflexes compared with AO or MI alone. In the previous study, the spinal reflexes during AO and MI were assessed only in a single muscle, but in fact, walking is orchestrated by the activation of multiple lower-limb muscles. Therefore, the purpose of this study is to investigate the effects of AO+MI on spinal reflexes in multiple lower-limb muscles. METHODS: Ten healthy males participated. To induce the spinal reflexes, an anode was placed over the abdomen and a cathode was placed on the midline of the skin between the spinous process of the upper lumbar vertebrae. Spinal reflex responses were obtained from the tibialis anterior (TA), the soleus

(SOL), medial gastrocnemius (MG), vastus medialis (VM), and biceps femoris (BF) muscles under the following three conditions: 1) control, 2) AO, and 3) AO+MI. While watching a monitor, participants maintained the supine position. In the control condition, participants looked at the fixation cross on the monitor. In the AO condition, the participants watched a video that showed a man walking and were instructed not to imagine anything else. In the AO+MI condition, participants observed the same video and imagined that they were walking alike the person. Spinal reflex amplitudes of AO and AO+MI conditions were normalized to those of the control condition. RESULTS: Spinal reflexes were greater in the TA, SOL, MG, and BF muscles during the AO condition. Also, in the TA, SOL, and MG muscles during the AO+MI condition compared to the control condition. These results showed that AO and AO+MI affected spinal reflexes in the muscles inverted from the lumbar and sacral spinal segments. AO+MI facilitates spinal reflexes in the muscles inverted from the sacral spinal segment, which is farther away from the brain compared to the lumbar spinal segment. A Pearson correlation analysis revealed significant positive correlations of spinal reflexes (% of control) between lower-limb muscles except the BF muscle in the AO condition, and between the lower-leg muscles (TA, SOL, and MG), and between the thigh muscles (VM and BF) in the AO+MI condition. These results showed that modulation patterns of spinal reflexes during AO+MI were different between the lower-leg and thigh muscles and suggested to be similar amongst the muscles inverted from the same spinal segment. CONCLUSION: The present study demonstrates that AO and MI of walking impacts the spinal reflexes in multiple lower-limb muscles inverted from the lumbar and sacral spinal segments. These findings should advance our understanding of the neural mechanisms involving AO and MI of walking, and in combination of both due to its relevance in neurorehabilitation concerning individuals with walking disabilities.

2-C-42 Smaller perturbation-evoked cortical responses are associated with better balance ability in healthy young adults

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Reactive balance recovery invokes hierarchical sensorimotor control, but the nature and role of cortical signals in balance recovery are unclear. Balance recovery behavior begins with an involuntary brainstem-mediated balance-correcting muscle response at ~100ms latency (Carpenter 1999) that can be followed by voluntary actions at longer latencies (Jacobs 2007). During the involuntary phase of balance recovery, EEG recordings have revealed a robust negative peak of activity (N1) over the supplementary motor area, peaking at ~150ms latency (Dietz 1984a/b, 1985a/b)(Marlin 2014)(Mierau 2015). While the processes underlying this balance-evoked cortical N1 are unclear, prior work has shown that it is influenced in amplitude by predictability (Adkin 2006)(Dietz 1985a)(Mochizuki 2008) and perceived threat (Adkin 2008) of a balance disturbance. My recent work shows that cortical responses are larger for shorter subjects, who had greater difficulty responding to the same support-surface perturbation, resulting in more compensatory steps (Payne, pending editorial review of minor revisions). Here, we hypothesized that the amplitude of the cortical N1 response reflects cortical involvement related to the difficulty of the balance task. We therefore predicted that cortical balance responses would be smaller for people with better balance. In 18 healthy young adults (11 female, ages 19-38) we measured the amplitude of the cortical N1 response evoked by 48 backward translational support-surface perturbations of unpredictable timing and amplitude. Perturbations included an easy perturbation magnitude that was identical across all subjects, and moderate and difficult perturbation magnitudes that were normalized to subject height to control for difficulty. To assess balance ability, we measured the distance traversed on a 12 foot beam of 0.5 inch width (Sawers 2015). We found that peak cortical response amplitudes at the Cz electrode 100-200ms after the onset of support-surface perturbations at all perturbation magnitudes were associated with greater distances traveled across the narrow balance beam (p=0.04 for responses to easy perturbations, p=0.03 for moderate perturbations, p=0.01 for difficult perturbations, and p=0.02 when responses were combined across all perturbation magnitudes). This association suggests that individuals may use greater cortical involvement to compensate for less effective involuntary balance control. Alternatively, it is possible that the larger cortical responses reflect greater perceived threat due to lower balance ability, or the greater cortical activation could cause poor balance ability by interfering with automatic balance control.

2-C-43 Speed-accuracy tradeoff in anticipatory postural adjustment for a forward step

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BACKGROUND AND AIM: Although variability is an essential property of motor performance and motor control, limited studies have reported variability and accuracy in postural tasks such as a forward step. Duarte and Latash (2007) measured movement time to step onto small and large targets and observed a speed-accuracy tradeoff relationship was observed in a forward step task. However, they did not separately analyze anticipatory postural adjustment (APA) and the following swing phases. Here, we investigated the movement time and variability of key performance parameters of APA and swing phases when subjects were asked to step as quickly as possible onto targets with different sizes. Two hypotheses were presented: one is the motor control before the take-off, i.e., to reduce the variability of center of mass (CoM) state by taking a long time for APA and the other is the step leg control after the take-off, i.e., to precisely control the foot in the air by taking a long step time. METHODS: Twelve healthy young male participants were asked to make a forward step to locate the foot thumbs at targets placed on the floor. Two target distance (20% and 40% of body height) and two target size (2 cm square and 10 cm square) conditions were made. The participants repeated 40 trials for each condition. Ground reaction forces and 3D motion data were measured. As APA parameters, the location of the center of mass (CoM), the velocity of CoM, and duration of APA were analyzed. As step parameters, time to complete the step and variability in the placement of foot thumbs were analyzed. These parameters were compared between conditions by using a two-way repeated measures ANOVA. RESULTS and DISCUSSION: The participants took a longer time to complete the step task to reduce the variability in the foot placement in the small-target conditions, which is consistent with the speed-accuracy tradeoff principle and the previous findings (Duarte and Latash, 2007). APA duration was longer in the small target condition than in the large target condition (small: 378±24 ms, large: 343±21 ms). The variability in anterior-posterior CoM position at the instance of take-off was smaller in the small target condition comparing with the large target condition (small: 9±2 mm, large: 13±3 mm). These results might be interpreted as a speed-accuracy trade-off in the control of APA. The CoM was located more at the support-foot side at the take-off under the small target condition (small: 44±6 mm, large: 34±4 mm). The shift of the CoM might contribute to the longer swing phase duration (small: 1156±82 ms, large: 1064±69 ms). CONCLUSIONS: Speed-accuracy trade-off was observed in the stepping task when the target size was manipulated. APA parameters were controlled so that the participants could make a slow

and accurate step. ACKNOWLEDGEMENTS: This research was supported by JSPS KAKENHI Grant Number 17H04750.

2-C-44 Sensor-based characterization of gait impairments during activities of daily living

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Advances in the motion capture systems and instrumented force plates have strengthened laboratory-based techniques to study abnormalities in neural control of gait. However, for gait assessments during functional activities of daily living to be effective, more portable technology is needed to interpret the underlying neural control of gait in the context of daily activities that extend beyond the confines of camera line-of-sight or force plate step locations. To achieve this goal, our group has developed and tested a system of body-worn sensors and automated detection algorithms that provide in-field assessment of physiologically relevant characteristics of gait that are of minimal encumbrance to the user and operator. We designed a case study of post medication monitoring among n=6 patients with Parkinson's disease to monitor deviations in neural control of gait (age: 60.8 ± 11 y; Hoehn & Yahr 1-3) during unscripted activities for a 3-hour period in a simulated home setting. Single sensors were placed on the tibialis anterior (TA) muscle of the most symptomatic leg to record the surface electromyography (sEMG) and inertial measurements (IMU) during voluntary movement. Using these data, we designed algorithms to autonomously detect and monitor, in real-time, 3 key characteristics of gait: 1) angular range and speed- to assess kinematics of leg movement; 2) muscle activity- to analyze the muscle activation patterns during different phases of gait cycle; and 3) heel strike and toe-off mechanics- to analyze take-off and landing mechanics of the foot. The automated algorithms were able to successfully detect instances of gait amidst other unscripted activities with 99.5% accuracy from all patients tested. When used to assess instances of gait between medication ON and OFF periods, all three metrics indicated significant differences ($p<0.05$) on per second basis with respect to expert-annotations of video recordings. These results demonstrate the proof-of-concept that a single body-worn sensor system can provide physiologically relevant gait metrics to characterize gait impairments. The impact of real-time, in-field analysis of gait activities expands the interpretation of neural control during functional activities to meet a multitude of health needs that stand to benefit from dynamically tracking natural physiological mechanisms of human movement. Acknowledgements: This work was supported in part by the De Luca Foundation and by a grant from the National Institute of Neurological Disorders and Stroke of the National Institute of Health under award R44NS083098.

2-C-45 Changes in postural synergy due to mechanical knee constraint on an unsteady stance surface

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Background and aim: Previous researches did not pay much attention to the coordination role of the knee joint during human upright stance, on account of a relatively small kinematic movement of the joint even during a stabilometer stance. This study aimed to characterize impacts upon postural synergy due to bracing of bilateral knee joints during a stabilometer stance. Methods: Sixteen young adults maintained 30 seconds upright quiet stance on a stabilometer plate wearing a pair of knee orthoses, either unlocked or locked, to restrict knee motion (the knee constraint (KC) and non-constraint (NC)

conditions). Stabilometer, ankle, knee and hip angular changes were recorded by either inclinometer or electrogoniometers. Constraint-induced changes in postural synergy was highlighted with joint angular velocities directly from derivatives of angular displacements. Principal component analysis (PCA) was used to reduce parametric changes in joint angular velocity in the kinematic chain. Results: More than 95% variance properties of joint angular velocities in the lower limb were explained by the first and second principal components (PC1 and PC2), attributable mainly to ankle angular velocity and combined angular velocity of the knee and hip joints respectively. Knee constraint added to regularity of the stabilometer angular velocity ($p < 0.001$) and PC1 regularity ($p = 0.003$), but reduced PC2 size ($p = 0.008$). Mutual information of the stabilometer angular velocity and PC1 (MISTBV-PC1) ($p = 0.000$) was potentiated with knee constraint. In the KC condition, the size of stabilometer angular velocity correlated positively to PC1 size ($r = 0.863$, $p =0.000$) and negatively to MISTBV-PC1 ($r = - 0.517$, $p =0.004$). In the NC condition, size of stabilometer angular velocity correlated positively to the size of PC1/PC2 ($r = 0.844$, $p =0.000$/ $r = 0.670$, $p =0.005$ respectively). Conclusions: Constraint-induced structural changes in stabilometer movement and PCs, which strongly suggested a substantial role of the knee joint in coordination control during the stabilometer stance. Knee constraint coerces increasing reliance on ankle strategy in maintaining a balanced posture on the stabilometer. The higher velocity coupling of ankle and stabilometer and the smaller ankle velocity, the better stance stability during the stabilometer stance with knee constraint.

2-C-46 Perceptive motor style at rest and during locomotion in humans

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Juan Mantilla and Danping Wang have equally contributed to this work in quality of first author. Humans exhibit various perceptive-motor styles, which reflect their intra- and inter-individual variability when they implement sensorimotor transformations. The different styles raise important questions: to what extent are these differences idiosyncratic and/or detrimental and at what point should they be readjusted to maintain optimal motor control. The perceptive motor style may reveal the onset of a pathological process and can help in following its rehabilitation and recovery. To investigate further how to define the concept, we used Codamotion system to quantify posture at rest and motor control of 18 healthy subjects in four different conditions at walking and running. Our results suggest that in humans, as in quadrupeds, at rest and during locomotion, motor control can be conveniently decomposed into a static component and a dynamic component. These skeletal configurations provide static markers to quantify the perceptive motor style of individuals because they exhibit a large variability among individuals. Also, by using four types of processing, we showed that dynamics were also very variable at both intra- and inter-individual levels during locomotion. Variability increased following a head to toe gradient. These findings led us to select several dynamic markers, which could define, together with the static markers, the perceptive motor style of a person. Finally, previous studies suggested that postural and motor control was sub-served by different neuronal networks in the frontal, sagittal and transversal planes. Our results support this view by showing that the dynamic markers we used to describe locomotion and running could markedly differ by plane of space.

D - Integrative Control of Movement

2-D-47 Haptic and visual information about the to-be-grasped object is integrated in specific parts of the movement planning and execution phases

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Grasping actions toward visuo-haptic objects are more accurate than actions toward visually or haptically sensed objects. However, it is still not clear where does the integration of visual and haptic information that leads to an improved performance occur along the movement: does the integration take place during action planning, action execution or both? In the present study we tackled this question by asking participants to perform grasping actions toward a handheld object without vision (Hfull), with vision provided for the whole duration of the movement (HVfull), or with vision provided only at specific stages of the action. In the latter case, vision could be suddenly removed (HV-) or added (H+) during the movement while haptic information about the target was constantly available. These perturbations occurred at the 5% (immediately after the movement onset) or at the 50% of the movement. Therefore, while in HV- participants had both visual and haptic information during the planning phase and early (but not late) stages of the movement, in H+ vision was available in combination with haptics only after the movement has already started. The analysis showed an overall smaller maximum grip aperture (MGA) in HV compared to H. Interestingly, whereas removing vision in HV- increased the MGA only moderately, adding vision in H+ after movement initiation reduced the MGA considerably, but only when vision was provided already at the earliest stage of the movement execution (5%). The analysis of MGA along the trajectory confirmed that seeing the object since the early stage of the action significantly reduced the MGA, which reached the same level of the HVfull condition. In contrast, while peak velocity was constant across the conditions, the analysis of the velocity profile along the trajectory showed that velocity was affected only when vision was removed or provided at the early stage of the movement. Taken together these results show that, when grasping a handheld object, the availability of visual information is crucial especially during the planning phase and at the early stage of movement execution, specifically, during the first 50% of the hand trajectory. It is within this space window that the sensory information and the motor commands can be best integrated. Indeed, when haptic and visual object information is available at the beginning of the movement, the removal of visual information at the late stage of the action has only minor consequences on the grasping performance. However, the integration of visual and haptic information can occur also once the movement has already started, if vision is provided shortly after the movement onset. Thus, the visuo-haptic integration in grasping that leads to an improvement in performance occurs in only specific parts of the movement, during planning or during the early stage of movement execution.

2-D-48 The reliability of the TMS-conditioned monosynaptic reflex in FCR muscle

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Assessing the excitability of the motor system can provide valuable information about the neurophysiological changes occurring after injury to the CNS or in response to therapy. In order to accurately assess these changes, objective, valid and reliable techniques are of fundamental importance

(Gray et al. 2017). Given this, the primary aim of this study was to establish the intersession reliability of parameters recorded from forearm muscles by using different noninvasive stimulation modalities. Thirteen healthy participants (mean age = 26.07, SD = 3.69, females = 6) were stimulated with either peripheral nerve stimulation (PNS), transcranial magnetic stimulation (TMS), or a combination of the two over three sessions. Electromyography (EMG) activity was recorded from the right flexor carpi radialis muscle in the forearm. Measures of spinal excitability included the maximal motor wave (Mmax) obtained upon stimulation of the median nerve and the monosynaptic reflex evoked at 10% of Mmax (H10%). Corticospinal excitability was assessed by measuring the motor evoked potentials (MEPs) obtained when delivering subthreshold TMS (90%_MT_TMS). Finally, we conditioned the monosynaptic reflex evoked in the FCR muscle by delivering TMS at intervals ranging from -7 to 7 ms from peripheral stimulation. The conditioning pulse significantly increased the amplitude of the monosynaptic reflex ($F_{2.3,23.4} = 12.83$, $P < 0.001$, $\eta p^2 = .56$) when delivered at a range of intervals from the test pulse, including: 1 ms ($P = 0.01$), 3 ms ($P = 0.014$), 5 ms ($P = 0.006$), 7 ms ($P = 0.03$) and 0 ms ($P = 0.012$). We found excellent reliability for Mmax (intraclass correlation coefficient (ICC) = 0.98), H10% of Mmax (ICC = 0.95) and conditioning at 3 ms interval (ICC = 0.83). Reliability dropped at all the other conditioning intervals (ICC ranging from 0.37 to 0.66). MEPs produced by the subthreshold cortical stimulation (90%_MT_TMS) were found to be only moderately stable across sessions (ICC = 0.42). Moreover, we report that the amount of facilitation observed upon conditioning negatively correlated with the baseline H-reflex, with the greatest increases in amplitudes observed when the size of the unconditioned H-reflex was smaller. Our data show that the conditioning effect of cortical stimulation on the monosynaptic reflex demonstrate moderate to excellent reliability over three sessions. The variability often reported both across sessions and participants in the outcome of conditioning the H-reflex with TMS may thereby arise from differences in descending corticospinal activity produced by the conditioning pulse. Measures need to be taken to ensure that the constituent elements of the conditioning protocol (conditioning and test pulses) produce the desired response in the recorded EMG throughout the session. The protocol we implemented can be used to assess changes in the excitability of corticospinal circuits occurring after lesion or novel motor skill learning.

2-D-49 Simultaneous MEG and articulography for the study of speech motor control

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Magnetoencephalography (MEG) recordings can provide detailed spatiotemporal patterns of brain activity that accompany hand and limb movements. However, there are few MEG studies of brain activity during overt speech movements, due to the lack of methods for tracking speech kinematics in the MEG environment, particularly motions of the tongue which requires non line-of-sight methods. We recently developed an MEG-compatible coil tracking system dubbed MASK (Magnetoarticulography for the Assessment of Speech Kinematics) designed to monitor brain activity in parallel with ongoing orofacial and speech movements [1] from up to 12 lightweight coils placed on the head, face and articulators. Here we present preliminary data demonstrating the ability to acquire speech kinematic data simultaneously with brain activity. Four healthy adults (aged 18-35) produces non-verbal utterances (lip smack), simple verbal utterances (/pa/), and complex verbal utterances (/pataka/). MEG

data were measured in a magnetically shielded room using a 160-channel whole head MEG system (Kanazawa Institute of Technology) simultaneously with kinematic data recorded from coils placed on the midline of the lips, lower jaw, tongue tip and tongue dorsum. Kinematic data were also collected in the same subjects using a commercial Electromagnetic MagnetoArticulography (EMA) system (WAVE, Northern Digital Inc, Waterloo, ON, Canada). The MASK system tracked orofacial movements at near EMA-resolution at rates up to 50 cm/s with less than 1 mm relative position error. MEG source analysis time-locked to the onset of each utterance revealed modulation of mu (8-12 Hz) and beta (15-25 Hz) rhythms in the ventral sensorimotor cortex, as well as a transient burst of high-frequency gamma (60-80 Hz) activity shortly after movement onset. We also observed co-activation of the dorsal (hand area) motor cortex confirming previous reports [2] that multiple regions of the sensorimotor cortex are activated during speech. These results show that detailed dynamics of the speech articulators can be directly and precisely related to measurements of brain activity obtained in the same experiment setup, providing a new approach to understanding the neural control of speech. We will also present pilot measurements from a second-generation MASK device currently under construction, with increased channel capacity and real-time visual display of speech movements. Supported by grants from the Australian Research Council (DP170102407) and Natural Sciences and Engineering Research of Canada (CPG-104310). [1] Alves N., Jobst C., Hotze F., Ferrari P., Lalancette M., Chau T., Van Lieshout P., Cheyne, D. (2016) An MEG compatible system for the measurement of orofacial kinematics: The MASK system. IEEE Trans Biomed Eng 63: 1709-1717. [2] Saarinen, T., Laaksonen, H., Parviainen, T., Salmelin, R. (2006) Motor cortex dynamics in visuomotor production of speech and non-speech mouth movements. Cereb Cortex 16, 212-222.

2-D-50 Inter-individual variability and predictability of throwing actions

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Overarm throwing is a fundamental human motor skill, involving complex whole-body motions. Skills as throwing involving many degrees-of-freedom may allow for multiple solutions and different individual strategies which may differ in their predictability. We aimed at characterizing how the predictability of a throwing action is related to the individual strategy and whether individual style affects catching performance. In a first experiment, we recorded whole-body kinematics from twenty non-expert participants performing unconstrained overarm throws at four different targets placed on a vertical plane. Throwing actions differed considerably across individuals and were classified into one of four typical styles using a low-dimensional representation of whole-body kinematics. To characterize the spatiotemporal structure of the information embedded in the kinematics of the throwing action about the outgoing ball direction, we performed a linear discriminant analysis on different body markers at different time intervals. For most participants it was possible to predict the direction of throw with an accuracy above 80%, as early as 400-500 ms before ball release. The spatiotemporal structure of throw direction predictability differed across individuals. The body parts that provided the most informative cues about throw direction varied across individuals and during the time course of the throwing action. To test whether the style of a throwing action affects catching performance, in a second experiment we recorded wrist movements of eight non-expert participants intercepting virtual throws while wearing a head-mounted display. The balls were projected by a human avatar animated according to the whole-

body kinematics captured in the first experiment from four subjects, each using a different style. Spatial interception errors were significantly smaller when the participants could see the throwing action in addition to the ball flight, indicating that they could extract throwing action information to improve their interceptive performance. Importantly, interception error differed significantly across individual throwers. In sum, these results suggest that throwing style affects catching performance because of the different spatiotemporal structure of predictive information available in whole-body kinematics characteristic of each style.

2-D-51 Representation of rotational and translational vestibular information in the human brain

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Vestibular information is a crucial source of information to sense our bodily state in the environment, and to adaptively control our body in the environment. Rotation of head movement, as well as translation of head movement is detected by the vestibular organs. However, where and how they are represented in the human brain is still unclear. Since these self-motions can co-exist independently (i.e. feeling the roll rotation while moving forward), we predicted that rotation and translation motions are independently represented in the brain, within the fronto-parietal vestibular network. Here we combined methods for eliciting virtual head motion sensations (rotation and translation) with fMRI to identify brain areas representing head rotation and translation. A four-pole Galvanic Vestibular Stimulation (GVS) was used in the fMRI scanner (n=16) to stimulate the vestibular organs and evoke virtual left-right roll rotation and forward-back translation sensations. In particular, the electrical current passing between the mastoids electrodes activates the vestibular organs inducing a perception of left-right head roll sensation, while the current passing between mastoids and temples evoked a forward-backward head translation sensation. To control for non-specific transcutaneous effects of GVS, we delivered a sham stimulation by placing two electrodes at the base of the neck, which does not induce any movement sensation. Voxel by voxel univariate analysis revealed GVS induced activations in the bilateral inferior parietal, premotor/anterior insula and prefrontal cortices. These areas are known to receive direct projections from the vestibular organs through vestibular nucleus. Furthermore, using a multi-voxel-pattern classification analysis, we show that the parietal regions reliably possess information about the four types of virtual head motions (left-right roll and forward-back translation). The described pattern of brain responses was vestibular input specific; such results were absent in sham stimulation condition. Finally, when the head roll and translation sensations were induced simultaneously, the activity pattern in the parietal regions were well described by the weighted sum of the sole roll and translation GVS induced brain activity patterns. Our study demonstrates that roll and translation form independent representation within the cortical vestibular network in the parietal regions.

2-D-52 Early developmental change in inter-muscle sensorimotor modules of human infants: Preliminary results

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Various human behaviors that use a small set of motor modules involving coordinated muscle activities have been reported. It is often assumed that some of these modules are acquired and augmented through sensorimotor experiences in the early developmental phase. However, whether and how a human infant acquires and augments these types of motor modules remains unclear. In this study, we collected detailed whole-body motion data from neonates and infants, and investigated the changes in the inter-muscle sensorimotor modules using musculoskeletal dynamic simulation. We first conducted a full-body motion capture of the spontaneous movements of 10 neonates (within seven days after birth) and 10 infants (3-months-old) with 12 infrared cameras. After obtaining the 12 joint movements with 20 degree-of-freedom through inverse kinematics, a total of 151 muscle activities and proprioceptive sensory inputs were estimated by a musculoskeletal dynamic simulation. Next, we quantified the sensorimotor interaction by calculating the information flow between all muscle pairs of muscle activities and proprioceptive sensory inputs using the Granger causality. Finally, we characterized the infantile sensorimotor modules among muscle activities and proprioceptive sensory inputs based on a network analysis. The maximum modularity was estimated with bootstrapping for the following three types of networks: i) among motor activities (MM-net), ii) among proprioceptive sensory inputs (SS-net), and iii) between motor activities and proprioceptive sensory inputs (SM-net). We consequently demonstrated that the infants had a significantly lower modularity than that of the neonates for all networks, and that the developmental changes varied from network to network (the comparisons between neonates vs infants were as follows, $p < 0.01$: MM-net 0.2 vs 0.06; SS-net 0.25 vs 0.21; and SM-net 0.24 vs 0.14). By combining the measured kinematics and musculoskeletal dynamic simulation, we quantified the infantile sensorimotor modules among muscle activities and proprioceptive sensory feedback during spontaneous movements. Our results demonstrated a developmental reduction in the modularity of the sensorimotor interaction, which is consistent with previous research that suggests the argumentation of motor modules in the early developmental phase.

2-D-53 Cortical local field potential control of epidural spinal stimulation for restoring forelimb movement after spinal cord injury

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In this study, we introduce a novel reanimation approach to restore voluntary control of forelimb function after spinal cord injury (SCI) via an artificial connection from the brain to the spinal cord. This approach includes recording from multi-channel intracortical electrodes and using a computational model to extract the intention to move the forelimb. This intention to move can then be used to control stimulation of electrodes on the spinal cord. To accelerate clinical translation, we deliberately selected both recording and stimulation methods with potential for near-term use in human subjects. This included intracortical Local Field Potentials (LFP) that provide more stable movement-related information and requires less power for hardware implementation compared to single unit spike sorting and decoding. We selected epidural stimulation of the spinal cord surface as it is clinically feasible and evokes fatigue-resistant contractions and synergistic movements. After animals were trained to press a lever for liquid reward, we used a Canonical Correlation Analysis (CCA) filter to predict the animals' movement intention from LFPs recorded on 16 electrodes in the forelimb region of primary motor cortex. After several weeks of cortical recording, the animals received a lateralized contusion on the right side of spinal segment C4 and an epidural implant on the right side of spinal segment C6. We then decoded motor intention from the recorded LFPs to continuously control the amplitude of epidural stimulation delivered to the spinal cord below the injury. When the stimulation was on, the animals produced robust and graded movements. With stimulation off, the LFP decoder output still predicted the forelimb movements, but the animal could not push the lever to obtain the reward. This system demonstrates that LFP-controlled epidural spinal stimulation can reanimate volitional forelimb movement in rats with spinal cord injury. The electrical stimulation artifact was managed by removal of 2ms of signal after stimulation using a sample-and-hold approach, which permitted robust decoding performance. To our knowledge, this is the first study that demonstrates the effectiveness of closed-loop continuous control of epidural spinal cord stimulation based on recorded LFP signals. LFP decoding required reduced experimenter input compared to spike-sorting and provided remarkably stable decoding performance across days without re-fitting the model. These are substantial benefits as we move toward implantable systems for clinical use.

2-D-54 Invasive Brain-Computer Interface for avatar arm control in virtual reality using a deep learning decoder framework

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Brain-Computer Interfaces (BCI) for rehabilitation of severely paralyzed patients have been used in several clinical trials. Usually an extracorporeal device, like a robot arm, is used as the effector of the system. For safety reasons robotic arms have to be placed in some distance to the patient and even if the robot arms are anthropomorphic it is clear to the user that they are external devices. Neural control strategies for the natural arm and the extracorporeal device could therefor differ significantly. To overcome this problem we are developing a virtual reality (VR) environment in which the patient will control the arm of an avatar, a digital representation of their body, instead of an external device. In a later step we want to use the neural signals to control a custom made upper-body soft exoskeleton which will move the patient's actual limbs. The lightweight and flexible exoskeleton will also be used for rehabilitation purposes with patients that suffer from arm and hand movement disorders. Another important part of our BCI system is the utilization of deep learning neural networks for decoding the intended movements from single unit and local field potentials. We have some first results for fully automatic unit detection which is a prerequisite for a fully autonomous decoding pipeline. Our neuron classifier has a high accuracy when used on offline data and we are in the process of making it usable in online mode as well. Similar to a human expert the spike classifier is not considering a single waveform for classification but a batch of waveforms which provide a context for comparison. The spike classifier shows a very high accuracy and can be used on neural data from multiple subjects and recording technologies once it is trained. We envision that our VR approach combined with deep learning will further improve the progress that has been made in the field of neuroprosthetics.

2-D-55 A comparison of neuronal activity between the dorsal premotor area and the pre-supplementary motor area in primates during a two-movement sequence task

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According to Lashley, serial actions are not just a chain of actions but coordinated actions. Indeed, both the medial motor areas [supplementary motor area (SMA) and the pre-SMA] and the dorsal premotor area (PMd; one of the lateral motor areas) contribute to the performance of memory-guided motor sequences. However, it remains unclear how the medial and lateral motor areas coordinate with each other to organize actions in an appropriate temporal order. To answer this question, we attempted to record single-unit activity in both the pre-SMA and PMd and compare timing and context-dependency of motor representations between these areas, while the animals performed a sequential motor task. Specifically, we trained two Japanese monkeys to memorize and perform multiple motor sequences consisting of two motor elements with an intervening delay. Each motor element could be one of four possible movements (left forearm supination or pronation, right forearm supination or pronation). The motor sequences were categorized into repetition sequences and non-repetition ones according to whether the two elements were identical or not. We found two major groups of neurons in both areas: (1) execution-related neurons whose activity was selective for the forthcoming motor element and (2) second-element selective neurons whose activity was exclusively selective for the second element. In this study, we focused on the second-element selective neurons and found differences in activity patterns between the PMd and pre-SMA. Specifically, the PMd neurons began their activities even before the first movement and the activities were persistent. In contrast, activities of neurons in the pre-SMA were generally phasic around the onset of the first movement and context dependent. Next, we examined the relationship between neural activities and the task performance. According to our behavioral analysis for error trials, the monkeys often performed the second element prematurely instead of the first one when a non-repetition sequence was instructed (replacement error). These errors implicate that the plan for the second motor element conflicts with that for the first. At a single-unit level, the pre-SMA neurons showed distinct activity in the non-repetition sequences while the activity was attenuated in the repetition sequence. Such context dependency was not observed in the PMd neurons. The firing rate of second-element selective neurons prior to the first element allowed us to predict the performance of the ongoing trial. These results suggest that the PMd persistently holds a motor plan specifying the second element until the movement is executed, whereas activity in the pre-SMA may suppress conflicting motor plan and/or aid to switch actions.

2-D-56 A communication subspace isolates population-level interactions between motor and somatosensory cortex

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During the control of reaching, motor commands are integrated with ascending sensory feedback to enable robust movements. Yet, it remains unclear how this integration is achieved across the sensorimotor cortical areas. Isolating cortical activity related to ongoing motor commands from the sensory-related signals within sensorimotor cortical areas will help us to understand the neural control of movement. Recent advances have shown how "subspaces" that capture population-level patterns of neural covariation can mediate specific functions, such as motor planning or adaptation. We hypothesized that interactions between primary motor (M1) and somatosensory (S1) cortex - such as efference copy to S1 or reafference to M1 - are captured at a population level within a "communication subspace" that is isolated from the other inputs to and outputs from these regions. We trained two monkeys to reach for, grasp and pull an object placed in different locations while we recorded limb kinematics, pulling force, and the activity of neural populations in M1 and area 2 of S1. We sought to identify a putative communication subspace within the M1 and S1 populations that could account for shared information between the regions. Using Principal Components Analysis, we identified a low-dimensional manifold within each region capturing the majority of neural variance. Since the communication between these regions is only a subset of the functions performed by each, expected the communication between them to be lower-dimensional than the full population activity. We thus used Reduced Rank Regression to identify subspaces of these M1 and S1 manifolds that were robustly linked by a linear mapping. These highly correlated components of M1 and S1 comprised the communication subspaces, while the remaining independent (orthogonal) components were the M1 and S1 "null subspaces". We then explored the roles of these subspaces during movement. Our hypothesis predicts that the communication subspace will reflect activity that has undergone some amount of cortical processing by M1 or S1. In contrast, the null subspaces will capture activity that most directly relates to the produced behavior - e.g., the descending commands to the spinal cord or sensory feedback from the limb. To test these predictions, we used linear regression to reconstruct limb kinematics from the activity of the communication subspace or null subspaces of M1 and S1. For both regions, we found that the communication subspace was a poor predictor of behavior when using the linear regression, while the null subspaces provided higher accuracy. These results indicate that population level interactions between M1 and S1 can be isolated from other features of the population, which may include inputs from, or outputs to, spinal circuits. This method could help us to understand rapid sensorimotor integration for feedback control, and enable robust decoding for brain computer interfaces.

2-D-57 Towards understanding the role of task-related sensory information in motor cortex during object interaction

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The ability to decode and leverage motor intent from cortical activity has dramatically improved since the introduction of early brain machine interfaces (BMIs). However, to control neuromotor prostheses in use today, the user must rely solely on visual feedback. In contrast, natural motor control integrates vision, proprioception, somatosensation, and other sensory inputs to generate and update a precise motor plan. Visual input alone is particularly insufficient during object manipulation. For example, information an object's weight, compliance, and texture, which cannot be determined through visual inspection alone, enables facile use of an object. To better understand how somatosensory feedback is used in the brain during motor control, we trained a nonhuman primate to perform a tactile object manipulation task. The animal was required to grasp a rotating manipulandum programed to spin at a velocity proportional to the applied pressure. Each trial, a different "target pressure" caused the manipulandum to stop rotating. A reward was delivered if the animal successfully detected this cue and held the target pressure for 300ms. In this way, the task required that the animal integrate a sensory input (manipulandum rotation) with its motor target (grip pressure). Additionally, the task was performed by the animal in its home environment. The task apparatus was designed to mount to the enclosure and an automated reward system was implemented to detect successful completion of a trial and deliver a juice reward. By implementing this in-cage paradigm, the animal could perform the task ad libitum allowing multi-hour, high throughput experimentation. Wireless neural transmitters were used to stream neural data from two implanted microelectrode arrays from inside the enclosure. One array was implanted in hand area of primary motor cortex and the other in finger area of primary sensory cortex to observe neural activity during the task. By directly attempting to decode the applied pressure from motor cortex we aimed to understand if a simple state-based "squeeze" or "hold" strategy was being employed or if intermediate output pressures were also being encoded. In addition, we searched for evidence that task related sensory specific information was present in motor cortex. By observing trials where a given pressure output was associated with different manipulandum rotational velocities, these two variables could be isolated and assessed separately within the neural data. Measuring the torque applied to the task's motor, allowed a metric of coefficient of friction to be additionally calculated and thus also correlated with the neural signals. In future work, we plan to stimulate sensory cortex to elicit artificial sensory percepts. Using biases in the animal's task performance as well as the trained sensory decoder in motor cortex as guides, stimulation parameters would be adjusted to best approximate the physiological perception of object rotation.

2-D-58 Motor cortex is an input-dependent dynamical system controlling dexterous movement

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Skillful control of movement is central to our ability to sense and manipulate the world. A large body of work in nonhuman primates has demonstrated that motor cortex provides flexible, time-varying activity patterns that control the arm during reaching and grasping. Previous studies have suggested that these patterns may be generated by strong local recurrent dynamics operating autonomously from inputs during movement execution. An alternative possibility is that motor cortex requires coordination with upstream brain regions throughout the entire movement in order to yield these patterns. Here, we developed an experimental preparation in the mouse to directly test these possibilities using optogenetics and electrophysiology during a skilled reach-to-grab-to-eat task. To validate this preparation, we first established that a specific, time-varying pattern of motor cortical activity was required to produce coordinated movement. Next, in order to disentangle the contribution of local recurrent motor cortical dynamics from external input, we optogenetically held the recurrent contribution constant, then observed how motor cortical activity recovered following the end of this perturbation. Both the neural responses and hand trajectory varied from trial to trial, and this variability reflected variability in external inputs. To directly probe the role of these inputs, we used optogenetics to perturb activity in the thalamus. Thalamic perturbation at the start of the trial prevented movement initiation, and perturbation at any stage of the movement prevented progression of the hand to the target; this demonstrates that input is required throughout the movement. By comparing motor cortical activity with and without thalamic perturbation, we were able to estimate the effects of external inputs on motor cortical population activity. Thus, unlike pattern-generating circuits that are local and autonomous, such as those in the spinal cord that generate left-right alternation during locomotion, the pattern generator for reaching and grasping is distributed across multiple, strongly-interacting brain regions.

2-D-59 Is the manual following response an attempt to compensate for inferred self-motion?

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When making a fast goal-directed hand movement, one can adjust this movement to changes in visual information. For instance, one can adjust the movement when the target moves. If the background of a visual target starts to move, the hand also responds and moves along with it. This latter behavior is known as the 'manual following response'. Background motion induces postural responses as well, to compensate for inferred self-motion. One explanation for the manual following response is that it is a compensation for this inferred self-motion. If this explanation is correct, other modalities signaling self-motion should have similar effects. We tested this by inducing apparent self-motion by galvanic vestibular stimulation. To test whether compensation for inferred self-motion is indeed responsible for the manual following response, we compared the responses to galvanic stimulation with responses to background motion. If the manual following response is a consequence of attempting to keep the hand on its trajectory during self-motion, inducing apparent self-motion in a visual or vestibular manner should influence hand movements. Standing participants tried to quickly tap on targets that we presented on a horizontal screen. On some trials, either galvanic stimulation or background motion induced apparent self-motion during the hand movement. We chose the stimulation strength such that the head responded in a similar manner to both types of perturbations. It took both the head and hand 50 ms longer to respond to background motion than to galvanic stimulation. The hand followed the background motion but was almost unaffected by the galvanic stimulation. We conclude that the manual response to background motion is not a direct consequence of trying to compensate for self-motion. The manual following response might be a consequence of an error in binding motion information to objects.

2-D-60 Exploring the limits of central pattern generators in quadruped locomotion using a musculoskeletal simulation model of mice

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Locomotion is due to the interplay of central pattern generators (CPGs), reflexes, musculoskeletal properties and descending modulation. In particular the interplay between CPG and reflexes are complex and difficult to investigate, and numerical models can help. In this abstract we focus specifically on using neuromuscular models to explore the role of CPG in locomotion. There have been several crucial findings in the literature regarding the neural circuits in- volved in producing feed-forward locomotor activity. One of the challenges has been to test these findings in a realistic model environment. The main reason being the lack of availability of neuromuscular simulation models. While there are many models available for humans, there almost none for quadrupeds. Currently we are developing a detailed three dimensional musculoskeletal simulation model of a mouse. The skeletal system of the model is made up of one hundred and eight degrees of freedom. But for the purpose of locomotion only the degrees freedom in fore limb and hind limb are made free while the rest are constrained to be fixed. The model used for locomotion study consists of sixteen degrees of freedom. The spine can have passive compliance to reflect the highly flexible spine in real mice. The free joints in the fore and hind limbs are actuated by hill-type muscles. Using the model described above, we are developing central pattern genera- tor circuits to produce different locomotion gaits. Central pattern generators are modeled based on the half-center model hypothesis. Each neuron in the CPG is modeled as a leaky-integrate and fire neuron with additional current channels. The model allows us to produce oscillations based on the mutual coupling be- tween two individual units, which makes up one oscillator. Individual oscillators influence a pair of antagonist muscles acting on a joint in each limb to produce flexion and extension movements. Every joint in the hind and fore limbs are actuated by separate oscillators. The individual oscillators are mutually con- nected to each other based on the nearest neighbor criteria. The parameters of the network are explored using evolutionary optimization techniques to produce different stable gait types. The model along with CPG will be subjected to several perturbations. Per- turbations include locomotion uneven terrains, random external forces applied on to the model during locomotion and addition of internal noise on to the muscle activation's. These conditions will allow us to systematically explore the different conditions under which CPGs perform well and conditions under which they do not.

2-D-61 Population dynamics in primary motor cortex during locomotion and obstacle avoidance

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Primary motor cortex (M1) is necessary in primates for generating precise, voluntary actions. However, the involvement of M1 during locomotion, which may not require online cognitive effort, as well as how M1 integrates voluntary actions onto ongoing locomotor rhythms, such as during obstacle avoidance, is not well understood. It has been postulated that voluntary limb movements like reaching and grasping may have evolved out of precise gait modifications during locomotion. To investigate the relationship between M1 activity during locomotion and the activity during directed, volitional actions, we employed an obstacle avoidance paradigm which requires the generation of directed limb movements both from rest as well as during locomotion. We recorded leg-M1 and arm-M1 activity with implanted microelectrode arrays from nonhuman primates (Rhesus Macaque) while the animals performed basic walking on a treadmill at 2.2 km/h ("autonomous" locomotion), stepping over an obstacle moving towards them at 2.2 km/h while stationary (volitional movements), and stepping over the obstacle while walking on the treadmill (integration and transition of states). To compare the cortical activity on a population level, we utilized a Poisson linear dynamical system (PLDS) model to explicitly extract the neural dynamics from recorded neurons. Low-dimensional trajectories in the latent state-space revealed similar rotational structure for both basic locomotion and stationary obstacle avoidance, despite the absence of rhythmicity in the obstacle avoidance movements. However, the neural trajectories also appear to separate along a dimension orthogonal to the rotational plane. During obstacle avoidance while walking, the neural latent state smoothly transitioned from the putative autonomous region to the putative volitional region while maintaining its rotational structure. These findings suggest that for voluntary movements and autonomous locomotion, rotational dynamics are conserved in motor cortex, but additional dimensions distinguishes the population activity between the two movement modalities.

2-D-62 The effect of individual traits on unintentional errors in skilled movement

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Clinical and neurophysiological studies have revealed that some psychiatric disorders affect motor systems. For example, the malfunction of forward model and monitoring function in schizophrenic patients and inefficient inhibition of motor control in ADHD patients have been considered to contribute to typical symptoms of each disease. Although a lot of evidence has shown that motor functions are influenced by various individual traits, there is still room for investigation how psychiatric traits that varies in healthy individuals affect motor control. Unintentional error that occur in voluntary movements is a key to reveal the mechanisms of motor function, because it provides information how intact motor execution process could be disturbed. The present study then aimed to reveal the relationship between individual traits and control of voluntary movements by analyzing unintentional errors in skilled motor sequences. Previous studies proposed that error in action sequences occurs when motor representations of intended action and several distinct related actions are simultaneously activated and incorrect one is triggered. Here we hypothesized that higher psychiatric tendency in healthy young adults accelerates the occurrence of unintentional error in skilled voluntary movement. To investigate unintentional errors in skilled movement in a laboratory setting, we experimentally induced slips of the pen using a method called Rapid Repeated Writing (RRW). RRW requires participants to write one character repeatedly as fast as possible for a few minutes. During RRW, some people mistakenly write different characters from what they intend to write. In the experiment, 41 participants performed a two-minute RRW task of one Hiragana character for five trials. To assess schizotypal and ADHD tendency, we used the Japanese version of the schizotypal personality questionnaire (SPQ) and Adult Self-Report Scale for ADHD (ASRS). SPQ has three subscales: Cognitive-Perceptual, Interpersonal, and Disorganization factors. ASRS has two subscales: Inattention and Hyperactivity/ Impulsivity factors. Result of the RRW task showed that slips of the pen occurred in 17 participants (41.5%). Correlation analysis showed a moderate positive correlation between the number of slips of the pen and SPQ score in the 17 participants ($r=0.50$, $t(15)= 2.24$, $p<.05$). The result suggested that individual traits in psychiatric tendency affect motor control of skilled movements. The present study suggested the possibility that the accuracy of the execution of skilled movements reflects individual differences in predictive motor control and monitoring system.

2-D-105 Neurophysiological mechanism underlying cervical transcutaneous spinal cord stimulation in humans

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Transcutaneous spinal cord stimulation (tSCS) can be used to evoke reflex responses of the lower-limb muscles, while neuromodulatory approaches can restore lower-limb sensorimotor function during spinal stimulation. Recently, remarkable recovery of the upper limb sensorimotor function during cervical spinal stimulation was demonstrated. Therefore, in this study, we evoked responses in the upper-limb muscles using cervical tSCS, with the aim to elucidate the neural mechanisms underlying the effects of tSCS of the cervical spine. Specifically, we hypothesized that cervical tSCS can be used to selectively activate the sensory route entering the spinal cord which transsynaptically converges on upper limb motor pools. The experiments were conducted on 10 healthy volunteers. To evoke spinal responses, a constant current electrical stimulator was used to apply monophasic pulses of 2 ms pulse width and stimulation amplitudes ranging from 50 to 90 mA. Participants remained at rest in the supine position for the duration of the experiment with both upper limbs resting on the bed alongside of the body. Four experimental protocols were evaluated: (1) double-pulse stimulation (DPS) - two stimulation pulses with 50 ms inter-stimulus interval were delivered and responses to the first and second stimulus compared; (2) passive muscle stretching - the wrist joint was extended manually by the experimenter to approximately 70o from the neutral position to apply a strong muscle stretch of the wrist flexors (i.e., FCR muscle) while participants remained at rest; (3) active grasping - participants were asked to produce an isometric grasp force set at 20% of their maximal effort and displayed on an oscilloscope, as fast as possible in response to an audio signal; and (4) muscle-tendon vibration - a constant vibration was applied on the palmar carpal ligament (i.e., wrist flexor). Control responses for the stretching, grasping, and vibration protocols were evoked prior to performing each condition while participants were at rest. Our results demonstrated significant inhibition of the second evoked response during DPS, inhibition of responses during passive muscle stretching and muscle-tendon vibration, and facilitation during voluntary muscle contraction (active grasping), which share similarities with responses evoked during lumbosacral tSCS in the lower-limbs. These results suggest reflexive nature of the evoked responses and that motoneuron excitability facilitated the evoked spinal responses. Overall, our work demonstrates the utility and sensitivity of cervical tSCS to engage the sensory pathway projecting to the upper limbs, demonstrating the utility and sensitivity of cervical spinal stimulation for electrophysiological assessments and neurorehabilitation.

E – Disorders of Motor Control

2-E-63 Patterns of oculomotor abnormalities in mild TBI

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Mild traumatic brain injury (mTBI) can result in significant problems affecting vision, vergence eye movements (Magone et al., 2014; Suhr et al., 2015), spatial orientation, movement, and balance (Hoffer et al., 2007; Hoffer et al., 2010), These issues can result in problems with gaze control, eye-head-coordination, and visual-motor transformations underlying goal-directed movements. This can occur after multiple head trauma events, and in some cases after a single mild TBI event. Also, there is evidence that symptoms can manifest years after the original trauma and become progressively worse over time. Effects of the natural aging processes probably interact with the pathophysiology resulting from TBI. This ongoing research is part of an effort to evaluate eye movements (saccades and pursuit eye tracking) during binocular viewing in mTBI. The general aim is to characterize the coordinated movement of the two eyes during changes in gaze in response to object movement (e.g., during saccades and visual pursuit of an object in three dimensional space) and during attempted visual fixation when there is head movement, to compare the eye velocity profiles of the two eyes in the presence of convergence, and to relate the velocity trajectories of the two eyes to vergence dysfunction in mTBI. For this presentation, the horizontal/vertical position and velocity of the left eye versus the right eye is being analyzed. Saccade targets are presented 5 to 25 degrees left/right of center and 5 to 15 degrees above/below center. Sinusoidal pursuit targets have 10 degree amplitudes at 0.15 to 0.60 Hz. For large saccade amplitudes there can be different velocities for the adducting eye versus the abducting eye in mTBI subjects who have convergence insufficiency or convergence excess. Furthermore, there can be a

velocity asymmetry for rightward versus leftward saccades and for upward versus downward pursuit. The preliminary results have identified eye velocity patterns that show promise for characterizing binocular eye movements and pursuit asymmetries in mTBI. Further work will evaluate gaze in three dimensions where there are changes in vergence. The results could provide further insight into the underlying pathophysiology affecting the control of gaze in mTBI and suggest possibilities for evaluating vision therapy.

2-E-64 Changes in the relations between postural control, eye movements and cognitive involvement related to the effects of Parkinson's disease and age

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Patients with Parkinson's disease (PD) and older adults exhibit reduced levels of synergy in both eye and body movements. Our first goal was to test PD- and age-related impairments in synergies between i) eye movements and ii) center of pressure (COP) and body (head, neck, lower back) movements. Our second goal was to test PD- and age-related impairments in the cognitive involvement associated with these aforementioned synergies between eye and COP/body movements (i.e. eye-COP/body synergies). Twenty patients (59.65 years±8.31; on-drug), twenty controls (60.95 ± 6.78 years) and twenty young adults (21.85 years±2.30) performed two visual tasks projected onto a large visual display (100°). In the free-viewing task, all the participants randomly looked at images of house rooms. In the search task, they had to locate five target objects in each image. COP, head, neck, lower back and eye movements were recorded in synchrony during each trial. The cognitive involvement was recorded after each task with a multidimensional subjective questionnaire. In the search task, significant negative Pearson eye-COP/body correlations were expected to be stronger in young adults than in older adults and to be largely weaker or inexistent in patients with PD (Hypothesis 1). The negative Pearson eye-COP/body correlations were assumed to be functional in showing that individuals reduce their COP/body movement when larger fixations need to be performed. These previous significant findings were expected to disappear when the influence of the cognitive involvement was controlled (in partial correlations, Hypothesis 2). Such a result was expected to show that functional - or synergistic - relations between eye-COP/body movements require a higher cognitive involvement. The free-viewing task only served as a control task, i.e. no significant eye-COP/body correlations were expected in such a task. As expected, the patients did not exhibit any significant negative, functional, eye-COP/body correlations in searching while the young adults mostly showed these negative correlations (90.6 % of the time) in this task. Unexpectedly, both older adults and patients with PD showed positive eye-COP/body correlations in searching. The patients with PD engaged their eye-COP/body correlations in destabilizing relations even more than the controls. The results also showed that 88 % of the aforementioned significant correlations were related to a higher cognitive involvement in the patients with PD and only 40-45 % of the time in older and younger adults. In brief, older adults and even more patients with PD increased their cognitive involvement to engage destabilizing eye-COP/body relations instead of using synergistic relations as younger adults did. These PD- and age-related changes in eye-COP/body relations may be due to a reduction of complexity in the triple relations vision-posture-cognition. Our novel, synergistic analyses were powerful to show these contrasted results.

2-E-65 Multiple causes of pathological oscillations related to ataxia in mouse cerebellum

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Since the emergence of 160 Hz local field potential oscillations (LFPO) in the cerebellum of mice deficient in calcium binding proteins, similar pathological LFPO were recorded in mouse models of Angelman and fetal alcohol syndrome, in Duchenne muscular dystrophy (MDX mice) and in myotonic dystrophy (DM1 mice). In all of these conditions ataxia was one of the common behavioural outcome. The Purkinje cells (PC) are in all of these pathological conditions the principal actor responsible of the fast LFPO emergence ranging from 160 to 200 Hz. We here analysed the different mechanisms responsible of these rhythmic abnormalities. Among these, the contribution of the granular cells in the absence of calretinin was firstly identified as providing an increase of parallel fiber excitation of the PC. It was demonstrated that the rescue of calretinin in the granular cells renormalized these abnormalities. As the 160 Hz LFPO was blocked by microinjection of gabazine and carbenoxolone in the Angelman mice, we may respectively proposed that the inhibitory synapses of molecular interneurons and PC collaterals and the gap junctions are key elements for the generation of the fast LFPO. The disruption of the GABAA receptors clustering at PC postsynaptic densities reported in MDX mice can leads to a decreased inhibitory input to the PC which is also responsible of the fast LFPO. In addition, we demonstrated that the presence of a 200 Hz LFPO and related ataxia in DM1 mice was explained by the existence of a marked RNA toxicity of the cerebellar Bergmann glia accompanied by a downregulation of the GLT1 causing PC hyperexcitability and glutamate neurotoxicity. This pathological situation (ataxia, PC firing, fast LFPO and excitotoxicity) were rescued by ceftriaxone injections upregulating the GLT1. The fact that the output of the cerebellum (except for the vestibular-prepositus nuclei) is assumed by the deep cerebellar nuclei (DCN) neurons it must be proved that the PC firing and LFPO abnormalities are transmitted to the DCN. For this, we studied in transgenic mice presenting a selective deletion of the BK channel in PC (BK-PC−/−), the signal transmission between the PC and the DCN. The latter in turn inhibit inferior olive nucleus, closing a positive feedback loop via the climbing fibers. Using multiple-unit recordings and antidromic neuronal identification in alert mice we found that the beta-range (15 Hz) bursting pattern and abnormal PC rhythmicity are transmitted to DCN with no effect on their mean firing frequency. In the same time, the intra-burst complex spike spikelets frequency was increased without modification of the mean complex spike frequency in BK-PC−/− mice. We argue that the ataxia present in these conditional knockout mice could be explained by rhythmic disruptions transmitted from mutant PC to DCN but not by rate code modification only. This suggests a neuronal mechanism for ataxia with possible implications for human disease.

2-E-66 Pre-movement excitability in post-stroke fatigue

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We have previously shown that resting motor cortex excitability is reduced in stroke patients with high severity of fatigue and suggest that this might be a reflection of reduced sensory attenuation. When preparing for an upcoming movement, one can predict the sensory consequences of one's own actions. These sensory predictions together with the ability to attend away from the resulting prediction errors (sensory attenuation), are a key feature of the active inference framework of sensorimotor control.

Motor cortex excitability and sensory attenuation are both dynamically modulated during movement preparation, before the onset of voluntary movement. Movement preparation has been studied extensively using reaction time tasks in which a delay separates an instruction stimulus from a subsequent "GO" cue. In humans, motor cortex excitability, assessed using Transcranial Magnetic Stimulation (TMS), is transiently suppressed during the delay period and then increases progressively after the "GO" cue before the onset of voluntary movement. Indeed, multiple sclerosis (MS) patients with fatigue show reduced pre-movement facilitation when compared to MS patients without fatigue and healthy subjects. By measuring motor cortex excitability using TMS during a simple warned reaction time task in stroke patients with varying severity of fatigue, I set out to answer the following question: does pre-movement motor cortex excitability change as a function of fatigue in stroke patients? Preliminary results suggest that high fatigue stroke patients show reduced modulation of motor cortex excitability during movement preparation when compared to low fatigue stroke patients. Those with reduced modulation motor cortex excitability during movement preparation also showed more variable reaction times. These results suggest that high fatigue stroke patients are not able to prepare or anticipate an upcoming movement as well as those with low fatigue which might be a result of reduced sensory attenuation.

2-E-67 Optogenetically mediated neuromodulation of trunk motor cortex paired with exercised based rehabilitation leads to axial reflex changes below a complete T9/T10 spinal cord injury

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After a complete T9/T10 spinal cord injury (SCI) in adult rats, trunk control becomes very important for postural stability, and crucial for function if stepping of hindlimbs is enabled. We have developed a neuromodulatory technique aimed at promoting plasticity and motor learning in the trunk motor cortex after SCI via subthreshold optogenetic stimulation using virally delivered Channelrhodopsin (ChR2). Virally delivered enhanced yellow fluorescent protein (EYFP) is used as a control. When optogenetically mediated neuromodulation is paired with a 25 day robot assisted rehabilitation paradigm, motor mapping studies reveal a significant increase in cortical representation of trunk muscle segments nominally below the injury (1-way ANOVA with Tukey-Kramer post-hoc comparisons, $p<0.05$) in the ChR2+robot rats, both with induced spinal stepping (N=8) and without (N=8), but not in EYFP+robot rats with (N=8) or without (N=8) spinal stepping enabled. Activation of caudal trunk enabled by these representational changes likely also causes plastic changes in spinal circuitry below the injury by influencing sensory input and motor output in the spinal cord caudal to injury. These plastic changes may be beneficial in functional recovery after injury, and understanding these effects may help direct future rehabilitation efforts. Functional tests, such as AOB or BBB scoring provide little insight into group differences at circuit levels, so a physiological probe is needed to understand the basis of functional differences. Monosynaptic reflex testing is used widely to test spinal excitability. To understand chronic below injury spinal circuit-level changes mediating trunk reflexes in external oblique and longissimus, we implant a stimulating cuff around the T13 spinal nerve, enabling monitoring of trunk muscle responses through a total of 13 trunk electromyogram electrodes, spaced both above and below injury, over the course of robot rehabilitation. Due to the proximity of the stimulating cuff to the spinal cord, in ipsilateral muscle segments caudal to injury, the motor response and the reflex response overlap. Artificial neural networks can be used to separate the two signals, however, we have also discovered a contralateral reflex of comparable latency, believed to be monosynaptic, which is readily analyzed. Varying stimulation frequency allows the effects of neuromodulation of trunk motor cortex on spinal excitability below the injury to be revealed. At high frequencies, lumbar external oblique reflex responses are significantly depressed in ChR2+robot rats with stepping enabled compared to EYFP+robot rats with stepping enabled (Three-way mixed model ANOVA with Bonferonni multiple comparison corrections). These data are an indication of spasticity reduction in the obliques, but in contrast there are no group differences with lumbar longissimus. This work has been supported by NIH NINDS NS054894, and NS072651 and the Craig Neilsen Foundation.

2-E-68 Delays in reticulospinal system are correlated with deficits in motor learning in older adults

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Motor skill acquisition, the process by which movements are honed and refined to become faster and more accurate, declines as we age. Older adults learn at a slower rate and to a lesser extent than younger adults. While there are numerous changes to all levels of the nervous system with age, the relative contribution of reticulospinal system deficits has not been explored. There is growing evidence that the reticulospinal system is critical during motor learning and becomes increasingly involved in movement as a skill is acquired. A recent study published in Neuron demonstrated that there is a shift from the use of cortical to reticulospinal structures following intense, repetitive training. Kawai et al. demonstrate that the initial learning of a task requires substantial input from the cortex; however following training rats with bilateral motor cortical lesions were still able to perform a sequence of precisely timed lever presses i.e. if sufficiently trained prior to lesion, rats can perform lever presses in the absence of the motor cortex. Importantly, rats could only perform the tasks if lesioning occurred after task training. Lesioning prior to training prevented rats from learning the task. This highlights the critical role of both the cortex and reticulospinal systems during learning but also notes that following learning the reticulospinal system becomes critical for execution of learned tasks. We recently demonstrated that this animal work generalizes to humans. The startle reflex, which is mediated by the reticulospinal system, was used as a probe of reticulospinal contributions. Reticulospinal contributions were shown to increase over the course of skill acquisition. Similarly, expert typists show larger reticulospinal involvement during individuated typing movements compared to non-experts. Our objective was to evaluate if deficits in the reticulospinal system are correlated to impairment of motor learning in older adult. In this study we evaluate 20 older adults were evaluated during skill acquisition of a task that simulated feeding. One-month retention of learning was compared to startle onset latencies taken prior to training. We found that there is statistically significant correlation between these two variables (Linear regression: $P < 0.001$). This indicates that deficits in the reticulospinal system may account for some of the learning deficits associated with aging. Further, this opens the possibility of startle being a predictor of learning deficits which could be used to facilitate better dosage of rehabilitation therapy.

2-E-69 Feedforward and feedback motor circuit dysfunction impairs reaching movements in EphA4 knockout mice

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Skilled reaching movements are initiated by feedforward motor commands conveyed by supraspinal motor pathways, and controlled by peripheral feedback as well as internal feedback systems for rapid online correction. Mutation of the axon guidance molecule EphA4 produces axonal misrouting of the corticospinal tract and spinal interneurons. Here we investigate how feedforward and feedback motor circuits controlling skilled reaching are affected by loss of EphA4 gene. The behavioral experiments show that EphA4 knockout mice display impaired goal-directed reaching movement. In vivo intracellular recordings from forelimb-innervating motor neurons demonstrate increased cortico-reticulospinal excitation, whereas decreased direct reticulospinal excitation and decreased direct propriospinal excitation in EphA4 knockout mice. Moreover, cerebellar surface recordings show a functional change in the internal feedback via the lateral reticular nucleus - cerebellar pathway in EphA4 knockout mice. Together, our findings reveal that loss of EphA4 disrupts both feed-forward and feedback motor pathways, resulting in deficits in skilled reaching.

2-E-70 Cortico-subcortical connectivity in stopping of ongoing movements

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The inhibition of prepotent motor responses and cautious cognitive control is thought to rely on an inhibitory network consisting of the inferior frontal gyrus (IFG), supplementary motor areas (SMA) and the subthalamic nucleus (STN). Subthalamic deep brain stimulation (STN-DBS) is an effective treatment option for Parkinson's disease (PD) and can be used to investigate behavioural effects resulting from the interference with STN signalling. Previous studies on STN-DBS have highlighted both the clinical benefits such as increased velocity and shortened reaction times in PD as well as a concomitant side-effect of an increase in erroneous responses under cognitive demand. Another clinical complication of STN-DBS can consist in involuntary movements, called dyskinesia. The role of the STN and the triangulated inhibition circuit in stopping of such ongoing motor output remains to be elucidated. 17 PD patients with STN-DBS performed ~20 continuous circular movements with a cursor using a digitizing tablet. Start and stop events for transition from movement to rest were visually cued. The task was performed both with stimulation ON and OFF. Reaction times for initiation and termination of movement were derived across conditions. Individual DBS electrode locations were reconstructed using fusion of pre- and postoperative imaging and transferred to MNI-space using the Lead-DBS toolbox. Next, functional connectivity values derived from a normative fMRI connectome from 1000 healthy subjects were analysed from all active contact pair locations in MNI space. A spatial connectivity fingerprint of stopping was mapped using whole-brain correlation of active contact pair connectivity with DBS induced change in stopping times. On average, stopping time significantly increased with DBS (ON: 796±121 ms, OFF: 754±135 ms, $P=0.018$), while the movement initiation time decreased (ON: 745±178 ms, OFF: 807±166 ms, $P=0.029$). The effect on stopping time was independent of the motor improvement through STN-DBS as assessed by the UPDRS-III ($P>0.05$). In contrast, the expected increase in movement velocity (ON: 22.8±6.1 a.u., OFF: 13.8±5.5 a.u., $P<0.001$) correlated with general improvement in parkinsonian symptoms ($R=-0.68$, $P<0.001$). Importantly, there was no significant correlation between stopping time and movement velocity ($P>0.05$). The fingerprint analysis of the connectivity pattern revealed that stronger connectivity of active contacts with SMA and IFG was associated with increase of stopping times with STN-DBS. Here we show that STN-DBS significantly increases the time needed to stop an ongoing movement, while decreasing the time needed to initiate it. Strong fMRI connectivity of active DBS contacts with SMA and

IFG regions seems associated with greater increases in stopping times. Our findings extend the current knowledge on the role of a fronto-subthalamic inhibitory triangle to the stopping of movements and may help explain dyskinesia as a DBS-related side effect.

2-E-72 Exploiting the Random Forest classification algorithm for identifying features of muscle synergy post-stroke

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In stroke rehabilitation, there has been much interest in finding reliable neurological markers that can reflect motor impairment, predict functional gain from specific interventions, and shed light on basic mechanisms of post-stroke motor control. Various parameters dependent on muscle synergies - hypothesized modules of motor control - have been suggested as potential markers. Muscle synergies are often extracted from multi-muscle electromyographic signals (EMGs) using factorization algorithms, which decompose the EMGs into a set of time-invariant muscle synergies (W) and their temporal activation coefficients (C). Different analytic techniques have been employed to search for hidden W- and C-features that may be clinically useful. However, it remains unclear if any specific muscle-synergy features can serve as reliable predictive or diagnostic markers in diverse stroke survivors. Our goal is to identify clinically and scientifically useful markers from features of EMGs and muscle synergies. We reason that any features that reliably distinguish the EMGs of a stroke-affected limb from those of a sound limb may be candidate markers. As a first step, we ask if a machine learning algorithm can discover muscle-synergy features that can be used for classifying whether a set of muscle synergies belongs to a stroke-affected or sound limb. To this end, we explore the utility of the Random Forest classification method, a supervised learning algorithm based on decision trees. In this method, an ensemble of decision trees is generated to avoid overfitting. Within each tree, features are randomly chosen, and a quantitative method is used to determine how well a feature can divide the test samples into different classes. Each tree then gives a vote to determine to which classes the data points belong, and the final classification is determined by combining the votes from all trees. We tested the performance of the Random Forest in a dataset derived from chronic stroke survivors (N=15). Surface EMGs were collected from the paretic and sound sides (14 muscles each side) during 3D center-out reaching over 2-3 sessions, and EMGs from a total of 77 limbs were analyzed. Muscle synergies were extracted from the EMGs using non-negative matrix factorization. We found that the Random Forest could successfully classify the stroke-affected- and sound-synergy sets (78% accuracy), but not the randomly shuffled synergy sets (40% accuracy). The synergy features most frequently used by the algorithm for classification include W components representing activations of biceps brachii (short and long heads), medial deltoid, trapezius (middle), and pronator teres. Our initial results here suggest that the Random Forest may be profitably employed for discovering new, potential markers during exploratory analysis of large datasets. The synergy¬ features we identified also highlight how some muscle synergies may be altered in a predictable way at the chronic stage of stroke.

2-E-104 Elevated beta oscillatory brain activity during balance recovery in patients with Parkinson's disease

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Introduction: Voluntary movement is preceded by reduced beta cortical oscillatory brain activity (13-30 Hz) in healthy young adults; beta cortical electrical stimulation can even slow ongoing voluntary movement. In people with Parkinson's disease (PD), beta oscillatory brain activity is abnormally high both at rest and during voluntary movement. People with PD also have balance problems, and likely rely more heavily on attentional mechanisms and voluntary balance control. Motor responses to balance perturbations are initially involuntary (150ms) and are followed by voluntary corrections at longer latencies (>250ms). We hypothesized that people with PD would display more beta activity during balance recovery compared to healthy older adults (HOA), which might interfere with voluntary balance-correcting behavior. Methods: We used support-surface translations to perturb standing balance in 15 people with PD (age 69±2, mean±stderr) and 9 HOA (age 74±2). Fluctuations in beta oscillatory power were quantified in single trial electroencephalography (EEG) data at the Cz electrode and subsequently averaged across trials within subjects. We then identified maximum beta power in for each subject in five 165-ms time bins: 1) during quiet standing before balance perturbation, 2-3) during involuntary balance-correcting behavior (0 ms-164 ms and 178-342 ms), 4) when voluntary control can contribute (356-520 ms), and 5) after the perturbation (533-697 ms). We used a two-way ANOVA to test effects of subject and time bin on the maximum beta power in each group. We use post-hoc Tukey tests to compare maximum beta power in each time bin after perturbation to pre-perturbation levels. Results: Both HOA ($p<0.0001$) and PD ($p<0.0001$) showed significant increases in beta power after perturbation onset. Relative to time bin 1, both groups showed significant increases in bin 2 (both $p<0.05$, 19±5 dB in PD and 18±4 dB in HOA) and bin 3 (both $p<0.05$, 28±5 dB in PD and 25±6 dB in HOA), whereas only the PD group maintained a significant increase in bin 4 ($p<0.05$, 18±3 dB in PD and $p>0.05$, 13±6 dB in HOA). In both groups, beta power was not significantly different in bin 5 relative to bin 1 (both $p>0.05$, 6±3 dB in PD and 5±4 dB in HOA). Discussion: We show that HOA have reduced beta during the period of balance recovery consistent with voluntary balance corrections. In contrast, people with PD have elevated beta throughout balance recovery which could indicate difficulty engaging voluntary balance recovery strategies. The elevated beta could be an indicator of impaired balance control, and potentially contribute to balance impairments.

F – Adaptation & Plasticity in Motor Control

2-F-73 Experienced prosthesis users exhibit accurate online error correction when reaching in the absence of visual feedback

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Introduction: Movements to targets within reach involve complex integration of feedforward and feedback control, including use of both vision and proprioception. Conventional upper extremity prostheses are insensate and this has led to the assumption that users rely heavily on visual feedback. However, recent evidence shows that experienced prosthetic-users also learn relationships between their body and the prosthesis and integrate such information into their internal body schema for the control of simple motor tasks. Whether these adaptations are sufficient to enable accurate control of the end effector in the absence of visual feedback remains uncertain. To address this issue, we had unilateral prosthetic users and controls undertake a reaching task with and without vision of the prosthesis/limb. Critically, on a minority of trials the location of the target was perturbed mid-reach, requiring actors to perform an on-line error correction. To the extent that vision is necessary to update the state of the end effector accurately, we expected that prosthetics users would exhibit decreased endpoint accuracy and slower movements times when required to correct reach trajectories in the dark. Methods: Nine upper extremity prosthesis users (two females, one left-handed, mean age = 60.0±8.6 years), with an average of 21.0 (±16.7) years of experience using a prosthesis an average of 27.5 (±16.2) hours per week, and nine age/sex/hand dominance-matched healthy controls (mean age = 57.44±9.55 years) participated. Response times, movement times and kinematics of the prosthesis endpoint were recorded (Optotrak Certus, Northern Digital) and compared with those from controls' the index fingers. Seated subjects executed a three-dimensional pointing movement to an illuminated target cube located either ipsilateral or contralateral to the tested limb. Target location varied pseudorandomly. Reaches were executed with the prosthesis/arm and in the dark and in the light during separate blocks (48 trials per visual condition per target location, a total of 192 trials). Within each block, target location changed during movement execution on 33% of trials (i.e., 64 perturbed trials in total). Results: Contrary to predictions, in all conditions prosthesis users performed similarly to controls, in terms of response times, trajectory lengths, and end-point accuracy ($p>0.2$ in all cases). Importantly, target perturbation in the absence of visual feedback had similar effects on reaches executed with the prosthesis or hand. Overall, however, movements performed with the prosthesis were slower ($p<0.02$), suggesting the need for additional time in order to maintain a high level of end-point accuracy. Conclusions: These findings suggest that experienced prosthesis users are able to predict the position of the device's endpoint relative to the state of the residual limb, allowing for accurate control and feedback-based error correction even in the absence of vision.

2-F-74 Challenging balance enhances generalization of visuomotor mappings across reaching and walking tasks

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The ability to transfer or generalize learned behaviours to novel contexts is an important component of learning. Limited generalization is often seen across different arm movements. However, most of these studies focus on isolated movements where participants are typically in a seated position, such that balance is not a concern. Yet balance challenges are inherent to everyday reaching and walking tasks, where the ability to complete these tasks depends critically on the control of the whole body. Generalization across different walking tasks appears more robust, suggesting that task dynamics may dictate the extent to which learned sensorimotor mappings can be transferred to new situations. We propose that balance challenges encountered during complex, whole-body movements require the nervous system to use a more complete internal model of the body's dynamics, and a more complete model may be a more generalizable model. Here we determined how challenging balance during standing-based reaching and walking tasks (i.e., whole-body movements) affects visuomotor adaptation and generalization. Four groups (n=12 each) of participants adapted to a new visuomotor mapping induced by prism lenses while performing either a standing-based reaching or precision walking task. In balance-unchallenged groups, participants performed the tasks without any additional balance manipulation. In balance-challenged groups, participants performed the task with inflatable rubber hemispheres (radii: 8.5cm) attached to the soles of their shoes to reduce the control afforded by shifting the center of pressure under the base of support. This manipulation appeared to have the desired effect as evidenced by increased effort (muscle activity: reaching, p=5.4e-6; walking, p=0.002), instability (trunk acceleration variability: reaching, p=0.006; walking, p=1.8e-8), and motor variability (limb-endpoint error variability: reaching, p=0.016; walking, p=1.2e-6). All groups adapted to the new mapping with no significant differences in adaptation rates. To assess generalization, participants performed a single trial of each of the other group's tasks (i.e., the non-adapted tasks) with non-prism lenses after the adaptation phase. Both the walking and reaching groups generalized within their respective non-adapted tasks (e.g., reaching balance-unchallenged generalized to reaching balance-challenged and vice versa). However, the balance-challenged groups showed greater generalization (transfer index: reaching, p=0.001; walking, p=0.009). Additionally, only the balance-challenged groups showed generalization across tasks, whereby the reaching balance-challenged group generalized to the walking balance-unchallenged task (p=0.01) and the walking balance-challenged group generalized to the reaching balance-challenged task (p=0.03). Overall, our results support the idea that challenging balance may lead to the construction of a more complete and generalizable internal model.

2-F-75 The complexity of tapping force and vertical displacement in finger tapping is higher for individuals who show repeated bout rate enhancement than for those who do not

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The behavioural phenomenon of repeated bout rate enhancement has been revealed and replicated [1,2]. The phenomenon consists of increased freely chosen finger tapping rate in the 2nd of 2 consecutive tapping bouts, separated by rest. Approx. 2/3 of tested individuals show the phenomenon (responders). But, the underlying motor control mechanisms remain undisclosed. What could explain why some, but not other (nonresponders), individuals show repeated bout rate enhancement? It has been argued that the study of motor variability can help to understand motor control linked to e.g. motor learning [3]. Besides, the study of intra-bout variability is a useful tool for deeper understanding of motor variability [4]. Sample entropy (SaEn), a measure of complexity, is frequently reported in relation to motor variability [5]. The aim of the present study was to test for main effects of group (responders, nonresponders), bout (1, 2), and time (3 epochs within a bout) on SaEn of tapping force and vertical displacement. We hypothesized that SaEn would be higher: 1) for responders than for nonresponders, and 2) in bout 2 than in bout 1. Healthy individuals (n=102) participated. Responders (32 men, 36 women) were 1.76±0.10 m, 74.9±13.0 kg, and 26.0±5.6 years. Nonresponders (16 men, 18 women) were 1.74±0.08 m, 73.9±12.0 kg, and 24.5±3.6 years. Each participant performed 2 3-min index finger tapping bouts at freely chosen tapping rate, separated by 10 min rest. Tapping was performed on a force transducer. A motion capture system synchronously recorded vertical displacement. SaEn was computed in agreement with [6] from 3 8-s epochs (start (0-8 s), mid (86-94 s), and end (172-180 s)) extracted from the force and kinematic recordings of the 2 tapping bouts. SaEn was evaluated using 3-way RM ANOVA and post hoc tests. There was a main effect of group on the SaEn of vertical displacement (p=.046). A post hoc analysis showed the SaEn of vertical displacement to be higher for the

responders than for the nonresponders (p=.046). For the responders, the SaEn of vertical displacement was higher for bout 2 than for bout 1 (p=.001). Also, there were main effects of bout and time on the SaEn of force (p=.009, p=.032, respectively). For responders, the SaEn of force was higher for bout 2 than for bout 1 (p<.001). SaEn of force increased for responders from start to mid and from start to end (p=.002, p=.002, respectively). The findings for responders may be interpreted in an 'expert dynamics' framework to suggest that responders had a greater adaptability towards performing finger tapping [7].
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2-F-76 Contralateral transfer of repeated bout rate enhancement in rhythmic movement

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Knowledge on the behaviour and control of human voluntary stereotyped rhythmic movement has relevance for sick, injured, and healthy individuals. In the present study, unilateral finger tapping was applied as a model of such a type of movement. We studied the phenomenon of repeated bout rate enhancement, which covers an increase of the freely chosen index finger tapping frequency during the 2nd of two consecutive tapping bouts performed with the same index finger (1,2). It is unknown whether tapping with the index finger on one hand can elicit repeated bout rate enhancement during tapping with the index finger on the other hand. We tested the hypotheses that A) the freely chosen frequency in rhythmic unilateral index finger tapping is highly correlated between the two index fingers, and B) a single 3-min bout of unilateral index finger tapping followed by 10 min rest results in a rate enhancement of the freely chosen tapping frequency performed by the contralateral index finger in a subsequent tapping bout. Healthy adults (n=32) participated. Freely chosen tapping frequencies from initial bouts were 167.2±79.0 and 161.5±69.4 taps/min for the index finger of the dominant and nondominant hand, respectively (p=.434). The correlation between the tapping frequencies recorded for the index finger of the dominant and nondominant hand was high (R=.86, p<.001). When the 1st tapping bout was performed with the index finger of the dominant hand and the 2nd bout was performed with the index finger of the nondominant hand, the freely chosen tapping frequency increased by 8.1±17.2% in the 2nd bout (p=.011). For the opposite order, the tapping frequency increased by 14.1±17.5% in the 2nd bout (p<.001). The increases were not statistically significantly different (p=.157). The present results were in line with a report of high correlations of unilateral freely chosen movement frequencies performed by the two legs separately during rhythmic leg exercise tasks (3). Stang et al (2016) suggested that involved spinal central pattern generators of the two legs might share a common frequency generator, or that separate frequency generators of each leg are attuned via interneuronal connections. It is possible (4,5), that the neural activity in the present 1st bout, via neuromodulation, excited the rhythm generating part of the central pattern generator controlling the contralateral index finger, and that this caused the generation of a higher tapping frequency in the 2nd bout. In conclusion, there was a high correlation between the freely chosen unilateral index finger tapping frequency performed by the dominant and nondominant hands, respectively. Furthermore, an interlimb transfer of repeated bout rate enhancement occurred. References: 1) Hansen et al 2015 J Mot Behav 47, 490-96. 2) Mora-Jensen et al 2017 Motor Control 21, 457-67. 3) Stang et al 2016 Front Hum Neurosci 10:36. 4) Perrier & Cotel 2015 Curr Opin Neurobiol 33, 1-7. 5) Gad et al 2017 Front Neurosci 11:333

2-F-78 The proficiency and strategy in tool-use grasping

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Previous studies have suggested that the proficiency of an effector influences motor control of reach-to-grasp movements, regardless of the distinction of tool and body. To further test this idea, the present study directly investigated how improvement in the proficiency of tool-use modify the kinematics of reach-to-grasping movement (experiment 1) and examined the effect of removing the priority of grasping accuracy on the kinematics without the proficiency of the tool (experiments 2), both of which were expected to bring about the hand-use like kinematics. In the experiments, participants carried out reach-to-grasp movements for a cylindrical object on a table with fingers (thumb and index finger) or a scissor-like tool. In experiment 1, participants practiced tool-use grasping movement for two weeks. The movement performance was evaluated before the practice and after one week and two weeks. In experiment 2, another participant group carried out reach-to-grasp movements with the tool but in three different speeds: normal, faster, and fastest speed; the participants were asked to prioritize speed instruction rather than successful grasping. The results showed that plateau duration, the length of which indicates how tool-use-like the grasping movement is, shortened as the tool-use practice proceeded. The results of experiments 2 also showed that the plateau duration shortened as the movement speed increased. These results together suggest that the kinematic features which have been supposed to be innate of tool-use grasping are just caused by a strategy to compensate the lack of proficiency of end effectors, supporting the idea that one single principle governs motor control of reach-to-grasp movements depending on proficiency of effectors.

2-F-80 Concurrent visuomotor and dynamic perturbations of one hand increase contralateral interference in a bimanual task

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During complex bimanual movements, the action of one hand can influence the action of the other through interference. For example, a visuomotor perturbation applied to one hand will result in directional error in the contralateral hand moving without visual feedback. Interestingly, dynamic perturbation of one hand results in only very little contralateral interference. Unimanual studies have demonstrated that when participants adapt to a dynamic perturbation, the response to a visuomotor perturbation is upregulated, suggesting that visuomotor and dynamic perturbations interact within the sensorimotor system. If this interaction is shared between hemisphere-effector systems, then interference to concurrent visuomotor and dynamic perturbations to one hand should result in greater interference in the contralateral hand than either perturbation alone. To test this hypothesis, sixty participants were randomly assigned to one of four groups: dynamic perturbation only, visuomotor perturbation only, combined perturbation, or no-perturbation. Participants moved two robotic manipulanda simultaneously from two home positions to two targets (at 90° or 270°), located 10 cm from the home positions. Hand position was represented by a cursor on a screen that occluded vision of the hands. Participants performed unperturbed reaches during two blocks of 30 trials; in the first block, visual feedback was displayed for both hands; in the second block it was removed for the left hand, requiring participants to rely on kinesthetic control for that hand. In the following exposure block of 250 trials, participants were exposed to the perturbation in the right hand, while the left hand continued moving without visual feedback. During the visuomotor perturbation, the cursor representing the right hand was rotated 40° clockwise, such that participants needed to adapt their movement trajectory to hit the target. During the dynamic perturbation, participants' right hand encountered a 20 Nms-1 force perpendicular to the movement direction. The combined perturbation group received both perturbations simultaneously, while the control group received no perturbation. Directional interference in the left hand was assessed at peak velocity, at the end of the initial ballistic movement, and at the end of the reach. Results show that the visuomotor and combined perturbation groups experienced the largest directional error in the left hand, while the dynamic perturbation only group showed smaller errors, though larger than the controls. Further, movement linearity was lower in the combined perturbation group compared to other groups. Overall, this suggests that visuomotor perturbations as opposed to dynamic perturbations dominate neural processes that cause interference between the hands.

2-F-81 Effects of volitional preemptive abdominal contraction strategies on co-activation of lumbar multifidus under different postures

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Introduction/Background: Low back pain (LBP) is the most common musculoskeletal disorder and lumbar multifidi (MF) atrophy has been identified. Co-contraction of deep core muscles is critical for sustaining spinal stability while studies have found MF is difficult to be specifically activated. Lumbar MF has proved to be co-activated during the abdominal drawing in healthy young adults. However, it is unknown whether other volitional preemptive abdominal contraction (VPAC) strategy is also effective and whether such responses may be affected by the postural conditions. Thus, the purpose of this study was to investigate the effects of VPAC on co-activation of l lumbar MF under different postural conditions in healthy young adults. Materials and Methods: Twenty-one healthy young adults were recruited. Thickness of the abdominal muscles including rectus abdominis (RA), external obliques (EO), internal obliques (IO), and transversus abdominis (TrA) along with the MF at the L4-L5 level were measured by the ultrasonography during 3 VPAC strategies (natural breathing, NB; abdominal draw-in, AD; and abdominal push-out, AP) under 3 postural conditions (lying, upright standing and single leg standing).. Two trials were obtained for each condition. A 3X3 repeated measure analysis of variance was conducted. Results:. Significant interaction effects were found for the thickness of the TrA and MF. . In the lying and single leg standing postures, the thickness of TrA and MF during the AD and AP were significantly greater than during the NB. In the upright standing, the thickness of the TrA during the AD and AP were significantly greater than during the NB but not MF. However, no differences were found between the AD and AP . Additionally, thickness of EO and IO were significantly smaller during the NB than the AD and AP. Conclusion: VPAC strategies including both AD and AP resulted in co-contraction of the MF in different postures. Nevertheless, not one of VPAC strategies is superior to the other. The effects of VPAC strategies on spinal stability in patients with LBP still needs investigation.

2-F-82 Looking for a sign of failure in actions: reaching errors triggered by slowing down of movement and specific brain activity in preceding trials

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As illustrated by a faulty pitch by MLB pitchers, even experts can sometimes make errors while performing well-practiced movements. Previous studies have reported patterns of electroencephalograms (EEG) specifically observed in failed trials 100-1000 ms before the movement onset (Babiloni et al., 2008; Bediou et al., 2012). However, how and why such failures in action and the associated brain activity patterns arise have not been fully investigated. Do they suddenly arise or is there any sign beforehand? By using a reaching movement adaptation paradigm, we tried to investigate if a sign of failure in action exists even in trials preceding a failure. We performed three experiments examining the presence of a sign of failure in movement patterns (Experiment 1) and in brain activity patterns (Experiment 2), and then tested whether providing feedback when detecting the sign could suppress failures (Experiment 3). In Exp. 1, 15 healthy participants were trained to reach toward a forward target (distance: 10 cm) in the presence of a rightward velocity-dependent force field (400 trials). We considered a lateral deviation from the straight path between the target and the starting position at the peak hand velocity as a reaching error (RE). Even after a sufficient amount of practice had been completed, REs varied from trial to trial and sometimes exhibited greater magnitude. Failed trials (FTs) were defined as trials in which the top 5% of REs were observed. There was no specific trial-dependent pattern in REs nor in reaction time in trials preceding FTs. However, we found that movement velocity had already started to decline before two trials preceding FTs ($P < 0.01$, compared to resampled trials). In Exp. 2, we tried to investigate if such a sign of failure could be detected in brain activity by measuring EEG. The task protocol of Exp. 2 was almost the same as Exp. 1 (8 participants, 600 trials) and we replicated the behavioral results in Exp. 1. In addition, EEG data obtained over the left sensorimotor cortex showed larger alpha and low-beta band (8-20 Hz) power before the movement onset in the trial immediately preceding a FT ($P < 0.01$, compared to resampled trials after cluster-based statistical testing). We speculated that the gradual decrement of movement velocity observed before FTs reflected a decrease in movement vigor and implicit motivation, as reported by Mazzoni et al. (2007). In Exp. 3, we tested whether a visual alert, "slow," provided when movement slowed down could suppress failures in the subsequent movements. In 3 out of 4 participants, the visual alert significantly decreased the absolute value of the REs. Our results suggest that failures in actions do not suddenly happen and there are signs in the preceding trials. Reduction of REs by visual alert based on detecting these signs suggests the presence of a causal relation between failures in action and velocity of movement.

2-F-83 Mechanistic determinants of interlimb transfer of visuomotor learning

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Generalization of motor learning across effectors, or interlimb transfer, has been widely demonstrated in the movement neuroscience literature, yet its mechanistic basis has not been well expounded. In particular, which of the mechanisms that drive motor learning contribute most strongly to interlimb transfer, remains largely unknown. Here we used as a starting point the widely held view that such learning is driven by multiple error-sensitive mechanisms that act in parallel but at different rates, and investigated their influence on transfer. Human subjects adapted to a counterclockwise visuomotor rotation for a varying number of trials with either their left or right arm, and were subsequently exposed to the same perturbation with their opposite, untrained arm in order to assess transfer of learning across the arms. We noted that transfer occurred only from the left arm to the right, and that its magnitude scaled with the number of left arm learning trials. Furthermore, the amount of transfer was principally associated with the level of a slowly developing, likely implicit memory of the perturbation and not by the net learning achieved at the end of the practice period or the state of other learning processes in this framework. Our results provide fresh insight into the mechanistic determinants of interlimb transfer, and are also significant from the point of view of understanding the mechanisms that drive the formation of effector-independent motor memories.

2-F-84 Reinforcement schedules to modify movement coordination in redundant motor tasks

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The human sensorimotor system has the ability to generate different movement patterns to perform the task, and often the goal in motor learning is to guide the individual from a pre-existing preferred movement pattern to a novel movement pattern. Reinforcement learning has been used as a powerful technique to modify motor performance, but its use in redundant tasks (where there are multiple solutions) is less understood. Here, we examined the use of different reinforcement schedules (abrupt, gradual and adaptive) to modify movement coordination in a redundant task. We designed a virtual throwing task where participants' goal was to control the sum of the trunk and hand velocity. This task is a redundant task because there are multiple combinations of trunk and hand velocities that participants can select, but typically the pre-existing preferred movement pattern has much hand velocities. The aim of this study is to guide participants to use a solution with higher trunk velocity by learning with reinforcement feedback. A pre-defined threshold of trunk velocity was set and participants got punished with a low score when the trunk velocity was smaller than the threshold. The goal of the participants was to learn to use higher trunk velocity by avoiding punishment. To investigate how to modify this threshold during training, we applied three threshold schedules -abrupt, gradual and adaptive. In the abrupt group, the threshold jumped immediately to the criterion value at the start of practice and stayed constant throughout practice. In the gradual group, the threshold changed incrementally so that the criterion value was achieved only near the end of practice. In the adaptive group, the threshold was modified based on the participant's performance - we set the threshold based on the average trunk velocity of the previous 6 trials. Participants performed 240 trials (8 blocks of 30 trials) that included a pre- and post-test without reinforcement. Results showed that the adaptive schedule had the best performance in terms of increasing trunk velocity in the post-test. The results suggested that the exploration triggered by reinforcement feedback is most effective when it is customized to individual performance. To further understand this exploration, we use a computational model to show how exploration interacts with uncertainty in the environment.

2-F-85 Changes in resting-state functional connectivity and behavior associated with a spaceflight analogue environment

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Following spaceflight, astronauts exhibit structural and functional remodeling of the brain, and impairments in sensorimotor function. Astronauts are exposed to microgravity and elevated CO2 levels onboard the International Space Station. Little is known about how microgravity and elevated CO2 combine to affect the brain and sensorimotor performance. Here, we used 6o head-down tilt bed rest with elevated ambient CO2 (HDBR+CO2) as a spaceflight analogue. We examined changes in resting-state functional connectivity (FC) and sensorimotor behavior in 11 participants over 58 days. Behavioral assessments included a rod and frame test to examine visual sensory biases, and a functional mobility test to examine whole-body locomotor behavior. First, baseline measures of resting-state FC and behavior were acquired 13 and 7 days prior to bed rest. Participants then underwent 30 consecutive days of HDBR+CO2. Resting-state fMRI scans occurred on days 7 and 29 of bed rest. Resting-state fMRI and behavioral testing were performed 5 and 12 days following bed rest. We first assessed the time course of FC changes from before, during, to after HDBR+CO2. HDBR+CO2 was associated with FC increases among visual, vestibular, and motor brain areas which reversed following bed rest. HDBR+CO2 was also associated with FC decreases between somatosensory and motor brain areas which reversed following bed rest. We then assessed if FC changes following HDBR+CO2 were associated with behavioral performance alterations. Increased FC among several sensorimotor brain regions after bed rest were associated with greater slowing during the functional mobility test. In contrast, increased FC among cognitive and visual brain areas following bed rest was associated with less slowing during the functional mobility test. These connectivity changes are suggestive of a compensatory benefit of visual and cognitive network interactions. We also found that FC increases between visual and somatosensory brain areas after bed rest were associated with improvements in response consistency on the rod and frame test. In contrast, FC decreases between premotor and vestibular cortex following bed rest were associated with performance improvements on the rod and frame test. These FC connectivity changes are suggestive of bed rest-associated multisensory reweighting. This study was supported by NASA grant #80NSSC17K0021

2-F-86 Unique excitation of the ipsilateral motor pathway in an elite high jumper with below-knee amputation

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Limb amputation induces large scale neural reorganization, such as, expansion of cortical representation of neighboring intact body parts of the amputated limb. Moreover, the extent of reorganization is depending on frequency in use of the remained body part. However, this knowledge is based on only non-athletes with amputation. Thus, it is quite interesting to examine what extent the brain of athletes with amputation has reorganized to control the stump muscles, because they frequently and hardly train to use their stump muscles for long term. We have already confirmed bilateral activation in primary motor cortex (M1) with an elite long jumper during stump muscles contraction using functional magnetic resonance imaging (fMRI). In this study, we focused on an elite Paralympic high jumper with below-knee amputation who holds the Asia record of high jump. His brain might be reorganized to

manipulate his prosthesis skillfully. The objective of this study was to clarify whether the elite high jumper shows bilateral activation similar to the elite long jumper using fMRI. Moreover, motor evoked potential (MEP) was measured to test if the excitability of ipsilateral cortico-spinal pathway would be specifically enhanced in the stump muscle by using transcranial magnetic stimulation (TMS). In fMRI experiment, we recorded brain activity during unilateral muscle contractions of lower limb, including ankle (motor imagery in amputated side), knee and hip joints. Each task was performed on the amputated and intact side. Bilateral brain activity in M1 was detected when the participant contracted knee joint muscles on the amputated side. In TMS experiment, MEP was measured from the rectus femoris (RF) on both sides in a resting state. Single-pulse TMS was delivered over the M1 lower limb area on both sides. Recruitment curves for the MEP were constructed to estimate corticospinal excitability. MEP on the amputated side was observed when the TMS was delivered over the ipsilateral M1 not only over the contralateral M1. The degrees of increase in MEP amplitude depending on stimulus intensity and the MEP thresholds were similar between the stimuli over the ipsilateral and contralateral hemispheres. On the other hand, MEP from the intact side was observed only when the TMS was delivered over the contralateral M1 but not ipsilateral M1. The world class high jump athlete with below-knee amputation showed existence of both the ipsilateral and contralateral motor pathways innervating the stump muscle which directly controls his prosthesis. This result is likely due to the long-term motor practice to develop enough control skills for manipulating prosthesis for his superior high jump. We confirmed this phenomenon using both MRI and TMS for a top athlete with amputation. This specific brain reorganization would support his superior sport performance.

2-F-87 EEG correlates of effort and reward processing during reinforcement learning

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Humans tend to adapt decisions and movements to maximize reward and minimize physical effort or energy expenditure. A frontocentral event related potential called the feedback related negativity (FRN) encodes a reward prediction error signal and is thought to be generated by a reinforcement learning process in the anterior cingulate cortex. We hypothesized that the FRN would be modulated not only by reward outcomes but also physical effort. We recorded EEG from human participants while they performed a task in which they were required to accurately produce specific levels of muscle activation to receive rewards. Participants performed isometric knee extensions while quadriceps muscle activation was recorded using EMG. Feedback indicating the combined muscle activation for both legs as a proportion of the target activation was displayed on a computer monitor. On a given trial, the target muscle activation was either "low" (approx. 15% MVC) or "high" (85% MVC). The required effort was determined probabilistically according to a binary choice indicated by button press, such that the "correct" and "incorrect" responses were associated with 20% and 80% probability of high effort, respectively. Periodically the effort contingency was reversed. Participants were told that in order receive a small monetary reward, they must exceed a minimum level of muscle activation indicated by a visual target while remaining as close as possible to the target. Once muscle activation reached the required target level, feedback displaying the magnitude of muscle activation was withheld, so that participants could not see the size of their errors relative to the target. After each trial, binary reinforcement feedback was provided to indicate success or failure. Reward frequency was controlled at approximately 0.5 in both conditions. We found that participants switched responses more frequently after non-reward relative to reward, and more frequently after high effort relative to low effort trials. We observed a statistically reliable interaction between reward and effort; the effect of reward on response switching was significant in the high effort condition but not the low effort condition. An FRN potential, peaking approximately 250 ms after feedback, was observed for non-reward relative to reward feedback. In addition, a sustained potential following the FRN was characterized by an interaction between reward and effort, such that a slow negative potential was observed for non reward relative to reward feedback in the high effort condition but not in the low effort condition. Our results indicate that during a reward based effort minimization task, the FRN reflects reward outcomes, while a later slow negative potential reflects an interaction between effort and reward that parallels the pattern of response switching.

2-F-88 Does motor variability predict individual differences in learning a redundant skill-learning task?

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Predicting an individual's ability to learn motor skills helps to more efficiently tailor the practice schedule to the individual; however, accurate prediction still remains one of the key challenges in motor learning. Recent evidence has suggested that motor variability may be an important predictor of learning because it facilitates exploration to find novel solutions faster. However, these findings have primarily been shown in adaptation tasks where the to-be learned movement is already in the participant's movement repertoire. Here we examined a skill-learning task that required learning to control variability. Specifically we used a redundant task where motor variability has two components - a task space component (which affects task performance) and a null space component (which does not affect task performance) to examine which of these components predicts future learning. The task used was a bimanual shuffleboard task, where participants held a bimanual manipulandum (KINARM) and made a discrete throwing motion to slide a virtual puck towards a target. The task was redundant in that the distance traveled by the puck was determined only by the sum of the left and right hand speeds at the time of release (with a perfect score achieved at VR + VL = 1.5 m/s). 50 participants performed the shuffleboard task in two conditions - first, at baseline, they performed in an 'unconstrained' version of the task, where they were free to use any combination of hand velocities they desired to reach the target. Subsequently, they performed a 'constrained' version of the task, in which we put an obstacle around the desired solution and controlled the horizontal position of the puck, so that participants had to choose certain combinations of hand velocities to make the puck go through the obstacle. In this case, only velocities around a '60%-40%' solution - i.e. corresponding to (VR,VL) =(0.9,0.6) m/s, would be successful in making the puck reach the target. After four blocks of practice in the constrained task, they then returned to the baseline unconstrained task for one block. Participants performed a total of 300 trials in a single day. Results showed that motor variability at baseline (in the unconstrained task) predicted learning in the constrained task, but contrary to previous findings, higher variability was in fact negatively correlated with subsequent task performance in the constrained task. Higher task space variability at baseline were associated with worse performance in learning the constrained task. Furthermore, the same relation also held with the null space variability (even though it has no effect on task performance), with higher null space variability at baseline being associated with worse subsequent performance. These results suggest that the relation between motor variability and learning is not direct, and point to the need to understanding the contribution of both exploration and noise to motor variability.

2-F-89 Individual optimal attentional strategy dependent social interaction during a dyadic motor learning task

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When we perform a cooperative motor task with another person, "social interaction" can affect the performance in each other. Although previous studies reported that the social interaction varies depending on the personal relationship such as a performer's gender, it remains unclear what kind of individual cognitive characteristics determines the social interaction. In this study, we investigated the effect of attentional strategy on the social interaction during a dyadic motor task. Focus of attention is one of the most influential factors facilitating motor performance, and previous studies have investigated the effect of two distinct attentional strategies on motor performance: internal focus (IF) and external focus (EF). Furthermore, we recently revealed that the EF strategy does not always lead to better motor performance. Based on our previous findings regarding the individual differences in the optimal attentional strategy, we hypothesize that combination of the optimal attentional strategy in performers modulates the social interaction. In other words, we expected that a consistent attentional strategy in each other induces a better social interaction and facilitate motor learning. Forty-two healthy young participated in this study (novice performer). The participants required to control a cursor on a monitor by hand movements. First, we evaluated the novice participants' optimal attentional strategy during the visuomotor task. Then, for dyadic visuomotor task, the novice participants were assigned into 4 groups based on their optimal attentional strategy and another expert performer's attentional strategy: Consistent-EF (Expert-EF and Novice-EF pair), Inconsistent-EF (Expert-EF and Novice-IF pair), Consistent-IF (Expert-IF and Novice-IF pair) and Inconsistent-IF (Expert-IF and Novice-EF pair). During the dyadic visuomotor task, we instructed pairs to cooperatively control a cursor. In the results, the Consistent-EF group showed higher motor performance compared with the Inconsistent-EF. Furthermore, the individual motor performance in the EF novices who paired with the expert applying the EF strategy improved after performing the dyadic visuomotor task. On the other hand, we did not observe the difference between the Consistent-IF and Inconsistent-IF groups. Current findings suggest that the combination of attentional strategy is a potential factor to modulate social interaction during a dyadic cooperative motor task. Social interaction optimized for each pair would facilitate a motor learning effect.

2-F-90 Exploration of distinct neural activity repertoire during learning of new arm dynamics

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The motor system can flexibly learn skilled movements and may implement distinct strategies in different learning contexts. In a visuomotor rotation (VMR) task, subjects learn new associations between visual feedback and the actual reach. Behavioral studies show that subjects employ familiar reaches but re-aim at different targets based on the rotation of visual feedback. In contrast, during force field learning, subjects reach in an environment of new forces, thus pure re-aiming cannot work, as it requires learning new arm dynamics. To facilitate this type of learning, the neural system likely cannot reassociate existing neural states but could explore a new repertoire of activity patterns. To investigate the neural strategy for learning new arm dynamics, we trained rhesus monkeys to first reach to 1 of 12 targets, and then adapt to a curl field active only for 1 target. After monkeys adapted to the force field, reaches to untrained targets using an "error clamp" were interleaved with the adaptation trials. Behaviorally, monkeys adapted gradually to the force field, and showed a bell-shaped spatial generalization of learning: newly learned hand forces were transferred to untrained directions proportional to their similarity with the trained reach. We recorded neural activity in PMd and M1 when monkeys performed the task. We applied dimensionality reduction methods and found that pre- and peri-movement neural activity showed different patterns of systematic changes to implement learning of new hand forces. During adaptation, pre-movement neural states gradually shifted away from the "baseline repertoire" (a set of neural states for reaching to all directions pre-learning). Baseline repertoire was separated from the after-learning repertoire mapped out by neural states in error clamp trials. This shift is intriguing as it occurred to both the trained and untrained directions. It showed that the pre-movement neural activity generated a global change correlated with learning but not specific to the trained direction. In contrast, peri-movement neural states shifted immediately from the baseline repertoire and reflected the online feedback control of compensatory hand force. After-learning neural states also shifted away from the baseline repertoire, but distinct from the global shift of pre-movement states, it was local and reflected the bell-shaped generalization. These results support the hypothesis that the neural population may utilize distinct activity patterns during curl field learning in a categorically different way from the "re-association" strategy found in a short-term brain-computer interface learning context (Golub et al., 2018) and VMR learning when there is minimal demand for generating novel arm dynamics. These findings are a first step towards understanding how systematic changes in neural population activity facilitate learning novel arm dynamics and how neural circuits learn to adapt activity patterns to changing task demand.

2-F-91 Variable brain states practice improves the retention of motor memory

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A fundamental issue in motor learning is how to better retain the skills. Previous studies showed an advantage of variable practice over constant practice in the retention of motor memories for familiar tasks such as ball throws (Kerr & Booth, 1978). Yet its neural underpinnings remain unclear mostly due to the complexity of the learning processes. Here, we trained healthy humans in an arm-reaching task in a velocity-dependent curl force field (FF) and applied computational modeling to test the hypothesis that the benefit of variable practice is mediated through variations in sensorimotor cortex (SMC) activity during the formation of skill memory. In a first experiment, 50 adults, divided into five experimental groups, performed 110 reaching movements in the FF. One group had a single visual target to be reached, which was shown 10 cm forward from the starting position. In the other groups, 11 visual targets uniformly distributed in the range of ±2.5°, 5°, 10°, or 20° from the front target were used for the learning (10 reaches for each target). After FF learning, all participants performed 50 reaching movements to the front target in a force channel (FC) in which errors were absent. The results showed that the motor memories, quantified using the force exerted against the FC, were most retained for the participants who learned the FF with the target position varying ±2.5°. A state space model, incorporating a context vector (Ingram et al., 2017) and natural movement variability, predicted that variability in the target positions during learning allowed to recruit a larger number of motor primitives and to improve the retention of motor memory. We conducted a follow-up experiment to empirically validate this prediction. To this end, we manipulated cortical activity using transcranial direct current stimulation (TDCS) while participants performed FF learning to a single target (120 reaches). 56 adults were assigned to one of four conditions. One condition applied four patterns of TDCS to the SMC in which current flowed anteroposterior, posteroanterior, mediolateral, and lateromedial directions relative to the central sulcus. The others used one or two patterns of the TDCS or the four patterns in which current passed through the parietal cortex. After FF learning, TDCS was terminated and all participants performed 54 reaches toward the target in FC. We found that the force exerted against the channel retained 40% of the learned skills after 54 FC trials in the participants receiving four patterns of the TDCS to the SMC, though the other conditions retained less than 30%. Note that the skills at the end of the learning period were not different among the conditions. We concluded that introducing variable brain states during practice, either by modulation of task features or by transcranial application of weak electric fields, enables to establish a more robust representation of the trained skills, resulting to improve the retention of motor memory.

2-F-92 Interlimb transfer of sensorimotor adaptation may not reflect interhemispheric transfer: New insights from patients with corpus callosum abnormalities

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When humans adapt with one limb to a sensorimotor perturbation in a given workspace, this adaptation can generalize to a different workspace, or even to the opposite limb. Such generalization across limbs is known as interlimb transfer, and despite being well documented in the literature, there are still questions surrounding the underlying neural mechanisms (Ruddy & Carson 2013). For instance, several theoretical models highlight the corpus callosum as a potential key structure for mediating transfer (Taylor & Heilman 1980; Parlow 1989), however, certain research supports the involvement of ipsilateral projections (Criscimagna-Hemminger et al. 2003). To investigate the role of the corpus callosum in interlimb transfer, we implemented a prismatic adaptation protocol to test for transfer from dominant to non-dominant arm and from non-dominant to dominant arm in a range of patients with corpus callosum insult. Based on the models indicating the corpus callosum as a key brain structure mediating interlimb transfer, it would be hypothesized that such patients should not show interlimb transfer in either direction. Results from two patients with recent naturally acquired lesions of the corpus callosum and one agenesis patient revealed clear sensorimotor adaptation of the arm exposed to the prismatic goggles. Our key finding was that the two patients with recently acquired corpus callosum lesions demonstrated significant interlimb transfer from the dominant to non-dominant arm. Further, the agenesis patient showed normal sensorimotor adaptation along with significant interlimb transfer from dominant to non-dominant arm but also from non-dominant to dominant arm. These results provide new insights into the theoretical models and mechanisms of interlimb transfer of sensorimotor adaptation: they show that interlimb transfer of sensorimotor adaptation can be observed despite lesions or even a complete absence of the corpus callosum. Our findings thus suggest that interlimb transfer of sensorimotor adaptation may not reflect interhemispheric transfer, but perhaps relies on ipsilateral projections connecting the hemisphere and the arm or subcortical structures such as the cerebellum.

2-F-93 Broadband masking noise contributes to speech motor control under formant transformed auditory feedback

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Auditory feedback plays an important role in the speech motor control. Transformed auditory feedback (TAF) experiments have been taken to investigate the effect of auditory feedback on speech production by measuring the compensatory responses against the perturbations given to the formant frequencies which determine the vowel sounds. However, it is unclear how the naturalness of feedback speech sound in TAF affects the speech production. Our previous study examined whether low-pass filtered feedback speech sound affects the compensatory responses in TAF. As a result, the lower the cutoff frequency of the low-pass filter was changed, the greater the error of the formant compensatory responses became. This result suggests that the high-frequency information of feedback speech sound is important for stable speech production. It is considered that the high-frequency information of speech sound contains speaker individuality. In this study, the low-pass filtered speech sound was fed back into a speaker through a headphone with or without a broadband pink noise in TAF. If the pink noise is added to the low-pass filtered feedback speech sound, it is expected that speaker individuality is recovered by auditory masking. As a result, when the pink noise was added, the error of compensatory responses decreased and was close to that for no low-pass filtered feedback sound. This result may suggest that speaker individuality was recovered by the high-frequency information of pink noise, and then the improved naturalness of the feedback speech sound stabilized the speech production. However, it is not clear whether speaker individuality is recovered by a pink noise in fact. To investigate this, speakers were asked to repeat a syllable three times, and then rate "Do you feel that the feedback speech sound was spoken by yourself?" under various conditions: with or without the high-frequency information of speech sound and with or without a broadband pink noise. As a result, there was a tendency that average score was higher under the conditions that the pink noise was added to the low-pass filtered feedback speech sound. This suggests that speaker individuality was recovered by the high-frequency component of the pink noise. Results of two experiments suggested that the presence of high-frequency information of speech sound improved the naturalness of feedback speech sound, and the addition of broadband noise to the feedback speech sound which lacked high-frequency information also improved the speech sound naturalness, thereby improving the speaker's "sense of agency in speech production" and consequently contributing stable speech control. Our future question is whether adding a broadband pink noise to feedback speech sound plays a role in a bone conduction masking or improvement of speech sound naturalness.

2-F-94 Climbing fiber synchronization emerges with skilled movement acquisition

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Synchronization has long been recognized as a key feature of neural activity in the olivo-cerebellar climbing fiber system. Theory posits that dynamic regulation of olivary synchronization may help to flexibly coordinate the spiking of disparate circuit elements as needed for differing patterns of motor output. To date, however, it has remained unclear how large-scale synchronization relates to the acquisition of skilled movements. We therefore imaged cerebellar Purkinje neuron complex spikes in mice learning to make skilled targeted arm-reaches. Large-scale coherent neural complex spiking actually became more common as task performance improved over days of learning. Moreover, the spatial scale of correlated activity among Purkinje neurons expanded by hundreds of microns during the skill acquisition. As a result, in expert mice, before movement onset, spiking transitioned from more disordered to internally time-locked synchronized activity, followed by coordinated silence. The extent of synchronization among Purkinje cell ensembles covaried with kinematic stereotypy across single trials. Optogenetic manipulation of cerebellar-olivary feedback bidirectionally modulated neural synchronization, demonstrating that olivary synchronization is internally regulated by the cerebellum during the execution of this task. These findings argue that to prepare learned movements cerebellar circuits enter a self-regulated, synchronized state promoting well-coordinated motions. Synchronized states may underlie the functions of other motor circuits and brain systems.

2-F-95 Pupil-linked arousal modulates trial-by-trial adaptation during reaching

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Recent evidence suggests that arousal state linked with central noradrenergic (NA) system has widespread effects on various cognitive functions, such as an individual's choice behavior. While the NA system's widespread projections include the motor structures, such as the primary motor cortex or the cerebellum, little is known about the specific role of NA/arousal on the motor learning process. Here we address this issue by monitoring pupil diameter to noninvasively assess central NA activity while human participants adapt their arm movement to novel velocity-dependent force fields. We tracked eye movement and pupil diameter of 55 participants while they reach to a target holding the handle of a robotic manipulandum. They were told to fixate on the target throughout the movement. In experiment 1, 29 participants were exposed to constant force field either clockwise (CW) or counter-clockwise (CCW) direction. During reaching with no external force applied (null trials), the participants' pupil showed typical dilation toward the end of the movement. When the force field was applied, the dilation became significantly larger. The significantß deviation started at as early as ~400 ms from the reach onset. The trial-by-trial change in the pupil dilation correlated with that for the magnitude of movement error; a large jump at the introduction of force followed by a gradual decrease (r=0.22, p=2.42e-7), suggesting that pupil dilation may reflect the size of prediction error or surprise during movement. To further assess the relationship between pupil dilation and motor learning, 26 participants were assigned to experiment 2, where we assessed the amount of single-shot learning to random perturbations. The perturbation included null, CW, and CCW force fields. Amount of single-shot adaptation was quantified by comparing forces measured during the channel trials between immediately before and after a perturbation trial. To evaluate the effect of NA/arousal on motor adaptation, we split the data into above- and below-median pupil dilation during perturbation trials and compared the amount of learning between them. We found significant modulation of learning by the size of pupil dilation during perturbation trials (p=0.038). A similar effect was not found for the physical size of error (p=0.32). These results indicate that rather than the physical size of errors, pupil dilation during movement may reflect internal variables such as subjective error or surprise. The results also suggest that the NA/arousal system can influence the amount of trial-by-trial motor adaptation.

G – Theoretical & Computational Motor Control

2-G-96 Saccade vigor reflects utility in effort-based decisions

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Saccade vigor has been shown to reflect how individuals evaluate financial outcomes and correlate with the intrinsic reward value of the saccade target. However, less is known when considering costly or effortful options. In contrast to reward, the saliency (magnitude of an option's reward or punishment) and utility (option's goodness) do not go hand-in-hand. When considering two effortful options the more effortful and more salient option, will be the option with lower utility. Will saccade vigor reflect the saliency of the option (i.e. greater cost) or the utility of the option (less cost)? To probe this, we provided subjects (n=19) effortful options consisting of varying inclines and durations on a treadmill while recording their eye-movements to determine the overall value of a preferred choice. Choices were between a reference incline and duration and an alternative option of varying inclines and durations. Decisions and eye movements were recorded in two distinct phases: a deliberation phase when subjects made saccades between the two options presented on screen, followed by a decision phase where subjects confirmed their decision by making a saccade to their preferred option. An iso-cost curve was fit to each individual's choices and used to assess an objective utility model where utility was joules of energetic expenditure quantified as energetic rate multiplied by duration. We also considered a subjective utility model that considered an unequal weighting on rate (i.e. intensity) and movement duration. Results show that subjects made their decisions using a subjective cost model which produced choices significantly different than otherwise predicted by an objective cost model. As cost differences increased, subjects responded more quickly. However, when the reference was the more metabolically costly of the two, subjects responded more slowly overall. By the end of the deliberation phase, saccade vigor was greater towards the preferred option, suggesting that saccade vigor reflects utility, not salience. Saccade vigor also responded to the magnitude of differences in costs, but only when the reference was the costlier option. During the decision phase, subjects' reaction times were greater the smaller the difference in cost, but overall slower when the reference was the poorer of the two. These results demonstrate that saccade vigor reflects the subjective utility of an option, rather than the salience of an option. Additionally, our results indicate the subject do not consider objective effort costs when considering options varying in intensity and duration but rather subjectively value effort, with most subjects avoiding high-intensity options despite the shorter durations. Together these findings help us understand movement-related decisions and reveal intrinsic links between decision making and movement.

2-G-97 Rotational neural population dynamics in motor cortex are differentially prevalent during reaching and grasping movements

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Reaching movements are associated with slow oscillatory, or "rotational", neural dynamics underlying the activity of populations of neurons in primary motor cortex (M1). These dynamics have been touted as reflecting a fundamentally different role for M1 than that posited by traditional neural coding hypotheses. We study the extent to which such dynamics are also prevalent during grasping movements. To this end, we record the time-varying kinematics of the hand using a camera-based motion tracking system and population activity in motor cortex using chronically implanted electrode arrays as monkeys grasp a variety of different objects. We also analyze kinematic and neural data recorded as monkeys performed a delayed center-out reaching task. We find that rotational dynamics are less prevalent during grasping than during reaching: Moreover, we find that the emergence and differential prevalence of these dynamics during reaching and grasping can be predicted from traditional neural coding hypotheses. Finally, we find that attempts to harness such neural dynamics to decode kinematics fails to offer an improvement in grasp decoders, even as they substantially improve reach decoders. Analysis of M1 as an autonomous dynamical system therefore appears to offer particular insight into the control of proximal limb movements. However, our results suggest that low-dimensional rotational dynamics in M1 may fail to generalize as a description of neural dynamics during grasp, rather than being a universal task-invariant signature of cortical motor control.

2-G-98 A revised computational neuroanatomy for motor control

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We discuss a new framework for understanding the structure of motor control. Our approach integrates the highly influential discussion of the neuroanatomy of motor control published a decade ago by Shadmehr and Krakauer (2008), and other existing models of motor control, with the reality of hierarchical cortical processing and the parallel segregated loops that characterize cortical-subcortical connections. We also incorporate the recent claim that cortex functions via predictive representation and optimal information utilization (Clark, 2013; Kanai et al., 2015). Our framework assumes each cortical area engaged in motor control generates a predictive model of a different aspect of motor behavior. In maintaining these predictive models, each area interacts with a different part of the cerebellum and basal ganglia. These subcortical areas are thus engaged in domain appropriate system identification and optimization. This leads to the radical notion that the cerebellum and basal ganglia actually perform different functions in the support of each of the cortical areas. It also refocuses the question of division of function among different cortical areas. What are the different aspects of motor behavior that are predictively modelled? We suggest that one fundamental division is between modelling of task and body while another is the model of state and action. Thus, we propose that posterior parietal cortex, somatosensory cortex, premotor cortex and motor cortex represent task state, body state, task action and body action, respectively. We demonstrate how this division of labor can better account for many recent findings of movement encoding, especially in the premotor and posterior parietal cortices. Preprint available at: www.doi.org/10.31219/osf.io/t6prj

2-G-99 Development of anatomically correct musculoskeletal model based on MRI images

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Musculoskeletal model has become an indispensable tool for motion analysis and simulation in a wide range of field, such as motor control, biomechanics, sports, and rehabilitation. Especially in the field of motor control, musculoskeletal model has been used for investigating whether EMG-derived muscle synergies truly reflect neural aspect or biomechanical constraints. However, conventional musculoskeletal models have an important problem in representing muscle function. Since the muscles are simplified as a straight line or a polygonal line without volume, it is basically difficult to accurately express muscle paths (i.e., moment arms) especially around the shoulder joint where many muscles interact with each other in a complex manner. To fundamentally solve this problem, we have developed a new musculoskeletal model that considers muscle volume and deformation due to interaction between muscles. In this model, the muscle shape was represented by many mass points located in a 3D grid manner (on average about 200 mass points for each muscle). Although usually computational burden in simulating such a large degree of freedom is very high, the model resolved this problem by using the GPU parallel computing method for solving the equations of the motions. Muscle deformation due to interaction between muscles was realized not by the conventional penalty force method which was essentially unstable due to sudden change of the penalty force, but by placing a buffer object that corresponds to fascia between mutually adjacent muscles. To accurately model the muscle path around the joint (i.e., moment arms), not only muscle and bone but also connective tissues such skin and fat is indispensable. The skin was expressed with multiple thin patches along the skin secant line to cover the surface of the muscles. By connecting the skin and muscles with a spring mass damper model, the effect of the skin binding up the muscles was expressed. The fast was also modeled to fill the gap between muscles. Lastly, we developed a method creating subject-specific musculoskeletal model based on MRI images. The experiment was approved by the ethics committee in National Institute of Information and Communications Technology. This new musculoskeletal model and technique allows us to analyze muscle function in an anatomically accurate manner.

2-G-100 Transient behavior and predictability in manipulating complex objects

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Humans dexterously manipulate a wide variety of complex objects. A mundane example is leading a cup of coffee to the mouth to drink: the hand applies a force to the cup, and also indirectly to the liquid, which in turn acts back on the hand. Previous work in our lab investigated how humans tune into resonant frequencies when rhythmically moving a dynamic object. Unlike in free movements, subjects did not minimize effort but adopted strategies that rendered interactions predictable. In those studies subjects started from rest, always at the same initial conditions; the transient was excluded from analysis, which focused on steady state. But transients can be complex, depending on initial conditions. This study examined whether humans would choose initial conditions to reduce transient duration prior to reaching steady state. We hypothesized that subjects would choose initial conditions to minimize the duration of transients and adopt steady state behavior to render object dynamics predictable. The experimental task consisted of interacting with an object simulated by a robotic manipulandum with haptic feedback. The cup of coffee was abstracted to a cart-and-pendulum system moving on a horizontal line, where the subject moved the cart, while the pendulum was only moved indirectly. The cart-pendulum system was visually presented as a ball rolling in a cup depicted as a semicircular arc. Importantly, movements of the cup also accelerated the ball, which in turn acted back on the hand.

Participants moved the cup back and forth rhythmically between two targets paced by a metronome at 0.6Hz without losing the ball. They were instructed to explore and choose their initial conditions within the start box before initiating the rhythmic movement by exiting the start box when they were ready. Participants performed 120 trials, each 15s excluding pre-trial exploration. Dynamic simulations were performed to understand the effect of initial conditions. To calculate transient duration, steady state was defined at the time when relative phase between ball and cup position was approximately zero. Mutual information between applied force and object dynamics evaluated predictability of the steady state behavior. Preliminary results showed that subjects indeed established a steady state defined by zero relative phase between cup and ball. The duration of the transient prior to reaching steady state decreased with practice. Subjects converged to different initial conditions. Simulations revealed that these initial conditions corresponded to shorter transients. Assessing the steady state segments revealed that mutual information increased with practice. These results present first support for our hypothesis that humans can identify initial conditions that minimize transients and favor steady state behavior that enhances predictability.

2-G-101 Discovering preference in human locomotion with robust inverse optimal control

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The study of motor control and learning is often concerned with the solution of inverse problems. Given an observed behavior, we seek to identify the underlying set of objectives that gave rise to the behavior. For example, a subject walking on a treadmill generally exerts a minimal amount of metabolic effort. When adding perturbations, more metabolic energy may be used. However, these measurements alone do not discriminate between the subject's choices. That is, the subject may spend more energy for a more stable gait, lowering fall risk. Or the subject may still prioritize energy, but perform more work due to unavoidable perturbed gait changes. To discriminate between such interpretations we propose an inverse numerical model optimization method to identify cost functions. We develop a computational method to describe preference in locomotion. This is called Inverse Optimal Control (IOC) because it inverts the optimal control problem of finding a behavior given a cost function. We seek to identify a cost function based on behavior. Here, we quantify tradeoffs between different costs in simple mechanical models of steady speed walking given a single step of the observed gait. The method assumes a mechanical walking model and the components of an underlying preference function. We assume the behavior results from an optimal controller, which chooses the gait by minimizing a linear combination of cost components. Cost components include squared joint torque or torque derivative integrated over the stride. An iterative process is used to propose and refine possible weightings of the cost components. We perform computational experiments to test robustness of our IOC to imperfections in measurements, modeling of the walker or task, and knowledge of the cost components. We expect all of these imperfections when applying IOC to experimental data. Without robustness to these imperfections, limited trust could be placed in the results with real data. In particular, we test 4 conditions: ideal, 10% speed mismatch, legs 10% heavier, 10% additive Gaussian noise, and a distractor case with 3 superfluous cost components. We test 4 sets of optimal gains in each condition, prioritizing different costs. IOC error is based on mean absolute normalized difference between estimated gains to optimal. Under ideal conditions, mean absolute error in weights was lowest

(16%). The speed or mass disturbed cases were worse (23% for both), followed by the distractor case (26%) and finally the noisy signal case (39%). Our method identified qualitative differences between cost functions, but is less robust to unknown cost components. This illustrates an issue with IOC, as a family of cost functions may yield similar behavior. Therefore care must be taken when choosing cost components, ideally as part of hypothesis and experimental development. IOC may allow identification of individual preference to help inform rehabilitative therapies for specific conditions.

2-G-102 Learning of generative neural networks models for EMG data constrained by cortical activation dynamics

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Recurrent Artificial Neural Networks (RNNs) are popular models for neural structures in motor control. A common approach to build such models is to train RNNs to reproduce the input-output mapping of biological networks. However, this approach suffers from the problem that the internal dynamics of such networks are typically highly under-constrained: even though the networks correctly reproduce the desired input-output behavior, the neural dynamics are not under control and usually deviate strongly from the ones of real neurons. Here, we show that it is possible to accomplish the dual goal of both reproducing the target input-output behavior and constraining the internal dynamics to be similar to the ones of real neurons. As a test-bed, we simulated an 8-target reaching task; we assumed that a network of 200 primary motor cortex (M1) neurons generates the necessary activity to perform such tasks in response to 8 different inputs and that this activity drives the contraction of 10 different arm muscles. We further assumed to have access to only a sample of M1 neurons (30%) and relevant muscles (40%). In particular, we first generated multiphasic EMG-like activity by drawing samples from a Gaussian process with covariance function opportunely chosen to have the samples resemble EMG activity during reaching. Secondly, we generated ground truth M1-like activity by training a stability-optimized circuit (SOC) network (Hennequin et al., 2014) to reproduce the muscle activity for the 8 different tasks trough gain modulation (Stroud et al., 2018). Critically, the neurons of such network have been shown to behave similarly to M1 neurons during the execution of limb movements. Finally, we trained two RNN models with the full-FORCE method (DePasquale et al., 2018) to reproduce the subset of observed EMG activity; critically, while one of the networks was free to reach such a goal through the generation of arbitrary dynamics, the other was constrained to do so by generating, through its recurrent dynamics, activity patterns resembling those of the observed SOC neurons. To compare the population activity of the networks, we first constructed low-dimensional neural response vector spaces by applying PCA to the activity vectors of all neurons, and then we measured the similarity of the EMG projected in such spaces. This analysis revealed that both RNNs were able to reproduce the EMG trajectories accurately, but the one with constrained internal dynamics showed a greater similarity in the neural response space with the SOC network. Such similarity is noteworthy since the sample used to constrain the internal dynamics was small. Our results suggest that this approach might facilitate the design of neural network models that bridge multiple hierarchical levels in motor control, at the same time including details of available single-cell data. Funding: BMBF FKZ 01GQ1704, DFG GZ: KA 1258/15-1; CogIMon H2020 ICT-644727, HFSP RGP0036/2016, KONSENS BW Stiftung NEU007/1

2-G-103 **A Model of speed-accuracy trade-offs based on human arm dynamics**

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In the previous studies, it has been shown that the speed-accuracy trade-offs in the human arm movements may be affected by kinematics, dynamics, and noise factors. However, it has not been proposed a unified model that concretely explains how each factor relates to speed-accuracy trade-offs. In this study, we clarified that the hand endpoint error can be expressed as a function of the movement duration, desired trajectories, velocities, acceleration, arm dynamics parameters (i.e., arm length, mass, distance from the center of mass to the joint, the moment of inertia, and joint viscosity), and signal-dependent noise parameters. This was derived from the relationship between movement duration and hand endpoint error based on the forward and inverse dynamics models of multi-joint human arm. In order to demonstrate how this theoretical model can explain the speed-accuracy trade-offs in observed movement, we conducted the experiment where 11 subjects carried out arm reaching movements in four directions (front, back, left, and right) in the horizontal plane while the movement speed was controlled. When comparing the endpoint errors estimated from the model with those of the actual movement, we found that the difference of the endpoint errors was small. Furthermore, we simulated the endpoint error in various directions when the dynamics parameters were gradually changed using the proposed model. In consequence, direction-dependent changes of the endpoint error were found relative to the changes of dynamics parameters and relationship between the endpoint error and the parameters are not merely linear. To our knowledge, it is the first time that a unified mathematical model of speed-accuracy trade-offs considering kinematics, dynamics, and noise factors was proposed. It might be one step closer to elucidating the speed-accuracy trade-odd mechanisms of arm movement in the human brain.

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