



1-A-1 Effects of transcranial magnetic stimulation of FEF on neurophysiological activity in contralateral FEF

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Transcranial magnetic stimulation (TMS) allows non-invasive perturbation of neural activity, induced by a rapidly changing magnetic field. Both single pulse and repetitive TMS (rTMS) have been shown to modulate behavioural output. Despite being considered an important methodology in cognitive neuroscience and as a potential treatment for neurological disorders, a precise understanding of the effect of TMS on neural activity in an interconnected brain network, and how such effects influence behavior, is largely lacking. To overcome this gap, we are developing an animal model of TMS, focusing on the oculomotor network in non-human primates (NHPs). Previous work has shown that delivering single-pulse TMS to the frontal eye fields (FEF) evokes feed-forward neck muscle responses, likely through the downstream superior colliculus, that can be used to localize optimal TMS position over the frontal cortex. Now having a reliable means of delivering TMS to the FEF, we are able to apply TMS either in a rapid pattern (e.g., single- or double-pulse TMS delivered at a precise time during a behavioural task), or in a repetitive pattern (e.g., 1-Hz TMS for 10-15 minutes). Our current focus is to examine the effects of TMS of one FEF on spiking and local field potential activity in the contra-lateral FEF. NHPs are performing either an intermixed pro- and anti-saccade task, or a memory-guided saccade task. In several recording sessions, we tested the effects of TMS on neurophysiological activity and behaviour after-single pulse TMS at various times of task execution, or by investigating the effects of rTMS in a block design. We present preliminary results from the inter-mixed pro- and anti-saccade task, which revealed a diversity of effects on single unit spiking activity, further contributing to optimization of our experimental approach.

1-A-2 Functional connectivity of the superior colliculus in macaques and marmosets investigated with resting-state ultrahigh-field fMRI

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Interest in the common marmoset monkey (*Callithrix jacchus*) is growing rapidly as it is poised to become the leading candidate transgenic primate model. In contrast to the very established Old World macaque monkey, little is known about the functional organization of the saccade circuitry in these small New World primates. Here we used resting-state ultrahigh-field fMRI collected from 12 anesthetized macaques and 4 anesthetized marmosets to examine and compare the functional connectivity of the superior colliculus, a major node in the neural network underlying the control of saccades in primates. Macaque data were obtained on a 7T Siemens MR scanner using a custom-built 8-channel transmit/24-channel receive coil and marmoset data were acquired on a 9.4T Varian MR scanner using a custom-built 2-channel transmit/15-channel receive coil. In both species, the seed region analysis revealed functional connectivity of a fronto-parietal network with the superior colliculus. In macaque monkeys, the network overlapped with the previously described functional connectivity pattern of the frontal eye fields and included also the intraparietal sulcus, dorsolateral



prefrontal cortex, anterior cingulate cortex, and supplementary eye fields. A visualization of the cortical functional connectivity map on a surface-based registration revealed the strongest bilateral connectivity in frontal cortex in areas 6DC, 6DR, 8AC and 8aD in and in parietal areas PFG and PF in marmosets according to the atlas by Paxinos and colleagues (Paxinos et al. (2012) The marmoset brain in stereotaxic coordinates. Elsevier). In addition, we found strong FC of the marmoset SC with areas MT, V4T, FST, and TE2, TE3, and TF. The results support an evolutionarily preserved frontoparietal system and provide a starting point for invasive neurophysiological studies in marmosets.

1-A-3 Cerebellar ataxia patients update inverse models for head movement control: lessons from a control systems model

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The cerebellum is considered essential for implementing internal models, of which inverse models generate motor commands for a desired movement and forward models predict sensory consequences of motor commands. Cerebellar damage impairs internal model adaptation, leading to deficient motor learning. However, cerebellar patients can adapt to perturbations in reaching experiments and re-optimize gaze shift kinematics to altered head plant properties. Here, we investigate possible mechanisms for such optimization. Using a physiologically consistent control systems model, we assess the contributions of inverse and forward model plasticity on updating head kinematics during gaze shifts to an increase in head inertia in nine cerebellar ataxia patients and ten controls. We find that the experimentally observed changes in head movements of cerebellar patients are explained by assuming that the inverse model, but not the forward model, is adapted to match the new plant characteristics. By adapting the inverse model it is possible to optimize head movement kinematics, i.e., to decrease suboptimal oscillations, maintain optimal movement durations, and increase peak velocity towards the new optimum. This suggests that the residual extra-cerebellar motor control network can implement inverse models, update intended movements and re-optimize without correctly predicting sensory consequences of action.

1-A-4 Automatic Classification of Saccadic versus Fixation Phases for Head-Free Gaze Shifts Using Supervised Support Vector Machines with Gaussian Kernels

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The gaze orientation system generates two major types of response: the saccadic (fast) phase and the fixation (slow) phase. The analysis of the responses of this system however, is often limited to either the slow-phase or the signal (eye or gaze) envelope, which is again dominated by the slow phase. This is in part because of the level of complexity associated with the fast/slow phase classification. In this work we propose a supervised learning method that automatically classifies noisy gaze signals with high accuracy. The applications of this method can be in fast and efficient automatic classification and identification of gaze orientation phases, as well as in diagnostic



protocols for the gaze system pathology. During the saccadic phase intervals, all plants (e.g., eye and head) collaborate to move the gaze to the desired target in space. Once the target is acquired, the gaze system switches to the fixation phase, in which the eye counter-rotates the head to keep the gaze on target. These phases have very different dynamics which are considered in any phase detection algorithm. To move forward on more accurate identification of nystagmus dynamics, objective (automated) classification is preferable. Few methods are currently available without user intervention to sort intervals in gaze nystagmus. In this work we introduce a new objective classification in the context of gaze shifts (saccade vs. fixation) using the supervised Support Vector Machine (SVM) method with the Gaussian Kernel. Simulations in this work are generated using the state-of-the-art Sensory-Motor-Fusion (SMF) model of the gaze orientation system (Haji-Abolhassani, Guitton, and Galiana - under revision for JNP), based on the Prsa-Galiana model. Gaze shifts were generated at the sampling frequency of 1KHz with Matlab Simulink[®] to train and test the classifier. The data was degraded by additive white Gaussian noise (AWGN) of different powers to evaluate the proposed classification method. The features used for the classification were low-passed versions of the eye and gaze position and velocity signals. To account for the filtering 'window leakage' effect at phase switching instances, multiple low-pass filter orders were used to create a rich feature set for classification. These features were fed to the SVM Gaussian Kernel Classifier for training using samples drawn randomly from the data. The size of the training set was set to different values to evaluate the learning curves, and training relied on few known switching intervals from the simulation. The results show very high F1 scores (above 97%) for even extremely noisy cases (much higher than experimental noise levels) that enable this method to be used for efficient classification of gaze signals. This non-subjective approach to classification opens doors for analysis and identification of both fast and slow-phases in any ocular or gaze nystagmus.

[1-A-5 Modeling multisensory evoked gaze shifts in dynamic double steps.](#)

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In a dynamic visual or auditory gaze double-step trial a brief target flash or sound burst is presented in midflight of a rapid intervening eye-head gaze shift (Vliegen et al., 2004, 2005). Our experiments have indicated that the subsequent eye- and head movements in such trials are goal directed, regardless stimulus timing, first gaze-shift characteristics, and initial conditions. This remarkable behavior requires that the gaze-control system has access to accurate signals about instantaneous eye-in-head, $EH(t)$, and head-on-body orientation, $HB(t)$, that it accounts for different internal signal delays, and that it is able to update the retinal (TE) and craniocentric (TH) target coordinates into appropriate eye-centered and head-centered motor commands on millisecond time scales. As predictive remapping (Duhamel et al., 1992) cannot account for this behavior, we propose that instead targets are transformed into a world-centered reference frame (TW) as soon as the sensory information becomes available (at $t=t^*$). In this way, visual target coordinates on the retina are mapped according to $TW,V=TE(t^*)+EH(t^*)+HB(t^*)$, and an acoustic target re. the head becomes $TW,A=TH(t^*)+HB(t^*)$. Note that the world-centered target coordinates are invariant to further intervening eye- and head movements. We present a computational model in which the recruited neural population in the midbrain Superior Colliculus drives eyes and head to the remembered



target location through a common dynamic gaze-displacement command, which is continuously derived from the stable world-centered goal (Goossens & Van Opstal, 2012; Van Grootel et al., 2011). The model successfully accounts for the complex, yet accurate, kinematic behaviors and trajectories of eye-head gaze shifts under a variety of highly challenging multi-sensory conditions, such as in dynamic visual-auditory double steps. Acknowledgments: Supported by Radboud University Nijmegen, The Netherlands, and by EU grant #604063 Marie-Curie FP7 'HealthPAC' References: Vliegen et al., J Neurosci 24: 9291, 2004; Vliegen et al., J Neurophysiol 94: 4300, 2005; Duhamel et al., Science 255: 90, 1992; Goossens & Van Opstal, PLoS Comp Biol 8: e1002508, 2012; Van Grootel et al., J Neurosci 31: 17497, 2011

1-A-6 Mechanisms of saccade initiation within the superior colliculus: insights following frontal eye fields inactivation

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Although the frontal eye fields (FEF) and intermediate layers of the superior colliculus (SC) are two key oculomotor areas in saccade generation, their relative contributions to saccade initiation and the manner in which the oculomotor system ultimately commits to a saccade remain unclear. Until recently, it was largely believed that saccades occurred when FEF and/or SC activity increased above a fixed threshold, so that any changes in saccade reaction time (SRT) relative to a go-cue were primarily due to the rate at which activity increased. However new evidence suggests saccade threshold may not be fixed and that other factors such as the onset of accumulation are also important determinants of SRT. Here, we study the contribution of the SC to saccade initiation when the FEF is inactivated; doing so provides a valuable opportunity to gain further insights into the brainstem mechanisms of saccade initiation. To examine this, we reversibly inactivated large portions of the unilateral FEF using cryogenics, and recorded saccade-related bursts within ipsilateral SC neurons while monkeys performed delayed visually- and memory-guided saccades. Since FEF inactivation caused the expected set of contralesional deficits in saccade generation (i.e., increased SRT, decreased amplitude, and peak velocity), we matched saccades generated before or during inactivation ($< 1^\circ$ horizontal and vertical displacement vectors, and $< 10^\circ$ radial peak velocity) to ensure that any changes in SC activity were not confounded by altered saccade metrics and kinematics. We specifically analyzed how FEF inactivation affected certain parameters of SC activity and SRT in a rise-to-threshold model (i.e., onset of accumulation relative to a go-cue, accumulation rate, and threshold activity immediately before saccade onset). We found that the increases in SRT with FEF inactivation were best explained by not only a decreased rate of accumulation of SC activity, but also by a delay in the onset of accumulation. In contrast, we did not observe any increase in saccade threshold with could have been predicted by the increased SRTs; in fact, SC threshold activity paradoxically decreased during FEF inactivation. We speculate that the differences in SC activity relating to increased SRTs are contingent on the integration of SC spikes within a short-time window in the downstream brainstem burst generator.

1-A-7 Dentate nucleus contribution to human eye movement control: insights from cerebrotendinous xanthomatosis patients



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The medial cerebellum (vermis and fastigial nuclei) is well known to be involved in saccade motor control. A role of the cerebellar hemispheres and dentate nuclei (DN) in oculomotion has also been suggested, but the extent and nature of their contribution to eye movement is not understood. Bilateral DN degeneration is a peculiar abnormality of cerebrotendinous xanthomatosis (CTX), which thus provides a unique opportunity to study the impact of DN on human oculomotor control. Nonetheless, eye movements have not been extensively investigated in this disease. CTX is an autosomal recessive lipid storage disorder due to mutations in CYP27A1. Pathological high plasma and tissue cholestanol concentrations lead to infantile-onset diarrhea, juvenile cataracts, tendon xanthomas, and progressive neurological dysfunctions including psychiatric and cognitive disturbances, pyramidal and extra-pyramidal signs, and cerebellar ataxia. DN abnormality is reported in about 75% of patients, but so far, no clinical differences related to DN involvement have been described in CTX patients. We analyzed the eye movements of nineteen CTX patients during the execution of horizontal and vertical visually-guided saccades and horizontal anti-saccades. Main saccadic dynamic parameters and anti-saccade error and correction rate were computed. Results were interpreted in relation to presence/absence of DN involvement at brain MRI. Data were compared with those of a matching group of 19 healthy subjects. We found that CTX patients could execute normally accurate saccades with normal main sequence relationships (peak velocity vs. amplitude and duration vs. amplitude), which indicates that the brainstem and medial cerebellar saccadic structures are likely spared. Patients with CTX also showed more frequent multistep saccades and directional errors during the anti-saccade task than controls, suggesting facilitation in releasing premature reflexive saccades. Patients with DN damage showed even more frequent directional errors, which were mostly not followed by corrections. DN would, then, participate in modulating complex voluntary behaviors such as suppressing reflexive saccades and executing self-paced movements. Moreover, patients with DN damage showed saccades with normal accuracy, but longer latency and worse precision than either controls or patients without DN involvement. This indicates that a network involving the medial cerebellum locates the movement target and determines the accuracy of the saccade. The DN would, instead, utilize different inputs, likely from frontal and prefrontal areas, to confirm and refine the location of the selected target, improving the precision of the movement. The medial and lateral cerebellar computations might converge on the superior colliculus, where the area corresponding to the movement target would be first broadly located and then refined.

1-A-8 Variations in Response Gain in Frontal Cortex Linked to Variability in Saccadic Reaction Time

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We revisited a fundamental question in oculomotor neuroscience: how does single-neuron activity in the frontal eye field (FEF) relate to the timing of eye movements? To investigate the neural correlates of choice, reward availability, reaction time (RT), and movement metrics, monkeys performed a RT variant of the one-direction-rewarded (1DR) task. In each trial, the animals maintained fixation at a central spot and made a saccade when an eccentric stimulus appeared at one of 4 possible locations, but crucially, only one location was associated with the primary reinforcer. Behavioral effects were clear: saccades to rewarded locations were precise and consistently short latency, whereas those to unrewarded locations were longer latency and of highly variable metrics. We exploited the large spread in RT and spatially distinct reward conditions in the 1DR task to study how individual FEF neurons contribute to saccade production. This exposed a novel, strong dependency: for most neurons, the maximum firing level either increased or decreased monotonically as a function of RT. This was true for all neuronal classes in FEF regardless of their visuomotor properties. Furthermore, modeling results suggest that the two complementary populations with similar response fields but opposite temporal selectivities serve a distinct purpose, to control, according to their relative gain, whether the ensuing RT is short or long. These findings are significant for two reasons. First, it is thought that saccades are triggered when the firing level in FEF reaches a fixed threshold, but according to our results, this is true only in an average sense; for individual cells, the presaccadic firing rate attained may vary substantially with RT, either positively or negatively. Second, the results pinpoint a fundamental source of variability in RTs -- fluctuations in the gain of fast- and slow-preferring complementary populations -- and propose a specific mechanism whereby cortical circuits may regulate the timing of motor commands.

1-A-9 Predicting future actions

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We designed a two-person competitive reaching task in a naturalistic setting. Two Subjects faced each other separated by a plexiglass screen. One (Attacker) was instructed to tap one of two targets on the screen and the other (Blocker) was told to tap the same target as quickly as possible. Blockers' reaction times were fast, almost 90 milliseconds faster than reaction times to a dot projected on the screen moving in the same manner. This suggests Blockers use subtle preparatory movements of Attackers to predict their goal. This was confirmed using spliced video recordings of an Attacker, where we removed the 90-millisecond segment before attacker movement initiation. Blocker reaction times were correspondingly slowed. Substituting putative preparatory videos of the reverse movements led the Blockers to initially choose the wrong target. We systematically occluded various body parts of the Attacker and showed that reaction times slowed down only when most of the body of the Attacker was occluded. This indicates that preparatory cues are well distributed over the body of the Attacker. We repeatedly saw no evidence of learning during the experiment, as reaction times remained constant over the duration of the session. We deem this lack of learning to be of particular significance as it suggests that humans have implicit knowledge of the biomechanical constraints of the bodily movements of others and use it to accurately predict their future actions. Furthermore, application of this knowledge is robust such that visibility of only small portions of the body is adequate for such predictions.



1-A-10 Beta oscillations between the subthalamic nucleus and substantia nigra pars reticulata during automatic and voluntary movement

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The basal ganglia (BG) network is implicated in switching between automatic and voluntary saccadic eye movement, and can influence saccade initiation via output to the superior colliculus and frontal eye fields. Previous electrical stimulation of the subthalamic nucleus (STN; BG input) and substantia nigra pars reticulata (SNr; BG output) suggested a juxtaposition of tonic activity in the inhibitory subthalamo-nigral pathway during voluntary movement (e.g., slower but accurate goal-directed movement), versus the facilitatory subthalamo-pallidal-nigral pathway during passive or automatic movement (e.g., fast automatic saccades, such as toward unexpected stimuli). We provide complimentary neurophysiological evidence, by examining changes in local field potential oscillation and coherence between simultaneously recorded electrodes in the STN and SNr. Two monkeys performed a free-viewing, pro- (look toward), and anti-saccade (look away) task, to recruit a continuum of automatic to voluntary control, while activity was recorded in both structures (n = 15 acute electrode pairs, 1500+ trials per pair). First, we found that coherence between the STN and SNr was strikingly decreased in beta frequencies (15-30 Hz) during the peri-saccadic period. Grouping trials according to high or low beta STN-SNr coherence revealed a robust increase in saccade latency during high coherence trials in all tasks. Second, we found a strong relationship between beta oscillatory power and saccade latencies, by grouping trials according to STN or SNr power. Beta oscillations in both structures were positively correlated with free-viewing saccade initiation, but had a mixed effect during pro-saccades, and were inversely correlated with anti-saccade initiation. Strikingly, beta oscillations were positively correlated (e.g., similar to free-viewing) and negatively correlated (e.g., similar to anti-saccades) with pro-saccade initiation, according to conditions with low or high STN-SNr coherence, respectively. Overall, this implies a task-dependent effect of beta oscillations that switches across the continuum of automatic to voluntary movements, which may be facilitated by STN-SNr coherence. We suggest these differences may be attributable to changes in BG networked activity during the suppression of reflexive responses and volitional execution of saccades, and are consistent with the juxtaposition of subthalamo-nigral and subthalamo-pallidal-nigral pathways implicated in these conditions.

1-A-11 Contextual influences on the behavioral effects of electrical stimulation with a vestibular prosthesis: eye and head orientation effects.

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Background: A vestibular prosthesis has the promise of restoring natural vestibular function using head motion modulated electrical stimulation of the vestibular nerve. One important function is the stabilization of gaze. In order to perform this function, the device must operate predictably in a variety of contexts, including different head orientations with respect to gravity, and different eye orbital positions. In our experiments, we examined the characteristics of electrically elicited eye



movements during electrical stimulation with one such device. Methods: Rhesus monkeys were implanted with a vestibular prosthesis identical to devices currently evaluated in human patients. The fully implantable device was activated to produce brief biphasic pulse trains that varied in current amplitude or pulse frequency. The animals sat in a chair positioned in front of a curved screen onto which point targets could be projected with a laser mirror galvanometer system. The chair and screen could be tilted together into different static orientations. Stimulation trials were performed in the dark, immediately following removal of a fixation target, to obtain stimulation trials initiated in different orbital eye positions and different static head positions. The resulting eye movements were recorded with implanted scleral coils. In some experiments, abducens field potentials were recorded during electrical stimulation using tungsten microelectrodes. Results: Both eye orbital position and static head position had significant effects on the velocity of the elicited eye movements. Both the direction and the magnitude of the eye velocity were affected. Horizontal eye velocities elicited by lateral canal stimulation generally increased with increasing initial eye position in the direction of the elicited eye movement. Vertical eye velocities elicited by posterior canal stimulation increased with increasing eye position opposite of the direction of the elicited eye movement. En block static tilt produced consistent changes in the velocity of elicited eye movements. These effects scaled with eye position, tilt position, and stimulation current. Limited abducens recording during stimulation revealed no changes in the evoked potentials based on initial eye position. Conclusions: Eye movements elicited by a consistent electrical vestibular stimulus are influenced by initial eye position and head orientation. The changes with respect to eye position occurred despite no observable change in abducens neural response to electrical stimulation. These results suggest that significant central modification of vestibular inputs are needed to produce consistent stabilization of the eye during head movement based on the eye position and head orientation context in which such movements occur, and that brief electrical stimulation may bypass this mechanism. Funding: NIDCD, NCRR-ORIP, Cochlear Ltd., Wallace H. Coulter Foundation

1-B-12 Neural mechanisms of predicting multisensory consequences of one's own action

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It has been proposed that the prediction of sensory action consequences is based on a forward model. This model generates predictions using the efference copy, and compares the predicted with the actual sensory outcome. Previous studies found that brain activity in parietal and temporal areas correlates with the amount of delay between action and sensory outcome, suggesting these are candidate comparator areas. However, so far only unimodal action outcomes were investigated. Since most actions lead to multisensory consequences we aimed to investigate the neural mechanisms behind multisensory action predictions. We tested 21 participants in our fMRI study. They were required to press a button at a self-chosen time, which led to the presentation of either a tone, a dot on the screen, or both, at various delays after the button press. Then, subjects had to report whether they detected a delay between button press and action outcome of the modality defined at the start of the run (referred to as task modality). Psychometric functions were fitted to the behavioural data. A repeated-measures ANOVA of the thresholds showed a main effect of condition (unimodal vs bimodal), with lower thresholds for bimodal trials, and a main effect of task



modality (visual vs auditory), with lower thresholds for visual trials. In our analysis of the fMRI data, we parametrically modulated the regressors for each stimulus type with the amount of delay. A cluster in the left angular gyrus correlated positively with delay for unimodal visual trials. For unimodal auditory trials, left and right angular gyrus were found. A conjunction analysis between the two identified a cluster in the left angular gyrus. For the bimodal conditions, a clear task effect arose. In the bimodal visual task, brain activity correlated with delay in the right superior temporal gyrus, whereas in the bimodal auditory task, delay was correlated with activity in bilateral visual cortex, bilateral angular gyrus, and anterior and posterior cingulate gyrus. A conjunction analysis identified anterior and posterior cingulate gyrus as the common areas for both tasks. In sum, the angular gyrus seems to be a supramodal comparator area, detecting delays in both visual and auditory unimodal trials. However, we show that bimodal action outcomes, and their temporal violations, are processed differently. ACC and PCC have been associated with self-other distinctions, which might be especially important when one's own action consequences are delayed in a multisensory context. Furthermore, areas in which neural activity correlated with delay in bimodal trials were influenced by the task, highlighting the relevance of top down processes during multisensory perception. These preliminary results suggest that the comparison of predicted and actual action outcomes may not be based on a single area, but rather on a network of areas fulfilling different roles depending on the task.

1-B-13 Proactive inhibition does not differentially affect preparatory activation between limbs

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Proactive inhibition enables the stopping of one response without affecting other responses. To examine this in a laboratory, it appears critical that participants are provided with a precue (e.g., maybe stop right), allowing them to prepare in advance which limb might have to be stopped in a task involving the two limbs. This proactive inhibition has been linked to a decrease in corticospinal excitability (CE) related to the limb that might have to be inhibited. It is unknown how proactive inhibition affects the uncued limb, which does not require stopping. Specifically, it is unclear how preparatory activation or activation related to the initiation of the response is affected. The startle technique was used to probe response preparation, as it has been shown that if a motor response is sufficiently prepared in advance, a startling acoustic stimulus (SAS: 120 dB white noise) can involuntarily trigger the initiation of the prepared response. As proactive inhibition is thought to exert an inhibitory influence on the activation of a specific response, it was hypothesized that the SAS would only trigger the response associated with the limb that did not require stopping (i.e., the uncued limb). Subjects were instructed to simultaneously initiate a bilateral isometric wrist extension upon the appearance of a visual go-signal. Occasionally, the go-signal was followed by a unilateral stop-signal after a variable delay. The stop-signal (M or W) instructed subjects to try to stop one response while still executing the other one. In each trial a precue was presented for 500 ms, consisting of either "maybe stop right" (MSR), "maybe stop left" (MSL), "maybe stop XXX" (MSX), or "null". The MSR and MSL precues provided foreknowledge about which response might need to be stopped (foreknowledge conditions), whereas the MSX cue was ambiguous as to which response might have to be stopped (ambiguous condition). The null precue indicated that no response was



necessary that trial. On every trial single pulse TMS (112% of RMT) was delivered 1000 ms following precue offset over the wrist extensor hotspot. The go-signal occurred 1500-3000 ms following precue offset, and a SAS was pseudorandomly presented concurrent with the go-signal in MSR, MSL & MSX conditions. Consistent with previous findings, reaction time (RT) of the responding limb was not affected by having to stop the other limb in the foreknowledge conditions, whereas RT was significantly delayed in the ambiguous condition. In contrast to previous findings, TMS results revealed no reduction in CE in the limb that was cued to potentially stop compared to both the uncued or ambiguously cued limb. The presentation of the SAS rarely led to response triggering, but resulted in the simultaneous triggering of both responses when it occurred. The results suggest that while proactive inhibition was being used in the foreknowledge conditions, both cued and uncued responses had similar levels of preparatory activation.

1-B-14 Enhancing tactile information during reaching movements

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Tactile stimuli presented on a moving limb are generally perceived weaker than they actually are. This phenomenon of tactile suppression has been explained by predictive and postdictive processes, like feed-forward mechanisms and reafferent masking, respectively. Suppressing tactile information is paradoxical, as humans need to rely on incoming somatosensory signals even when performing simple daily movements. In order to examine whether the perception of tactile stimuli during a movement depends on the relevancy of the upcoming somatosensory information, subjects performed reaching movements either to a visual (LED) or a proprioceptive (digits of their unseen hand) target. Two brief vibrotactile stimuli (50 ms, 250 Hz) were simultaneously presented: a reference stimulus to the little finger of the left static hand, and a comparison stimulus to the index finger of the right moving hand. Two reference stimuli were combined with thirteen comparison stimuli that differed in intensity. Subjects were asked to discriminate which of the two stimuli felt stronger. We fitted the data to a psychometric function and determined the point-of-subjective-equality (PSE). PSEs were substantially higher when reaching to the proprioceptive than to the visual target. Thus, subjects seem to suppress the tactile stimulus on the right moving hand more strongly when reaching to the proprioceptive than the visual target. However, this stronger suppression could also be caused by tactile enhancement of the left target hand. In order to test this, we conducted a second experiment, with the reference stimulus presented to a location irrelevant for the task (sternum), while subjects performed the same reaching task as before. In that case, the PSEs did not differ when reaching to the visual or the proprioceptive target, suggesting that the stronger suppression during proprioceptive reaching in experiment 1 was likely caused by enhanced tactile perception of the reference stimulus on the left static target hand. This suggestion is based on the fact that the reaching movement was always the same, but the tactile information was more relevant when reaching to the proprioceptive target; i.e., tactile information can inform about the performance of the proprioceptive but not of the visual reaching movement. In a third experiment, we examined whether such tactile enhancement is specific to the target digit or spread across the target hand. Subjects reached with their right index finger either to their left thumb or left index finger. A reference stimulus was presented to the left little finger and a comparison stimulus to the



left thumb or left index finger. We found that tactile perception can be specifically enhanced at the location where somatosensory information is relevant. In sum, we suggest that tactile perception can be flexibly modulated in a predictive manner depending on the relevancy of the somatosensory information for the movement.

[1-B-15 Strong coding of grasp force planning and execution in macaque areas F5, M1 and AIP](#)

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It is known for a long time that hand and wrist force is represented in the primary motor cortex (M1) and, to a lesser extent, in the premotor cortex. These classical studies focused on force exertion in a restricted setting without a reach component. With the advancements of neural prosthetics, studies now tend to focus on understanding the motor system by investigating more natural movements. Also, planning activity before action initiation is often analyzed to predict upcoming movements. Much progress has been made in recent years in extracting kinematic planning and movement information from cortical activity, but only few have looked at how cortex plans force. Here, we investigated grasp force planning and execution for two grip types in the monkey (*Macaca mulatta*). In addition to the hand area of M1, we recorded from ventral premotor cortex (F5) and the anterior intraparietal area (AIP), which are both involved in grip type planning. We trained two macaque monkeys on a delayed grasping task, in which a handle had to be grasped with either a whole-hand grip or a precision grip. Every grip had to be held for 1 s at one out of three force levels. Both the grip type and the required amount of force were cued simultaneously before the monkey was allowed to act. Neural activity was recorded from F5, M1, and AIP in the hemisphere contralateral to the moving arm using chronically implanted floating microelectrode arrays (FMAs; MicroProbes for Life Sciences). Two 32-electrode FMAs were implanted in each brain area (M1 only in 1 animal: 128 electrodes in monkey S and 192 electrodes in monkey B). We present single- and multi-unit spiking activity. Grip force was strongly represented in F5, M1, and AIP during movement, similar to grip type. During movement, higher percentages of M1 units were significantly tuned for grip type than F5 and AIP units (cluster-based permutation test; $p < 0.05$), but grip force modulation was surprisingly similar among all areas. During the planning epoch, grip type tuning was prevalent in all areas, but grip force planning was mainly found in F5. Fewer AIP than F5 units were tuned for force planning in monkey S, and only very few M1 and AIP units were tuned in monkey B. While holding the handle, grip force tuning became more dominant in all areas and exceeded grip type tuning in F5, but not in M1. Grip force modulation was strongly affected by grip type, especially in M1, indicating that these populations control both factors simultaneously. Neural responses could increase or decrease in relation to an increased grip force, and both was observed in similar proportion. Only while grasping, when the applied grip force was dynamic, but not during holding, F5 and M1 units showed a higher proportion of the increasing type. These results demonstrate a clear and potentially different involvement of F5, M1, and AIP for the planning and execution of grasp forces. Supported by DFG (SCHE 1575/1-1 & SCHE 1575/3-1).

1-B-16 Relating neural and kinematic trial-by-trial variability



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Trial-by-trial kinematic variability is a hallmark of human motor behaviors. Many models of motor control stress the advantages of such variability: it is essential for motor learning/flexibility and enables exploration of alternative motor solutions through trial-and-error. We asked whether behavioral motor variability is a stable characteristic of the individual subject and whether we can identify neural sources that generate behavioral motor variability in humans. Here we present evidence from several fMRI experiments, which demonstrates that neural variability and kinematic variability are stable individual traits that appear in a consistent manner across targets and effectors. Furthermore, a significant portion of the kinematic trial-by-trial variability can be explained by the trial-by-trial variability of fMRI responses in specific motor system areas as well as by global fluctuations in neural activity that are measured across the entire cortex. This suggests that kinematic trial-by-trial variability is generated in part by global neural activity fluctuations that may be associated with arousal and neuro-modulatory mechanisms. Our findings reveal that: 1. Behavioral variability of individual subjects is correlated across targets and effectors (behavior of some subjects is "noisier" than others). ; 2. Brain response variability is correlated across targets and effectors (neural responses in some subjects are "noisier" than in others). ; 3. Global and local brain response variabilities are correlated with behavioral variability of specific kinematic variables (subjects with "noisier" brain responses have "noisier" behavior). Specifically, global and local brain response variabilities were correlated with extent variability but not direction variability when movements were performed with the dominant hand and vice versa when movements were performed with the non-dominant hand. We, therefore, conclude that neural and kinematic variability are individual traits that are relatively stable across different movements and effectors. In addition, the relationship between neural and kinematic variability seems to differ when movements are performed by the dominant or non-dominant hand. This may be related to the different specializations of the two hands as suggested by previous studies.

1-B-17 Quantifying the kinematics of hand movements towards a flying ball

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The analysis of 3D hand movements in interceptive tasks, like ball catching, is methodically difficult. Depending on how adequate the catcher anticipates the ball's trajectory in space and time the overall movement can be curved in a complex manner and can have an irregular velocity profile [Cesqui B, d'Avella A, Portone A & Lacquaniti F (2012) PLoS ONE 7: e31770]. We present a method to analyze and quantify hand movements, while intercepting moving objects, making use of the facts that planned movements are fitted well by minimum jerk trajectories [Hogan N (1984) J Neurosci 4: 2745:2754] and that freely flying objects tend to move along a determined, parabolic, trajectory.
 20 subjects caught 20 balls which were gently thrown in the frontal plane. In the full vision (FV) condition an assistant threw a tennis ball over a horizontal bar, which was fixed at the subject's height in a sagittal plane through the subject's non-preferred shoulder. The subjects caught



these balls using their preferred hand. In the occluded vision (OV) condition, the throwing action was occluded by a cloth draped over the horizontal bar. Kinematic data (400 fps) were used from movement initiation until the first intersection of the hand palm with the ball's parabola. For all successful trials (FV: N=184; OV: N=183), we calculated a 1D hand trajectory, which was defined as the shortest distance of the midpoint of the hand to the parabola over time. A minimum jerk trajectory was fitted to the longest interval ending with the hand entering the parabola, whose average error was less than 1 mm. In the FV condition, a significantly longer movement interval was fitted by a minimum jerk trajectory than in the OV condition (FV: $0.21s \pm 0.04$, OV: $0.18s \pm 0.03$, $p < 0.003$, Bonferroni-adjusted, paired t-test). Furthermore, in the FV condition, the catcher's hand intersected the parabola for a significantly longer duration than in the OV condition (FV: $0.14s \pm 0.04$, OV: $0.08s \pm 0.04$, $p < 0.001$). We found no significant effects of the initial distance of the catcher's hand to the parabola and the flight duration of the ball. On average, the balls flew for 0.71s, the first 0.16s of which were occluded in the OV condition. Our method was able to detect differences between the FV and OV condition. Our finding that the FV condition had a longer minimum-jerk like interval indicates that the subjects needed fewer ongoing corrections. This is consistent with result that the hand also moved for longer on the parabola. This method also allows for the possibility that the movement goal is adjusted over time, as the movement enrolls. This affects the duration of a minimum jerk-like interval, which can be quantified. Moreover, the method has the advantage, that it reduces a complex 3D-movement towards a moving object to a 1D-trajectory, which focuses the analysis on essential features of interceptive movements.

1-B-18 Cerebellar regions involved in fine motor control and learning to control dynamic objects

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INTRODUCTION: A current topic in motor learning is the involvement of the cerebellum in learning to control dynamic objects. Most previous studies have been focusing on goal-directed reaching movements perturbed by spring-damper dynamics. In this study, it was examined which cerebellar regions support (i) fine motor control as measured by the precision in hand movement amplitude and timing, and (ii) the capability of learning to control a dynamic object, namely a simulated cart-pole system. **METHODS:** 19 young adult subjects with chronic surgical cerebellar lesions (mild to moderate ataxia symptoms) and 9 age-matched healthy controls learned to balance a virtual cart-pole system by applying continuous forces to the cart using a joystick-like input device. On each of five subsequent days, subjects (i) performed two tasks of fine motor control, and (ii) trained the cart-pole balancing task for 30 minutes. In the cart-pole simulation, the gravity was increased after every 30-seconds long trial increasing task difficulty. Cerebellar subjects' lesions were manually traced in individual 3D magnetic resonance imaging (MRI) data sets and spatially normalized using a method optimized for the cerebellum (www.diedrichsenlab.org). To identify structures involved in the examined tasks subtraction analysis and, for statistical confirmation, Liebermeister tests were applied. **RESULTS:** Cerebellar subjects showed in average a decreased precision of amplitude and



timing in the fine motor control tasks. In the cart-pole balancing task all healthy subjects reached the maximum gravity, but only eleven of the 19 cerebellar subjects. Four of 19 cerebellar subjects reached a cart-pole balancing performance comparable to controls. There was a significant but weak correlation between the performance in the fine motor control tasks and the cart-pole task, suggesting the influence of additional factors. Cerebellar subjects who reached the maximum gravity but were not able to balance the system on average as long as the healthy controls showed significantly decreased precision in movement timing ($p < 0.05$). Based on control subjects' performances in the different tasks cerebellar subjects were divided into an impaired and unimpaired group (99% CI) allowing for subtraction and binary statistical analysis. Lesions of the interposed nucleus, lobules V and VI were associated with reduced precision of movement amplitude, whereas decreased precision in movement timing and cart-pole balancing performance were associated with lesions of the dentate nucleus, lobules V, VI and Crus I. **CONCLUSION:** Learning to control dynamic objects such as the cart-pole system depends on the integrity of the cerebellum. Intermediate and lateral cerebellar regions play a role. Although precise fine-motor control is a necessary requirement, it is not sufficient to perform well in the cart-pole balancing task. Funded by Studienstiftung des deutschen Volkes, CIN PP-2013-1, DFG TI 239/10-2 and TI 239/16-1

1-B-19 Determining the components of follow-through that activate separate motor memories

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When different follow-through movements are associated with motor skills that normally interfere, they can be learned simultaneously, suggesting that distinct future actions activate separate motor memories (Howard et al, 2015). However, it is unknown which features of the follow through, such as planning or action, are crucial for such learning. We examined four groups of human subjects reaching in a randomly selected clockwise or counter-clockwise curl field from a start target to a goal target. On some trials we applied a force channel to assess learning. For the first group, a follow-through target (to the right or left of the goal target) was displayed from the start of a trial. After the movement through the field the subjects continued on to the follow-through target (with no force field) and the direction of the field applied on the first movement depended on the follow-through target. As expected strong learning was seen. For the no-follow through control group the subjects stopped at the goal target and did not follow through. As expected no learning was seen. For the third group, the follow-through target only appeared as they reached the goal target and the participants then followed through. This allowed us to examine whether the follow through movement could retroactively separate motor memories. A fourth group planned a follow through movement similar to the first group but the follow-through target disappeared as they reached the goal target and they were required to abort the movement. However, on channel trials the follow through was performed. This group therefore planned different follow-throughs but did not enact them. These groups allowed us to separate the effects of planning and the motor act of follow through. Howard, I. S., Wolpert, D. M., & Franklin, D. W. (2015). The Value of the Follow-Through Derives from Motor Learning Depending on Future Actions. *Current Biology*, 25(3), 397-401.

1-B-20 Neural signals associated with task-irrelevant movement variability in humans



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Mechanical redundancy in the human body is associated with task-irrelevant variability (i.e. many different muscle activation patterns achieve the same task). Uncovering the neural signals associated with task-irrelevant movement variability could have important consequences in understanding differences in motor performance among important subpopulations including healthy individuals, those with chronic pain, and those attempting skilled performance from the amateur to professional level. Here we report the first attempt, to our knowledge, to determine if the brain contributes to task-irrelevant variability in motor output in humans. We first measure whole-scalp electroencephalography (EEG) during a bimanual task where the subject repeatedly matches the sum of abduction forces generated by left and right index fingers to a single target force level presented using visual feedback. The analysis of fingertip forces during repetitions of the task indicated that all of our subjects exhibited task-irrelevant variation in left and right index finger forces. For each subject, we attempted to classify 500 milliseconds of pre-movement EEG signals using Common Spatial Patterns (CSPs) in order to distinguish between two states based on task-irrelevant finger force variation: one state when more right finger force than left was applied, and one state when more left finger force than right was applied. We employed a leave-one-out cross-validation analysis that learned the CSPs of the two states using all but one repetition of the task; then applied linear discriminant analysis to classify the remaining repetition based on the learned patterns. Our preliminary data suggests that this algorithm can successfully distinguish between different pre-movement brain states associated with task-irrelevant variability, even in individual participants. To spatially map brain signals associated with task-irrelevant variability, we additionally show preliminary results from a single subject using a complementary functional magnetic resonance imaging (fMRI) study design that utilizes the same task. Regions within the motor and sensory representation of the hand were found that were more active when task-irrelevant variability favored the contralateral hand. These results suggest that the brain is involved in producing task-irrelevant variability. *Kanso and Kutch have equal contribution in this work.

1-B-21 Task demands change online coordination of eye and hand movements

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When capturing objects with the hand, for example in reaching movements, gaze is usually directed to the target. Indeed, studies showed that gaze is anchored at the reach target, since initiating a saccade elsewhere is remarkably delayed (Neggers and Bekkering, 2000). This finding demonstrates tight eye-hand coupling, and suggests that saccades to non-target locations during a reach should have definite costs. From a theoretical view, the brain should compute the optimal solution for eye and hand motor coordination according to the cost and task-demands. Here we asked whether eye-hand coordination is fixed, or whether it can be modulated by experimental manipulations that independently motivate eye and hand movements, based on reward contingencies. Participants (n=18) made forward reaching movements (20cm) while holding a planar robotic manipulandum.



Visual feedback was provided on a monitor placed above the robot. Participants initiated a reach to a visual target (square, 1.5x1.5 cm) while maintaining gaze on a fixation cross (1.5x1.5 cm) presented inside the reach target. In randomly selected trials, the fixation shifted to right or left (7cm) just after the start of reach. In these trials, participants were asked to make a saccade to the new fixation as rapidly as possible while reaching to the central target. Participants received a monetary reward on each trial based on the combination of reach endpoint error and saccade latency. There were three reward conditions: (1) only reach accuracy mattered (HAND), (2) only saccade latency mattered (EYE), or (3) both these measures mattered equally (BOTH). To match reach behavior among conditions, participants were asked to keep the peak velocity (38-52 cm/s) and the movement time (550-800 ms) of reaching within the instructed range. On average, we found that both reach error and saccade latency varied systematically depending on reward conditions (reach error: HAND < BOTH < EYE, saccade latency: EYE < BOTH < HAND). Additionally, when saccade latencies were rewarded, saccades were generally initiated during the reach. These findings suggest that gaze-anchoring is not an obligatory feature. Rather, eye-hand coordination can be flexibly modulated depending on reward contingencies. Meanwhile, when reach accuracy mattered, lower saccade latencies seemed to be achieved by sacrificing reach accuracy. This tradeoff suggests that reaching movement incurs a cost when making rapid saccades. This cost might be related to the implicit effect of saccade on online reaching control, since reach trajectories deviated in the opposite direction from saccade direction at the timing of saccade onset. In summary, our findings highlight the possibility that the brain optimally modulates eye-hand coordination during reaching, depending on the reward-based task demands and the cost of eye movement. Motivation can cause eye and hand coordination to tradeoff against each other, instead of inherently synergizing.

1-B-22 Heterogeneity of neuronal activity in multiple putative premotor cortical areas of the cat during visually-guided locomotion.

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In primates, multiple premotor areas have been identified in the frontal lobe. One of the important functions of these premotor areas is thought to be the preparation of voluntary movement [Wise (1985) *Behav Brain Res*, 18(2), 79-88]. In cats, several cytoarchitectonic divisions have also been identified in the frontal portion of the cortex. Many of these have direct connections to M1 [Ghosh (1997) *J Comp Neurol*, 388(3), 371-396]. Although it is tempting to postulate that these divisions are analogous to primates' premotor areas, their functions have been poorly characterized to date. To investigate the roles of the putative premotor areas of cats in voluntary motor control, we trained two cats to walk on a treadmill moving at speeds of 0.35 to 0.5 m/s and to step over obstacles attached to a second moving belt. Once the cats were overtrained, we recorded single-unit activity in the dorsal and ventral banks of the cruciate sulcus (areas 4_d, 4_{sfu}, 6a_d and 6_{iffu}) as well as the dorsal (lateral) bank of the presylvian sulcus (area 6a_l) during locomotion. We identified a group of neurons in area 6_{iffu} that exhibited a progressive increase in activity before the lead forelimb passed over the obstacle and frequently diverged from control several steps before the gait modification (step-advanced cells). Such step-advanced cells were often independent of ongoing step cycle related activity and were also occasionally found in area 6a_l. In contrast, neurones in areas 4_d and



4sfu often showed rhythmic activity synchronized with the step cycle and they changed their activity only during the step over the obstacle. Generally, neurones in area 6aá did not show task-related activity. These results demonstrate for the first time details of the neuronal discharge patterns in cats? putative premotor areas when they have to perform a voluntary gait modification based on visual input. The early onset of the discharge activity in areas 6iffu and 6aã suggests that these areas might be involved in planning the gait modification. In contrast, activity in areas 4ä and 4sfu seems more closely related to execution of gait modification rather than planning it, at least during treadmill locomotion. However, more complex locomotor activities might produce context-dependent changes in activity, as in primates. Together the results suggest the presence of several premotor areas in cat frontal cortex. Future anatomical and physiological studies are required to determine the extent to which these subregions might correspond to the different premotor areas defined in primates. (Supported by the CIHR)

[1-C-23 Symmetry is Not Always Optimal: Mapping the Metabolic Cost Landscape of Walking on a Split-belt Treadmill](#)

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When adapting to walking on a split-belt treadmill, the nervous system gradually reduces step length asymmetry while simultaneously reducing metabolic cost. However, the causal relationship between these variables is unknown. In other words, is symmetry the end result of an optimization of energy or is the observed reduction in metabolic cost a byproduct of adaptation. Here, we use explicit modification of step length asymmetry to test the hypothesis that symmetry is the most economical strategy for walking on a split-belt treadmill. Twelve healthy individuals (27 %2B/- 5 years old) walked on a dual-belt treadmill under three conditions: 1) a 5-minute BASELINE period at 1 m/s; 2) a 5-minute period walking at 1 m/s with feedback (FBK) of baseline step length asymmetry (SLA); and 3) a 5-minute split-belt walking period (SPLIT) with the left and right belts moving at 1.5 m/s and 0.5 m/s respectively. Seven different SPLIT trials were conducted, and for each trial participants were provided with feedback of the desired SLA. Target values consisted of 0% SLA (Symmetric), %2B/- 5% SLA, %2B/-10% SLA to %2B/-15%. Negative SLAs indicate longer steps with the slow leg and positive SLAs indicate longer steps with the fast leg. Kinematics were recorded using an optical motion capture system and real-time visual feedback of step lengths was provided using Vizard. Metabolic power was calculated from the rate of oxygen consumption and carbon dioxide production using standard techniques. We found a significant metabolic power associated with walking while making precise foot placements (FBK condition) that was 16%2B/-7% higher than BASELINE ($p < 0.001$). Moreover, walking with 0% SLA in the split condition increased metabolic power by 32%2B/-23% relative to FBK. The relationship between metabolic power and SLA in the split condition was highly variable across participants. Consistent with our previous findings (Finley et al., 2013), we found that negative values of SLA (longer steps with slow leg) increased the metabolic cost of walking, with 7/12 individuals having the greatest metabolic cost at -15%SLA (54%2B/-30% greater than FBK). Surprisingly, in 6/12 participants, positive asymmetries of 10% or 15% were the most economical strategy. Only 3/12 individuals experienced the lowest metabolic cost at 0% SLA. These results suggest that symmetry is not the energetically optimal solution for all participants, but may instead



be the first point at which the gradient relating metabolic cost and asymmetry becomes too shallow to drive further optimization.

1-C-24 Modifying Adaptive Locomotor Learning using Body Weight Support

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It was recently demonstrated that adaptation to walking on a split-belt treadmill is associated with a reduction in the metabolic cost of walking. Though it has been proposed that energetic optimization may drive split-belt adaptation, a causal relationship between energetic cost and adaptation has not been explicitly investigated. A potential approach to address this issue is to manipulate the metabolic cost of walking and determine if this modification affects adaptation. If, for example, one could reduce the energetic cost of asymmetry, this should attenuate adaptation if adaptation results from energetic optimization. Here, we modified the metabolic cost of walking by providing body weight support. We hypothesized that providing body weight support would reduce the metabolic cost of asymmetry, thereby diminishing the need for adaptation during split-belt walking. Two groups of participants, Body Weight Support (BWS) and Control, adapted to walking on a split-belt treadmill. Each group performed 10 minutes of baseline walking at 1.0 m/s. For the BWS group, this consisted of 5 minutes with no support and 5 minutes with 50% body weight support. During adaptation, both groups walked for 15-minutes without body weight support (Control) or with 50% body weight support (BWS) while the left and right belts were set to 1.5 m/s and 0.5 m/s, respectively. During post-adaptation, both groups walked without body weight support for 10 minutes. Kinematics were measured using an active marker-based motion capture system. Step length asymmetry (SLA) was calculated by computing the difference between the step lengths of each leg. The time course of adaptation was quantified by the number of strides required for SLA to reach a plateau. Additionally, metabolic power was calculated based on measures of oxygen consumption and carbon dioxide production. During baseline walking, the BWS group reduced metabolic power by $10 \pm 7\%$ relative to the no body weight support condition ($p < 0.05$). There were no significant effects of body weight support on metabolic power or asymmetry during early or late adaptation (all $p > 0.05$). However, despite there being no differences in the magnitude or time course of the changes in symmetry during adaptation, the BWS support group had a more rapid washout during post-adaptation relative to the Control group (40 ± 23 strides vs 106 ± 67 strides, $p < 0.05$). Since body weight support had no effect on the online changes during adaptation, but led to an increase in washout rate, these results suggest that sensory information related to force is critical for determining the strength of the motor memory acquired during adaptive locomotor learning. Supported by NIH K12HD073945 and a James Zumberge Individual Research Award from the University of Southern California

1-C-25 Can cognitive training substitute treadmill motor training to resist a fall?

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Motor and cognitive learning sometimes can be referred to as implicit and explicit learning. Little is known pertaining to their relationship and whether one can substitute the other to reduce falls among older adults. The purposes of this Randomized Control Trials study were to determine 1) whether treadmill perturbation training (TPT) and cognitive prevention training (CPT) can reduce falls upon a novel slip trail during overground walking, and 2) whether both are similarly better than the controls (CTR). The study included 135 community-dwelling older adults, and they were randomly assigned to these three groups (N[TPT] = 45, N[CPT] = 44, N[CTR] = 46). All groups started with three regular (overground) walking trials at their preferred speed. Then TPT received 40-repeated "slip-like" trials on a computer-controlled treadmill. CPT watched videos made from previous experiments with identical setup and slides demonstrating where and how to use flat-foot landing and knee bending to resist a fall. CTR received the same amount of walking time on the treadmill without perturbation. Finally, everyone returned to the same walkway and a real slip occurred after three regular trials, induced by an electronic mechanical release of a pair of low-friction platform. None were told at the time the slip occurred. The between-group center of mass (COM) stability was compared. While TPT (22%) fell less than CTR (48%) ($p < 0.05$), CPT (36 %) did not ($p > 0.05$). This can be explained by TPT's significant improvement made in proactive (prior to slip onset) control of stability (TPT vs CTR $p < 0.05$, but not CPT vs CTR $p > 0.05$). Nonetheless, both groups had better reactive (at protective step liftoff after slip onset) control of stability than CTR ($p < 0.05$). The improvement in stability was mainly due to anterior shift of COM position ($p < 0.05$), rather than COM velocity ($p > 0.05$). We found that while CPT did improve the control of stability, yet that it was not sufficient to significantly reduce the rate of falls. It clearly cannot substitute the effect of the sensory motor input experienced by TPT that was necessary to improve their proactive and reactive control of stability.

1-C-26 Stochastic Vestibular Stimulation Alters Vestibular Cortical Representation

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The addition of low-level noise to a sensory system has been shown to result in more sensitivity for signal detection. Here we assessed the effects of one, 45-minute session and four 45-minute sessions of noisy, subthreshold stochastic vestibular stimulation (SVS) coupled with balance training on vestibular brain activation and postural control. Since falls are the current leading cause of fatal and nonfatal injuries in older adults, we further investigated the effects of noisy, subthreshold SVS with regard to age. We hypothesized that this stimulation would enhance vestibular cortical activity and postural control in a dose-dependent fashion. Subjects underwent three fMRI scans over the course of 6 days: baseline (day 1), short-term effects (day 2), and long-term effects (day 6). We measured posture control on a force platform on days 1 and 6 (i.e. pre and post intervention). The subthreshold, noisy SVS was applied 45 minutes per day for 4 days (days 2-5). We evaluated subjects' perceptual thresholds each day and modified the stimulation level to be 40% of subjects' perceptual threshold for SVS application. Our preliminary results document that one session of stimulation plus balance training results in increased activity of frontal, parietal and occipital regions,



and decreasing activity in fusiform and lingual gyri and the thalamus (N=4). Four sessions of stimulation plus balance training resulted in decreased activity in canonical vestibular regions (superior and middle temporal gyri), suggesting more efficient vestibular processing. Age and balance exercises amplified these effects; meaning that these changes were greater in older adults than young adults, and in exercise group than control group. This pattern of alterations was not limited to brain activation, as older adults in exercise group showed the most improvement in measures of body sway. The results of this pilot study suggest that application of subthreshold noisy SVS leads to improvement of vestibular function (more prominently in older adults), which correlates with enhanced postural control.

1-C-27 Anticipatory postural adjustments as a function of response complexity in simple reaction time tasks

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The predictive motor response to counteract postural destabilization due to a forthcoming voluntary movement is known as an anticipatory postural adjustment (APA) (Woollacott, 2009). These postural adjustments are considered to be anticipatory because they occur prior to electromyographical (EMG) activation in the relevant effector of the primary voluntary movement (e.g. a moving arm in a reaching task) (Massion, 1992). Furthermore, APA sequences are elicited at a shorter latency when a startling acoustic stimulus is applied during the foreperiod of a simple reaction time (RT) paradigm, indicating that APAs are planned in advance (MacKinnon et al, 2009). Increasing the complexity of a task in a simple RT paradigm has been shown to delay RT as a result of additional programming (Henry and Rogers, 1960), sequencing requirements (Klapp, 1995), or timing preparation (Maslovat et al., 2014). It is currently unknown if increasing the complexity of a task results in a similar APA delay. The purpose of the present study was thus to investigate if task complexity modulates APA onset in a manner analogous to that observed in the primary effector. Five participants completed 150 trials of both a simple (1 target) and complex (2 or 3 target) arm movement sequence using a KINARM robot. Simple and complex sequences were completed while standing on a force plate and again in a seated position. Results indicated that participants had significantly faster arm movement RTs in the simple compared to the most complex condition (simple: 350 ms; complex: 370 ms; $p = 0.035$). Furthermore, RTs were significantly faster when participants were seated compared to standing (seated: 355 ms; standing: 366 ms; $p = 0.02$), in agreement with previous studies (e.g. Dietz and Colombo, 1996) attributing this to the fact that postural adjustments required while standing must precede voluntary arm movements. APA onset quantified by the initiation of EMG activity in the tibialis anterior (TA) muscle also demonstrated a trend towards significance (simple = 250 ms; complex: 262 ms; $p = 0.08$). These preliminary findings demonstrate that similar to the primary effectors, APAs are sensitive to task complexity suggesting that APA parameters are planned in advance.

1-C-28 Modulation of cortical excitability with changes in base of support during standing

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There is growing evidence that the primary motor cortex (M1) plays a role in maintaining upright balance both in response to external perturbations and during anticipatory adjustments. Also, studies have found differences in motor cortical activity between conditions that impose different demands on the postural control system, despite minimal differences in background muscle activity. This suggests that cortical excitability may be modulated based on postural stability/ demand, even when there is no difference in background muscle activation between conditions. The purpose of this study is to determine differences in cortical excitability of the tibialis anterior (TA) between 2 different postural conditions - standing with a wide base of support (BOS) i.e. feet shoulder width apart (Stand WB) and standing with a narrow BOS i.e. feet together (Stand NB). Methods: 5 healthy adults (2 males; 27 ± 1.73 years) were recruited for the pilot study. Fine wire electromyography (EMG) signals were recorded from the right TA. Transcranial magnetic stimulation (TMS) was applied using a double cone coil connected to two Magstim 2002 units via a BiStim module. The hot spot for TA was determined in the sitting position and the motor threshold (MT) was determined in standing. Short Interval Intra-Cortical Inhibition (SICI) was measured by applying a conditioning pulse at 80% MT followed by another pulse at 120% MT after 3ms. 10 single pulses at 120% MT (test MEP) and 10 paired pulses (conditioned MEP) were applied in random order. These measurements were repeated in both conditions. MEP peak to peak amplitudes were computed and SICI was quantified using the formula: $(100 - (\text{conditioned MEP} / \text{test MEP} * 100))$, with a higher percentage indicating greater inhibition. Results: Background EMG measured 100ms before the TMS pulse was applied was not significantly different between the 2 conditions ($p=0.5$). In all participants it was less than 10% of maximal voluntary contraction. In 4 of the 5 participants, the test MEP amplitude was significantly higher in Stand NB compared to Stand WB ($p=0.001$; Cohen's $D_z = 5.9$). Also, in 4 of the 5 participants there was a trend for lower SICI in Stand NB compared to Stand WB ($p=0.064$; Cohen's $D_z = 1.4$). Conclusions: The pilot data shows a trend for higher corticospinal excitability and decrease in SICI when standing with a decreased BOS, despite similar background EMG levels. From a mechanical perspective, a smaller BOS represents a smaller margin of safety for maintaining balance. The higher corticospinal excitability may indicate an increase in the general state of 'readiness to move' in the condition where it would be more difficult to maintain balance in response to perturbations. The concurrent decrease in SICI suggests that at least part of this change in excitability is mediated supra-spinally. In general, these findings support the argument for involvement of the motor cortex in postural control.

1-C-29 Cooling-induced cortical deactivations reveal the contributions of parietal area 5 to memory-guided stumbling correction in the walking cat

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Tripping over an unseen obstacle can evoke the stumbling corrective reaction, resulting in limb hyperflexion to lift the leg over an impeding obstacle without interrupting forward locomotion. In quadrupeds, this coordinated action must extend to both the forelegs and hindlegs for successful avoidance. As this reflexive action persists following lower spinal transection, its neural circuitry



likely resides within spinal segments. However, supraspinal cortical structures related to motor planning and memory are important for locomotion in more complex or memory demanding settings. For example, parietal area 5 has been shown to play a role in maintaining a visually-acquired memory of an obstacle used to guide hindleg stepping. To test the hypothesis that area 5 is likewise engaged for a visually-independent memory of an obstacle, the stumbling corrective reaction was evoked in walking cats, resulting in foreleg clearance over an obstacle. Forward locomotion was paused for delays up to 120 s, during which the obstacle was covertly removed from between the fore- and hindlegs. When walking was resumed, elevated hindleg step height and trajectories indicated that obstacle height and position were retained during the delay. However, this visually-independent obstacle memory did not appear as long-lasting as its previously studied visually-dependent counterpart, with attenuated hindleg step height after 40 seconds. Interestingly, visually-independent obstacle memory appeared more robust when both forelegs contacted the obstacle before the delay. To assess the role of parietal cortex in visually-independent obstacle memory, cooling loops were placed bilaterally over area 5. Reversible, cooling-induced deactivation of area 5 throughout the obstacle avoidance test resulted in reduced hindleg step height and altered trajectories, suggesting significant obstacle memory impairment. Furthermore, memory deficits remained when area 5 deactivation was temporally restricted to the approach phase involving foreleg contact and clearance over the obstacle, or when cooling was restricted the subsequent delay period. These results demonstrate the role of area 5 in both the acquisition and maintenance of a visually-independent memory of an obstacle used to coordinate hindleg avoidance. As area 5 deactivation resulted in memory deficits similar to those observed in previous visually-dependent obstacle memory tests, area 5 may store information about an obstacle regardless of input sensory modality.

1-C-30 Movement Planning and Postural Adjustment in Single and Multiple Step Initiation

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In step and gait initiation task, the anticipatory postural adjustment (APA) patterns and duration offers a unique window to probe the cognitive motor planning process for step execution and locomotion control. In this study, we investigated the difference between single step and multiple step initiation tasks to better understand the mental chronometry for locomotion planning. Eight healthy young college students participated in this study. Subjects were asked to stand upright without shoes on a force platform and to initiate forward stepping as quickly and accurately as possible in response to a visual cue displayed on a TV screen placed at 1.7 m height and 4 m ahead of them. The visual cue consists of six 10 cm by 10 cm squares placed equally distanced at the center of the screen in a three row by two column manner. The three rows indicated that there were 1-3 possible forward steps, and the two columns on either side of the screen indicated the side of the landing foot. During the task, only one of the six squares was displayed in color, which required subjects to plan their steps corresponding to the location of the cue. After the swing foot corresponding to the visual cue landed, the subject brought the stance foot next to the swing foot and stood upright. Each subject first performed 60 trials in a simple reaction task (SRT) condition, in which each visual cue condition was performed in a block schedule (10 trials per block). Subject then



performed 60 trials in a choice reaction task (CRT) condition, in which each visual cue was displayed with a 1/6 probability. The visual cue was displayed by a customized MATLAB PSYCHTOOLBOX program, and the kinematic and kinetic data during stepping was collected through a Qualisys motion tracking system in sync with two AMTI force plates. Center of Pressure (COP) displacement during step initiation was used to identify the type and duration of the APA during step preparation. Vertical and horizontal ground reaction force (GRF) were calculated and analyzed to identify the difference between single and multiple steps motor planning. The CRT induced significant longer reaction time and APA duration than the SRT for step preparation. The multiple step initiation task induced a longer APA duration than the single step initiation task, but did not alter the reaction time for movement onset. This indicates that the motor planning for single and multiple steps differs only during the postural adjustment period. Interestingly, the single step initiation task induced a longer double support phase (DSP) duration, reduced propulsion force, and increased brake impulsion compared to the multiple step initiation task. This indicates the motor planning for step termination was programmed and executed in the double support phase, and not during the APA period.

1-C-31 Automatic step detection and gait variability evaluation using inertial sensors

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Given its sensibility to evaluate pathological gait, gait variability is a key gait parameter which is traditionally evaluated with the standard deviation of the step duration or step length, two quite unspecific parameters. For the computation of these parameters, step detection is needed, which can be an issue for real time analysis or in the case of a big amount of data. This study proposes an update for these two issues and proposes a method that performs robust step detection and evaluates gait variability. We present the results on a cohort of 30 slightly impaired Parkinsonian patients, 20 slightly impaired patients suffering from toxic peripheral neuropathy and 20 healthy controls performing a 20 meter walking task in daily medical practice condition wearing four inertial sensors at the head, the pelvis and both feet. The step detection algorithm gives the heel off and the foot flat of each gait cycles (97% recall and a 96% precision) and our gait variability parameter offers a precise and more specific insight on gait variability which could be of great help for gait visualization in daily medical practice.

1-D-32 Coupled pairs do not necessarily interact

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Previous studies that examined paired sensorimotor interaction suggested that rigidly coupled partners negotiate roles through the coupling force [1-3]. As a result, several human-robot interaction strategies have been developed with such explicit role distribution [4-6]. However, the evidence for role formation in human pairs is missing; to understand how rigidly coupled pairs negotiate roles through the coupling, we systematically examined rigidly coupled pairs who made point-to-point reaching movements. Our results reveal the consistency of the coupling force during



the movement, from the very beginning of interaction. Do partners somehow negotiate the roles prior to interaction? A more likely explanation is that the coupling force is a by-product of two people who independently planned their reaching movements. We developed a computational model of two independent motion planners, which explains inter-pair coupling force variability. We demonstrate that the coupling force alone is an unreliable measure of interaction, and that coupled reaching is not a suitable task to examine sensorimotor interaction between humans. [1] Reed KB, Peshkin M (2008), IEEE Trans Haptics 1: 108-20. [2] Stefanov N, Peer A, Buss M (2009), Proc Worldhaptics 51-6. [3] van der Wel RPRD, Knoblich G & Sebanz N (2011), J Exp Psychol 37: 1420-31. [4] Evrard P, Kheddar A (2009), Proc Worldhaptics 45-50. [5] Oguz S, Kucukyilmaz A, Sezgin T, Basdogan C (2010), Proc Worldhaptics 371-8. [6] Mörtl A, Lawitzky M, Kucukyilmaz A, Sezgin M, Basdogan C, Kirche S (2012), Int J of Robotics Research 31(13): 1656-74.

1-D-33 Quantifying Ipsilateral Silent Period in Electromyography to Measure Interhemispheric Inhibition

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The ipsilateral silent period (ISP) is considered an index of interhemispheric inhibition (IHI) during active movements measured by transcranial magnetic stimulation (TMS). ISP is characterized as a brief disruption in EMG activity following TMS applied to the primary motor cortex (M1) during ipsilateral volitional muscle activation. ISP is mediated by the transcallosal pathways, which allow balanced interaction between the two hemispheres to precisely perform coordinated movements. ISP has become a widely-used tool to measure IHI given its accessibility and simplicity using a single pulse TMS paradigm. As a result, it is essential to utilize a consistent method to quantify ISP. ISP can be measured by either duration or amplitude of EMG reduction to reflect the amount of IHI. However, it has not been shown which method can better quantify ISP consistently. Therefore, the current study aims to compare different ISP quantification methods to accurately assess IHI. We previously established that ISP measured during 50% maximal voluntary contraction (MVC) was easier for participants to generate repeatedly compared with 30% and 100% MVC. Thus twenty-five young right-handed individuals were instructed to exert 50% MVC of isometric right thumb abduction with visual feedback. A supra-threshold TMS pulse (130% of resting motor threshold) was applied to the right representational area of the abductor pollicis brevis. Fifteen trials of raw EMG activity were averaged and rectified to generate a processed EMG trial. ISP onset and offset were determined as the periods when the processed EMG activity crossed a pre-defined threshold. Three different measurements of ISP were compared. One method quantified ISP duration in milliseconds as the time difference between onset and offset; and two methods quantified ISP amplitude: i) ISP area: area between the threshold and the depth of EMG reduction, and ii) ISP inhibition: area under the reduced EMG activity, normalized to pre-stimulus EMG area over an equal duration. ISP was quantified by each method described above in the processed EMG activity. Measurement consistency as determined by the homogeneity of variance test and by the coefficient of variation (CV) was compared across all methods. Homogeneity of variance showed significantly different variance across three quantification methods ($p < 0.01$). ISP inhibition resulted in the least measurement variability (CV = 44.45%, 83.17%, 23.18% in ISP duration, ISP area, ISP inhibition,



respectively). In summary, the ISP inhibition method, which generates less variability, is a better choice to quantify ISP to indicate IHI. We suggest that future studies utilize ISP inhibition, which takes both duration and amplitude into consideration, to determine the role of interhemispheric interaction in complex task performance and in refined movements.

1-D-34 Current grasping theories cannot explain kinematic changes in grasping when only seeing one digit

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Grasping an object seems to be an effortless action, but the underlying mechanisms are still unclear and the models proposed to explain it still controversial. Our study was designed to examine the role of visual feedback in reach-to-grasp movements and, specifically, the influence that the visibility of each finger has on the action kinematics. We know that grasping movements are slower and the grip opens wider when performed without visual feedback, than when grasping with full vision, but little is still known on how the kinematics of the movement changes when either the finger or the thumb is occluded. On the basis of current theories on grasping, we made the following alternative predictions: we expected that when only one digit was occluded, either only the occluded digit's trajectory would deviate (independent control of the digits), or both digits' trajectories would deviate to some extent (to increase the grip aperture). We also considered the possibility that occluding the thumb would have more influence than occluding the finger (due to a possible guiding role for the thumb, and to the finger often disappearing from view behind the object in natural grasping). To test for these hypotheses and the different models, we used a see-through monitor to separately manipulate the visibility of both the digits and their respective contact points. We tested 20 participants grasping a sphere (\varnothing 40mm) located at different distances from the hand along the fronto-parallel axis (300-400mm) in four randomly interleaved conditions: 1. Both fingers and contact points visible (baseline), 2. Thumb and its contact point occluded, 3. Index finger and its contact point occluded, 4. Both fingers and contact points occluded. We compared the index fingers' and the thumbs' trajectories between the conditions with occlusion and the baseline. Our results do not satisfy any of the predictions. When the thumb was occluded, the trajectories of both fingers deviated away from the body, as if participants tried to avoid the occluder by following a more curved path, although the extent of the deviation was much too small to achieve that goal. When the index finger was occluded, both digits mainly moved away from the body again, but only later in the movement, when they were closer to the object. The analysis of the trajectories also suggests that the index finger might have a guiding role in these actions. The two fingers did not approach the object in the same way but the thumb showed a more prominent movement outward and inward to open and close the grip. This aspect is confirmed by the analysis of the time to contact, showing that the index finger makes contact with the object before the thumb in all conditions except when the index finger was occluded, in which case the digits (on average) made contact simultaneously. Taken together, these results do not satisfy any of the predictions based on the current theories on grasping.



1-D-35 Practice order effects of tactile and visual guidance during movement on tracing performance and cortical activation

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Previous work has indicated cortical regions that are uniquely activated by tactile (bilateral frontal areas) versus visual (bilateral posterior areas) guidance during tracing movements. However, the way brain activation changes during performance improvement, and the relevance of the order of touch- and vision-guided movements during practice is unknown. In this study, we investigated the effects of sensory modality and order on performance and cortical activation during the practice of tracing tasks. Sixteen right-handed, healthy adults (19-34 yrs) were included in this IRB-approved study. Volunteers traced 6 irregular shapes (path length = 45.7 ± 3.6 cm on a 156 cm² plate) with the right index finger using 1 of 2 sensory modalities for guidance. In the tactile modality (TM), movement was guided only by tactile feedback of semi-circular bumps along the path (height = 0.13 cm, spacing = 0.76 cm). In the visual modality (VM), movement was guided only by vision of dots along the path (dia = 0.13 cm, spacing = 0.76 cm) seen through a circular window (dia = 3 cm) at the tip of the finger. They performed 60 serial trials (5 blocks of 12 trials each) of each modality and the trace time of each trial was recorded. Eight participants performed the TM task, followed by the VM task, and vice versa for the other 8 participants. EEG data were recorded from 28 scalp leads. Cortical activation was quantified by the drop in task-related power (TRP), the log-ratio of spectral power during the task to rest. Full-factorial repeated measures ANOVA was used to model trace time, alpha (8-12 Hz) TRP, and beta (13-30 Hz) TRP (within-subject factor: block; between-subject factors: modality, order, and lead for TRP). Trace time decreased across blocks. The decrease was similar when the TM task was done first or second, while the trace times were faster in the second versus first VM task (blocks x order x modality: $p = .043$). Cortical activation in the alpha and beta bands decreased to zero across blocks when the VM task was performed second, but slightly increased when the VM task was performed first and when the TM tasks were performed (alpha: blocks x order x modality: $p < .001$; beta: blocks x order x modality: $p < .001$). Cortical activation was greatest in bilateral sensorimotor areas, with more in the left than right hemisphere. Notably, cortical activation in the "VM first" group was more widespread across leads than in the "TM first" group, even when participants switched tasks to the other modality. This study provides evidence that performing TM-guided movements first may promote improved performance on future VM tasks, but the specificity of this effect to TM guidance remains to be tested. Improved performance on the second VM task maybe related to the observed global decrease in cortical activation. These results may be of relevance to the order of task practice and the understanding of cortical mechanisms of improvement in hand neurorehabilitation.

1-D-36 Keeping and object vertical: The emergence of a basic skill

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Keeping an object vertical: The emergence of a basic skill Luis F. Schettino, Christopher Kelbaugh, Michael Leff, Nada Fadl and Raphaela Gassanov Humans develop a number of basic sensorimotor skills in their early years. Among them walking, talking and grasping. Grasping itself offers an interesting window into the interplay between innate and learned components. For example, the natural opposition of the thumb to the fingers, present in the first few months of life, undergoes considerable diversification into a number of handshapes as the child interacts with objects with varied physical properties. The ability to maintain a tall object vertical, such as a glass filled with a beverage, is a common skill which most human adults express effortlessly. However, the choice of digit contact points on the object is critical to reduce object roll (Lukos et al., 2007). Particularly, the location of the thumb along the vertical axis of the object must change to oppose the force exerted by the fingers (Schwark et al., 2008). Our study looked at the choice of digit contact points of (1) 17 normal young adults and (2) 15 children of ages 58 to 88 months on a tall vertical object which precariously supported a rubber ball at its tip. There were three different circular object tips of different diameters (L=20.5 mm, M=16 mm, S=8 mm). The smaller the diameter, the smaller the roll angle at which the ball would drop. Participants were asked to produce precision grasps to the object either above (T) or below (B) the object's center of mass (CoM). In order to facilitate the task for the children participants, the object employed was scaled at 2/3 of the adults' size and the rubber ball was smaller (5.3 vs. 4 cm diameter). Digit contact point position on the vertical dimension of the object was captured using a high-resolution camera (7.2 pixels/mm) placed parallel to the object plane. Our results indicate that adult participants modulated the position of the thumb relative to that of the midpoint of the opposing fingers in such a way that the thumb was closer to the line of the midpoint when grasping below the CoM of the object (-3.3 mm vs. -12.8 mm). The data for children participants showed little thumb position modulation in children younger than 70 months of age with a concurrent drop in task success under the more stringent conditions (Low grasp, small tip diameter) followed by a rapid increase in both success and behavioral similarity to the adult pattern after that age.

1-D-37 Cerebellar responses to auditory errors in musical material after piano training

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Playing the piano requires sophisticated auditory-motor interactions. It is likely that predictions for upcoming auditory input are generated during performance via internal forward models. Forming such predictions relies on training of the playing material and likely involves the cerebellum. However, prediction and expectation also form part of the process of listening to music. Neural correlates of expectations in listening to music can be measured via the mismatch negativity, an EEG/MEG component elicited after deviant tones in a recurrent melody. Here we show that cerebellar activation is involved in the generation of the mismatch response to material that was previously trained in a piano duet situation. Eight pairs of musically untrained subjects learned to play a small piano piece as a duet. Training consisted of eight sessions of half an hour each within two weeks. Training progress was monitored by MIDI recording. Afterwards, each subject was tested with an excerpt from the training piece in which occasionally either one of the notes that the subject had played or one of the notes that the partner had played was altered. The altered note could



either be lower in pitch than expected, or be presented 70 ms earlier than expected. Brain responses to these stimuli were recorded with a 275 channel MEG system. The mismatch negativity was determined by contrasting trials with deviant tones and standard trials in the time interval after the onset of the deviant tone. Beamformer analysis was used to localize the sources of the mismatch negativity from the MEG sensor data. Significant source activity was found in auditory cortex, in inferior frontal and parietal cortices, all part of the cortical mismatch network, but also strongly in the cerebellum. These results suggest that the cerebellum is involved in predicting the auditory outcome of musical sequences available in the motor repertoire.

2-B-1 CONGRUENT AUDITORY STIMULI INCREASE THE PROPORTION OF CORRECT RESPONSES IN AN INSPECTION TIME PARADIGM.

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Inspection time is a measure of the amount of time required for a visual stimulus to be presented in order for it to be accurately perceived by a participant. The visual stimulus most commonly used is a "pi" figure with differing leg lengths which is briefly presented (e.g. 20-200 ms) and then rapidly backward masked to prevent further visual processing. Participants are to indicate which side (left or right) of the "pi" figure has the longest leg. Correct identification is no better than chance (50%) when the figure is presented for a very short amount of time (e.g. 20 ms), whereas longer presentations of the figure result in more correct identifications. In this way inspection time is used to evaluate perceptual processing speed by determining the presentation time required to correctly identify the figure at a preset threshold level (e.g. 75%). In reaction time (RT) paradigms an irrelevant accessory stimulus has been shown to affect a participant's RT (i.e. Simon effect); however, the origin of this effect is unclear. It is possible that the stimulus "primes" the associated motor response, but it is also possible that the stimulus aids or impedes perceptual processing. Although the inspection time paradigm has long been used to investigate perceptual processing speed alone, it is unclear how accessory stimuli may impact perceptual processing. As such this study examined whether the presentation of spatially congruent/incongruent acoustic stimuli would alter perceptual processing of visual stimuli. A warning tone was followed by a visual fixation cross presented on a computer monitor for 500 ms. Following fixation offset a "pi" figure where the left or right leg was longer (22 vs 15 mm) was presented for between 15 and 135 ms (in 15 ms steps) and was then backward masked for 500 ms. Participants manually responded via keypress indicating which leg of the pi figure was longer. On some trials, the appearance of the pi figure was accompanied by a 15 ms duration auditory tone presented through headphones. In an equal number of trials at each visual stimulus duration a congruent auditory stimulus (a tone presented to the ear on the same side of the longest leg of the pi figure), incongruent auditory stimulus, binaural tones, or no auditory tone was presented. All combinations of visual stimulus duration and auditory condition were randomly presented. Results showed that congruent auditory stimuli lead to an increase in the proportion of correct identifications at short presentation times, whereas incongruent stimuli decreased the proportion of correct responses at these times. Importantly, although the acoustic stimulus was irrelevant to the task, participants were more likely to respond congruent with the tone at these short presentation times. This pattern of results suggests that in



cases of sensory uncertainty, stimuli with higher saliency are provided a higher weighting regardless of relevance.

2-B-2 Curved movement trajectories when reaching diagonally

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BACKGROUND AND AIM: Human reaching studies often focus on reaching forward in the sagittal plane, which commonly results in straight trajectories [1]. However, slightly curved reaching trajectories were also observed [2], [3]. Reported curvatures were very small, possibly due to small movement amplitudes. We investigated whether large amplitude movements outside of the sagittal plane show larger deviations from straight line trajectories. **METHODS:** Ten healthy, seated males (20 ± 2.7 years) reached with their dominant right arm to a virtual target using a haptic manipulator, which constrained the motion to the horizontal plane at shoulder height and emulated a uniformly viscous media. The virtual target (width 5 mm) was centered to the subject's shoulder and positioned at a virtual wall at 95% of arm length. Reaching movements started from random starting points (SPs) evenly distributed within $\pm 45^\circ$ around the target at distances of 15% (three SPs), 37.5% (five SPs), and 60% (seven SPs) of arm length. Subjects were to position the cursor at a given SP and move anytime following a ready signal. Movement duration, from self-initiated reach onset to reaching the virtual wall, was calculated for each reach and subjects were instructed to hit the target as many times as possible in a total movement time of 100 s. Each target hit was rewarded by € 2.5. Accumulated reward, remaining time, target, SP, and visual feedback of the hand cursor were shown in real time. Overall reach accuracy was comparable across all SPs. Kinematic data were analysed for reaches starting from 45° (rightward diagonal reach), -45° (leftward diagonal) and 0° (straight) at the three SP distances. Trajectory length and movement duration were calculated for 307 accurate target hits and averaged over subjects and SPs. Following a paired t-test 45° and -45° SP data were collapsed. Statistics were conducted at $\alpha = 0.05$. **RESULTS:** Trajectories differed significantly from the Euclidean distances between the SP and the target for all 45° SPs (0.9 - 1.3 cm longer, paired t-test all $p < 0.02$) and for 0° SP at the shortest distance (2 mm, paired t-test $p < 0.02$). Angle influenced both trajectory prolongation and duration, but distance between the target and the SP affected only movement duration ($p < 0.02$ for all, repeated measures ANOVA). **CONCLUSIONS:** Subjects reached the target with equal success from all SPs, but their movement trajectories were curved when reaching at 45° , unlike mostly straight movements at 0° . Such behavior might reflect task generalization to reaching forward in the sagittal plane [4], possibly due to complexities caused by different SPs. Computational modelling of this behavior, taking into account the underlying muscle activity, is underway. **REFERENCES:** [1] Thoroughman et al, Nature, 2000. [2] Izawa et al, JNeurosci, 2008 [3] Uno et al, Biol Cybern, 1989 [4] Barton et al, SfN meeting, 2014

2-B-3 Motor cortex but not muscles approximate a dynamical system during a novel cycling task

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The principal computation of motor cortex remains the subject of much debate. It has been postulated that motor cortex activity might 1) code high-order commands (e.g. hand velocity), 2) code muscle activity, or 3) function as a dynamical system that generates patterns from which muscle activity is built. These hypotheses derive primarily from the study of reaching - a small subset of all possible movements. To further explore and compare the above hypotheses, one desires a task where a broad set of brief and extended movements are evoked, and where the three hypotheses predict different time-evolving patterns of activity. To this end, we designed a novel task in which monkeys navigate a virtual environment by grasping a hand pedal and cycling forwards or backwards for a variety of prescribed distances. In this way, the evoked movements have a straightforward relationship at the kinematic level (forwards and backwards pedaling are essentially mirror images). Yet, the temporally complex patterns of muscle activity are very different for forwards versus backwards movements and are far from being mirror images. This creates the desired dissociation between kinematics and muscle activity. The task also creates the desired dissociation between muscle activity and internal dynamics: the patterns of muscle activity are poorly described by a linear dynamical system. We recorded neural responses from motor and premotor cortex of two monkeys (114 and 106 neurons) and EMG recordings from the arm, shoulder, and chest (36 and 22 recordings). Neural activity did not resemble any kinematic variable. Although kinematics could be decoded reasonably well from neural activity ($R^2 = .88$ and $.89$), generalization performance from one set of conditions to another was often strikingly poor. On the other hand, neural activity fit muscle activity well ($R^2 = .95$ and $.95$) and generalization performance was typically good. Yet despite these resemblances, neural and muscle responses were different in a number of ways. This was especially true when considering the population response (i.e., a population of neurons or muscles). Fitting a linear dynamical system to evolution of the population state was much more successful for the neural populations ($R^2 = 0.73$ and 0.69) compared to the muscle populations ($R^2 = 0.36$ and 0.21). Furthermore, we found that the neural population displayed a particular distinction between forwards and backwards movements that was not observed in the muscle population. In neural space, the activity during these conditions evolved orthogonally to one another and thus did not produce opposing flow fields. This was not true in muscle space. Thus, the neural responses obey population dynamics to a degree not observed in the muscles, yet muscle activity can still be decoded from neural activity. These results are compatible with the hypothesis that motor cortex acts as a dynamical system that produces complex muscle commands.

2-B-4 The sensorimotor properties of the fast visuomotor system

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When a novel visual stimulus appears, a transient signal sweeps through the neuraxis; this signal also generates a rapid stimulus-locked response (SLR) within 100 ms of stimulus onset on both neck and upper limb muscles in humans. This fast visuomotor system has been proposed to be distinct from that mediating voluntary motor control, involving reticulospinal rather than corticospinal pathways. To test this, we compared the sensorimotor properties of these two systems by measuring the EMG activity of the right pectoralis major muscle in 14 healthy subjects. First we tested the reference frame of the SLR. For a visually-guided reach movement, retinotopic visual input is converted into a



limb-centric motor output. To dissociate whether the SLR is encoded in a retinotopic or a limb-centric reference frame, subjects reached toward a visual stimulus from different starting eye and hand positions. We found that, similar to voluntary control, the SLR is encoded in a limb-centric reference frame. Hence the fast visuomotor system is able to rapidly integrate limb position with the retinotopic visual input. Next we tested the SLR when the visual stimulus was spatially dissociated from the voluntary motor command. To do this, subjects were instructed to reach either towards (pro-) or 180° (anti-) from the visual stimulus. Unlike voluntary control, the SLR still generated a response towards the visual stimulus in the anti-reach condition. However the magnitude was modulated by cognitive control, being attenuated before anti-reaches. Furthermore, we found a reversed relationship between the SLR and ensuing reaction time for pro- and anti-reaches; larger SLRs preceded short-latency pro-reaches and longer-latency anti-reaches. Finally, we investigated the SLR during motor learning. Subjects performed a visuomotor rotation task, where the sensory mapping of the visual stimulus was altered so that a new voluntary command was required to accurately reach the visual stimulus. We found that although the preferred direction of the SLR adapted during the task, the degree of adaptation was comparatively less than that of the voluntary movement. Previous studies have shown that both implicit and explicit forms of motor learning contribute to solving this task for the voluntary motor command; we speculate that the SLR represents only the implicitly learnt component. Together, these three results suggest that the human fast visuomotor system, indexed by the SLR, has a different set of sensorimotor properties compared to the voluntary motor system. While the SLR is a rapid feed-forward response to a novel visual stimulus, it can exhibit a surprising degree of sophistication, as indicated by the integration of proprioceptive and visual signals and modulation by both cognitive control and motor learning. Overall, the SLR appears to provide a unique way in which further properties of the fast visuomotor system can be studied.

2-B-5 Temperature Response in Motor Unit Firing Patterns

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Motor control response can vary depending on the environment the body moves through. It has been documented that muscle response changes with external and internal body temperature. Performance tends to improve in higher temperature environments and decreases during lower temperature environments. While performance has been well documented changes in the descending neural drive have not been explored. It is assumed that as the temperature of the muscles and motor units change the neural drive to control those bodies will be altered. The question this study addresses is the effects of colder temperatures on motor unit response. Studying motor unit firing rates and recruitment patterns found from decomposed surface EMG signals allows us to identify neural adaptations when the muscle is introduced to an altered environment. To study this question we took surface EMG measurements from the first dorsal interosseus (FDI) of the right hand in index finger abduction. Ten healthy subjects were recruited with no history of hand injury or pathology. Surface EMG was measured via a specialized sensor (Delsys® Inc.). Subjects were required to track a trapezoidal shaped curve by abducting their index finger into a load cell. Subjects were allowed to practice to become comfortable with the task. Once the task was completed subjects



submerged their hand in cold water, approximately fifty (50) degrees Fahrenheit, for three periods of five minutes with a thirty second break in between. The subjects again were requested to repeat the force tracking immediately following the cold bath. The specialized sensors used to collect the EMG allowed for specialized software to decompose the raw EMG into motor unit action potential (MUAP) trains. These trains represent the firing instances of all motor units identified by the software. It was found that the firing rates of motor units after the cold bath for each subject were significantly lower than in the un-altered state. Many subjects also seemed to recruit more motor units at the beginning of the contraction curve after the cold bath, rather than spaced along the curve as was common in the control state. Due to these results it can be assumed that the neural network adapted to the changing morphology of the muscle system by recruiting motor units earlier and with lower firing rates in an attempt to better control the system. Because the targeting task was the same in both the control and altered states the output kinetics were the same in both cases. Thus the changes in the firing rates can be fully attributed to the altered muscle state due to the temperature variation. This study aimed to show how motor unit strategies are changed when the muscle environment is altered.

[2-B-6 Context-dependent use of the upper limb for balance](#)

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Galvanic vestibular stimulation (GVS) artificially activates the vestibular nerve, producing a false sense of head movement. This evokes a whole body sway response towards the anode electrode when standing. When holding a fixed support, the upper limb has been shown to contribute to this sway response. Here we determine how the upper limb response is altered by the nature of the manual interaction with the surface. GVS was applied under three conditions of quiet standing; 1) no contact (NC); 2) light finger-thumb grasp (<1N) with a fixed support situated 45° forward/right of the subject (LG); 3) firm hand grasp of the same support (FG). Ten volunteers stood on a force plate with feet together and eyes closed while bipolar GVS was applied between the mastoid processes (2mA, 2s). Ground reaction forces and centre of pressure (COP) were obtained from the force plate, while upper limb forces were detected using a triaxial strain gauge. When standing freely (NC), subjects exhibited a clear balance response to GVS. This was characterised by a lateral ground force impulse, generating body sway towards the anode electrode to compensate for a false sense of movement towards the cathode. During LG this sway response was significantly reduced (~44%) in magnitude. Upper limb forces simply reflected the direction of evoked body sway response. During FG, sway magnitude was reduced even further (~69% from NC). However, the initial upper limb forces were in the opposite direction to the LG condition. This indicates that the arm was actively involved in generating the initial sway response to GVS during FG. Following this initial response, the upper limb forces resembled those seen during LG. These results suggest the upper limb performs two functional roles in maintaining balance. During LG, the arm acts like a passive spring, providing sensory information about bodily movement which can feed into the control of body sway via ground reaction forces. In contrast, during FG, the arm is actively involved in generating forces to compensate for sensed body motion. The switch between these two modes of action is not simply



due to limitations on maximal force output during LG; peak hand forces were similar during both FG and LG. Instead, the simple context of grasping in itself changed the role of the upper limb.

2-B-7 Different population structure in primary motor cortex and the supplementary motor area during reaching

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Different cortical areas are typically thought to perform different computations. Consider the supplementary motor area (SMA) and motor cortex (M1). SMA appears to be involved in movement timing. M1 participates in generating descending commands. SMA and M1 thus process different information and presumably perform different computations via different network dynamics. We analyzed SMA and M1 (including the adjacent premotor cortex) population responses recorded while monkeys performed a reaching task. We employed a novel ?hypothesis-guided dimensionality reduction? approach which translates a hypothesis into a cost function. In this framework, dimensionality reduction is viewed as an optimization. By specifying a cost function appropriate to a given hypothesis, one can find a projection that reveals the presence or absence of the hypothesized structure. Motivated by a central motif found in M1 data and simulations [Churchland et al., 2012; Sussillo et al., 2015; Kaufman et al. in preparation] we hypothesized that a large translation of the neural state activates strong dynamics, yielding a basis for outgoing commands to the muscles. Thus, we designed a cost function to seek projections where some dimensions show a condition-independent translation (the same for leftwards vs. rightwards reaches) while other dimensions contain trajectories that are fit well by a dynamical system. We allowed any linear form of dynamics, including but not limited to rotational dynamics. This approach thus seeks a 6 dimensional motif with 2 condition-independent dimensions and 4 dynamical dimensions. –The M1 population response displayed the hypothesized structure. Just before movement onset there was a large condition-independent translation of the neural state. Subsequently, the neural state evolved according to rotational dynamics. The rotational dynamics produced oscillatory patterns, which were partially reflected in the patterns of muscle activity. However, the full structure observed in M1 (the large translation followed by rotational dynamics) was not present in the muscles. Furthermore, the SMA population response did not display same structure seen in M1: no clear rotations or linear dynamics were present. Yet while SMA did not exhibit simple linear dynamics, there was one potential commonality between SMA and M1: both areas showed the large condition-independent translation just before movement onset. That translation may reflect a key shared dimension linking the different computations performed by the two areas. This finding supports the idea that the SMA performs a very different computation from that in M1. This result also puts the central M1 motif into context: that motif is absent in the downstream muscle population and in upstream SMA. Such specificity supports the hypothesis that the central motif in M1 is related to pattern generation rather than generic aspects of the data.

2-B-8 Coordinating goal-dependent modulation of the long-latency stretch response across muscles.



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We recently showed that goal-dependent modulation of the long-latency stretch response (muscle activity 50-100 ms following a mechanical perturbation: LLSR) is coordinated across shoulder, elbow and wrist muscles during goal-directed reaching movements (Weiler et al, 2015: JNP). In that work, participants used our 3 degree-of-freedom (shoulder, elbow & wrist) exoskeleton robot to reach in the horizontal plane towards visual targets following an unpredictable elbow flexion or extension mechanical perturbation. The targets were placed such that elbow perturbations displaced the participant's hand directly into the target or away from the target. We found that perturbations that displaced the hand away from the target compared to into the target elicited larger LLSR from the stretched elbow muscle, as well as larger LLSR from the shoulder muscle that counteracted interaction torques generated by the required elbow movement and from the wrist muscle that assisted in transporting the hand to the target. Here, we further probed the coordination of the LLSR between shoulder, elbow and wrist muscles during goal-directed reaches. In Experiment 1 we tested whether the goal-dependent modulation of the LLSR was coordinated across the shoulder, elbow and wrist muscles. Participants reached towards targets following elbow perturbations that could be of small, medium or large magnitude that displaced their hand towards or away from the target. As in our previous work, perturbations that displaced the hand away from the target compared to into the target elicited larger LLSR from the stretched elbow muscle, from the shoulder muscle that counteracted the interaction torque generated by the required elbow movement and from the wrist muscle that assisted in transporting the hand to the target. Furthermore, when the hand was displaced away from the target the magnitude of the LLSR across these muscles scaled linearly with the linearly increasing perturbation magnitude. In Experiment 2 we tested whether the magnitude of the LLSR was coordinated between shoulder, elbow and wrist muscles on a trial-by-trial basis. Participants reached towards visual targets following elbow perturbations of a single magnitude that displaced their hand towards or away from the target. Perturbation trials that displaced the hand away from the target resulted in reliable positive correlations between the magnitude of the LLSR from the stretched elbow muscle and shoulder muscle that counteracted the interaction torque generated by the required elbow movement, and between the stretched elbow muscle and wrist muscle that would transport the hand to the target. Taken together, our experiments provide additional evidence that the goal-dependent modulation of the LLSR is flexibly coordinated across multiple muscles to meet the demands of the intended goal-directed action.

2-B-9 Exploring the role of increasing task and null space variability during motor skill learning

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Although the role of variability in motor learning has been examined from different theoretical perspectives, much less is known about the type of variability that needs to be introduced, especially in skill acquisition tasks. In redundant tasks, variability can be introduced along dimensions that affect task outcome (task space) or along dimensions that have no effect on task outcome (null



space). Here, we investigated the effect of both the amount and the dimension that variability is introduced in learning a skill acquisition task. The task we used was a virtual shuffleboard task, which involved sliding a virtual puck towards a 1-D target. The distance traveled by the puck was entirely determined by the velocity of the puck at release. Participants held a bimanual robot and made discrete throwing movements. The velocity of the puck at release was defined as the average of the left and right hand velocities, making the task redundant (as multiple combinations of left and hand right velocities could be used to move the puck to the target). We used the robot to introduce variability by applying different force perturbations to the two hands from trial-to-trial. For participants in the task space variability groups, perturbations were introduced along the task space (i.e. both hands were sped up or slowed down simultaneously). For participants in the null space variability groups, perturbations were introduced along the null space (i.e. one hand was sped up while the other was slowed down). We manipulated both the dimension that variability was introduced (task space/null space), and the amount of variability (low/high) by changing the magnitude of the perturbation experienced. Healthy college-aged participants ($n = 50$) were assigned to one of five groups - task space-low, task space-high, null space-low, null space-high, and a control group (where no perturbation was introduced by the robot). Participants learned the task over two days (800 trials of practice) and we compared the groups in test blocks where no perturbations were applied (i.e. from pre-test to post-test). Results showed that all groups improved with learning, but the high variability groups (task space-high and null space-high) showed significantly worse performance at the end of practice compared to the control group. In contrast, the low variability groups (task space-low and null space-low) were not significantly different from the control group. There was also an effect of the dimension in which variability was introduced, with the null-space groups showing greater exploration of the null space after learning. These results show that in a task requiring reduction of motor variability, the amount of variability introduced is a more critical variable for skill acquisition than the dimension along which variability is introduced. Future tests are necessary to examine if the greater exploration of null space leads to greater flexibility in using different solutions.

2-C-10 Assessing the precision of vestibular coordinate transformations for balance

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Vestibulo-spinal reflexes are vital for fall prevention. For these reflexes to be useful, head-referenced vestibular information must be transformed into body coordinates, if a person detects leftward head motion while facing forwards, to maintain balance the appropriate response is a compensatory body movement to the right. If the head is turned rightward by 90 deg, the same pattern of vestibular afferent feedback would require backward body movement. Galvanic vestibular stimulation (GVS) is used to investigate this transformation process. It involves a small current applied between the mastoid processes, modulating the firing rate of the semi-circular canal afferents (i.e. increased firing on the cathodal side and decreased on the anodal side) and inducing a virtual signal of head roll towards the cathode electrode. When standing this evokes a compensatory sway response towards the anodal ear. The direction of the evoked sway is fixed in head coordinates, rotating in line with head yaw. Previous research has examined this cranio-centric



principle by calculating the average response direction over multiple GVS trials. This approach does not reveal trial-by-trial variations in response accuracy which may be important for revealing degraded control of balance. Here we studied the GVS-evoked sway direction on a single-trial basis, to determine its directional variability. GVS (2mA; 1s) was applied while subjects adopted one of five head yaw angles (0, ± 30 and ± 60 degrees). Full vision was compared to an eyes-closed condition. We hypothesized that greater proprioceptive sensation of head orientation in the presence of vision would improve the coordinate transformation process, as evident by more precise sway responses (i.e. less inter-trial variability in sway direction). The peak ground reaction force vector between 180-800ms post-stimulus was used to calculate sway direction, and circular statistics were used to analyze angular data. GVS evoked significant ground reaction forces which tended to push the body towards the anodal ear. Mean response direction was significantly altered by head yaw angle, as previously reported ($p < 0.05$; ANOVA). Analysis of individual trial data revealed a significant clustering of angles towards the mean sway direction, confirming the validity of our analysis ($p < 0.05$; Rayleigh R). However, contrary to our hypothesis, response directions variability was actually greater during the eyes-open condition (mean angular deviation \pm SD: eyes-open= 0.278 ± 0.07 , eyes-closed= 0.178 ± 0.09 ; $t(11)=4.8$, $p < 0.05$). Simultaneously, response magnitude was significantly greater during the eyes-closed condition. Therefore the precision of the response direction seems to be inversely proportional to response magnitude. We suggest that, when the eyes are open, the resulting down-weighting of vestibular information for balance may manifest as less accurate transformation into whole-body coordinates. Further research is needed to confirm this theory

2-C-11 A brain-to-brain neuroprosthetic interface between sensorimotor cortex and MLR for neuromodulation therapies based on intended movement after spinal cord injury in rats

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Neuroprosthetic interventions in the brain and spinal cord showed efficacy to enable locomotion. Moreover, timely and controlled neuromodulation has been shown to increase the quality of motor output and promote activity-dependent plasticity after spinal cord injury (SCI). Electrical stimulation of the Mesencephalic Locomotor Region (MLR) triggers walking, trotting and galloping for increasing level of charge in healthy rats, and increases the hind-limb kinematic level in chronic lumbar SCI rats. Despite these remarkable effects, external triggering in MLR stimulation delivery remains unpractical, and likely suboptimal to take full advantage of spiking-time-dependent-plasticity for strengthening synaptic connections between disconnected regions of the central nervous system. To remedy these limitations, we elaborated a computational infrastructure whereby neuronal ensemble modulation from the sensorimotor cortex directly triggers the neuromodulation therapy delivered in the MLR. First, multi-unit activity is recorded via a 32-channel intracortical array during execution of a few seconds of quiet standing and walking on a linear runway. Then, an unsupervised-learning method is applied to segregate two main cortical states. Last, the decoded intention to walk was used to deliver cortical-state-dependent neuromodulation of mid-brain locomotor-related circuits in real time, with a granularity of decision of 10ms. We validated this complex interconnected technology in rats with lumbar SCI, 5 weeks after lesion, trained to walk bipedally



with partial body-weight support provided by a robotic platform. This artificial connection amplified the cortical motor command to walk by directly stimulating the MLR, resulting in stronger kinematic output. These results demonstrate the feasibility of establishing an electronic bridge to amplify the cortical command during communication between the brain and the spinal cord in order to facilitate rehabilitation after spinal cord injury. Moreover, the developed computational infrastructure and associated methods provide the opportunity to evaluate whether interfaces between the motor cortex and other locomotor-related regions of the brain and spinal cord can enhance activity-dependent plasticity and functional recovery after SCI. Funding: European Research Council, ERC "Walk Again"; European Union Framework 7 Project "NeuWalk"; Swiss National Science Foundation, Project "Dynamo"; NanoTera Programme, Project "SpineRepair"; National Center of Competence in Research in Robotics.

2-C-12 A brain to spinal interface to alleviate lower limb deficits after neuromotor disorders in non human primates

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CONCEPT: Various neurological disorders disrupt communication between supraspinal centers and spinal circuits that control lower limb movements, thus leading to a range of motor disabilities. Here, we aimed to develop a Brain Spinal Interface: a neuroprosthetic system able to re-establish communication between the brain and the spinal cord after injury. **METHODS** Two rhesus macaques were implanted with an epidural spinal electrode array that was tailored to access lower limb flexor and extensor "hotspots" independently. Electrical stimulation delivered over these specific spinal cord regions induced whole-leg flexion versus extension movements. The spinal electrode array was connected to an implanted pulse generator from Medtronic with a modified firmware, which enabled real-time control over multiple stimulation sites using Bluetooth wireless protocols. In addition, each monkey received a 96-channel microelectrode array into the leg area of the left motor cortex to wirelessly record neural ensemble activity. A computer running a custom made software received neuronal signals and used them to decode foot-off and foot-strike events with an accuracy of up to 97% (LDA) during continuous locomotion. These motor predictions were used to update the location, timing, and frequency of electrical spinal cord stimulation. **RESULTS OBTAINED:** We first tested our Brain Spinal Interface in intact animals. We were able to finely and independently modulate the degree of flexion and extension of the lower limbs during continuous locomotion without disrupting the natural dynamics of gait movements. The decoder correctly anticipated the initiation and end of locomotion, turning on and off the specific electrodes with the appropriate timing based on the detected intentions to walk or rest. Second, we tested our Brain Spinal Interface in a model of spinal cord injury. We performed a unilateral lesion of the corticospinal tract at the thoracic level. Seven days after the lesion, both monkeys showed severe paralysis of the leg ipsilateral to the lesion site. The brain spinal interface enabled the monkeys to regain plantar stepping movements while walking on a treadmill and along a corridor. Both monkeys progressively



regained leg motor control capacities but a number of deficits remained apparent, including foot drop and reduced hip flexion, which affected balance and weight support during quadrupedal gait. The brain spinal interface corrected these remaining deficits and normalized the gait patterns of both monkeys. **CONCLUSION:** We integrated technologies that have been approved for use in humans to demonstrate the feasibility of interfacing leg-area cortical neuronal signals with a selective spinal neuroprosthesis. This brain spinal interface restored coordinated walking in two monkeys in the acute phase of a unilateral spinal cord injury, and alleviated the remaining gait deficits in the chronic phase.

2-C-13 Swimming Attenuates Age-Related Declines in Balance

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Background: The present study is part of a larger study from the Counsilman Center for the Science of Swimming at Indiana University concerned with the benefits of habitual swimming participation on the aging process. Postural control decreases with age due to the cumulative declines in afferent input, central integration, and efferent output of the systems controlling upright balance. Both high- and low-intensity exercise has been shown to improve balance, but this had not been investigated looking at swimming as a form of exercise in older adults. **Purpose:** The purpose of the study is twofold: first to investigate whether older swimmers demonstrate enhanced static and dynamic balance compared to age-matched inactive controls and, second, to determine whether or not low-intensity recreational lap swimming induces similar improvements in balance as high-intensity Masters swimmers. **Methods:** Sixty-three subjects over 55 years old were recruited based on their current exercise participation into three groups: Masters Swimmer (MS), Lap Swimmer (LS), and Inactive Control (C). Static balance was measured on a Kistler force plate 3x90 second trials under two conditions: eyes open (EO) and eyes closed (EC). All data was analyzed in MATLAB to determine mean sway velocity and the rambling and trembling components of center of pressure (COP). Dynamic balance was assessed using the Timed Up and Go (TUG) test. The groups were compared using a one-way ANOVA, covarying for age. **Results:** The MS and LS swayed significantly less than the inactive C group. The MS and LS demonstrated similar sway velocities and trembling trajectories in the AP direction, but the MS had smaller sway velocities and trembling trajectories in the ML direction. In addition, the MS performed the TUG test significantly faster than both the LS and C groups. While sway velocity and ML trembling deviations were significantly greater during EC trials compared to EO, no group by condition interactions were found. **Conclusions:** Swimming participation has a beneficial role in attenuating age-related changes in both static and dynamic balance. MS performed better on the dynamic TUG balance test than the LS and C. The LS tended to have similar static balance to the MS indicating that any level of swimming participation in the aging population is better than not performing any exercise. The similarity of rambling trajectories and differences in trembling trajectories between groups indicate that physical activity in the older population improves the peripheral control of balance, but not the central control.

2-C-14 Contribution of the support leg to online movement adjustments during tripping



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BACKGROUND AND AIM: Online movement adjustments allow for rapid changes of responses to perturbations, for example when avoiding a dangerous landing after tripping. We have shown that such online adjustments are successful even during trip recovery, usually by step shortening [1] involving a two stage muscle activity response in the tripped leg [2]. During tripping, muscle activity responses occur synchronously in both legs [3], as the support leg generates push-off and counteracts the forward angular momentum of the body [4]. Here we investigated whether muscle activity during online adjustments of tripping responses is also bilaterally synchronous. **METHODS:** Sixteen young adults walked at their comfortable speed over a walkway equipped with hidden obstacles that could cause a trip in mid swing (eliciting an elevating strategy; [4]). They were tripped 10 times in between a random number of normal walking trials and 5 trips included a projection of a forbidden zone (FZ, 30x50 cm) at the subject's preferred landing position. Stepping into the FZ (if presented), was to be avoided. Support leg data were analyzed for seven subjects (24.6±3.2 years, 1 female), who consistently used step shortening and avoided the FZ in all trials. Electromyographic data of gastrocnemius medialis (GM), tibialis anterior (TA), rectus femoris (RF), and biceps femoris (BF) and kinematic data on ankle, knee, and hip joint angles were collected. EMGs were preprocessed, averaged normal walking activity was subtracted from the trip activity and the residual activity was aligned to trip onset and normalized to maximal normal walking EMG. Performance on trips with a FZ, requiring movement adjustment was compared to normal trips using wavelet functional ANOVA [5] with statistical significance set at $p < 0.05$. **RESULTS:** Step shortening and earlier landing of the tripped leg in the FZ condition was accompanied by decreased muscle activity in the support leg's BF (from 250 ms) and GM (from 190 ms) and increased muscle activity in TA (from 280 ms), leading to less knee and hip extension and decreased ankle plantarflexion, consistent with less need for propulsion and support during trip recovery. Muscle activity changes related to online adjustments of trip responses started 15 - 109 ms later in the support leg compared to the tripped leg (BF 235 ms, GM 107 ms, TA 171 ms) and we did not observe two stage responses, which existed in the tripped leg [2]. **CONCLUSIONS:** Step adjustment needed to avoid the forbidden zone appears to be primarily a reaction of the tripped leg, quickly followed by changes in muscle activity on the support side. This sequence is probably a consequence of the tripped leg adjustments to meet new mechanical requirements of a shortened recovery step. **REFERENCES:** [1] Potocanac et al., *ExpBrainRes*, 2014 [2] Potocanac et al., *JNeurophysiol*, 2015 [3] Pijnappels et al. *JBiomech*, 2005 [4] Pijnappels et al., *GaitPosture*, 2001 [5] McKay et al, *JNeurophysiol*, 2013

2-C-15 Augmented visual feedback during a rhythmic postural task differentially modulates cortical activity in patients with Parkinson's disease and age-matched controls

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Background: In individuals with Parkinson's disease (PD), augmented visual feedback (VF) may offer benefits similar to those of rhythmic external cues. This may be due to the recruitment of non-affected brain areas. The involvement of the cerebral cortex during postural tasks with and without VF has not yet been studied. Our primary goal was to see whether there is neurophysiological evidence for the recruitment of additional cortical networks when VF about postural behavior is available. While VF may potentially be a useful avenue for promoting motor behavior and learning, there is also some evidence that subjects with PD overly rely on visual information, making them vulnerable to incongruity of visual information. Our secondary goal was hence to investigate electroencephalographic (EEG) activity in the cortex under conditions of incongruent VF. Methods: 28 individuals with PD and 16 healthy, age- and gender-matched controls performed rhythmic swaying movements, while standing on a force plate facing an LCD monitor and wearing a 64-channel EEG head cap. Feedback of subjects' center-of-pressure was presented either in real time (congruent), delayed by 250 or 500 ms (incongruent), or withheld (control). We used linearly constrained minimum variance beamformers of broadband filtered EEG to estimate neural source activity. We concentrated on the following bilateral regions-of-interest: primary visual cortex, primary motor cortex, primary somatosensory cortex, and the superior temporal sulcus/gyrus. Outcome measures were mean normalized power and event-related (i.e. at maximal lateral excursion) modulation in various frequency bands. Analyses of group differences in event-related power focused on the following contrasts: 1) VF versus no VF; and 2) incongruent VF versus congruent VF. Results: Preliminary results revealed most movement-related and task-discriminating activity in the alpha and beta bands (8-14 Hz and 15-30 Hz, respectively). For control subjects, mean normalized beta power and event-related beta modulation were lower under conditions of VF than under conditions without VF. Patients with PD showed stronger beta modulation that increased under conditions of VF, in particular the incongruent conditions. Discussion: Our results lend support to the hypothesis that cortical activity is modulated when VF is available versus when it is not. Furthermore, mean normalized beta power and the event-related beta modulation across the motor network discriminated between both condition and group. This supports previous results that showed altered movement-related modulations of alpha/beta activity in patients with PD, and it is in line with behavioral data showing greater reliance on congruent VF in patients. Alpha and beta power and especially event-related alpha and beta modulation thus also appear to be associated with relative changes in attentional load or task difficulty.

2-C-16 Comparing muscle activity patterns post-stroke with normative profile at self-selected walking speeds

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A primary locomotor impairment post-stroke is insufficient and inappropriately timed muscle activity. Currently there is a lack of a standardized method to quantify electromyographic (EMG) patterns during walking in individuals post-stroke that allows comparison of different training parameters to determine which paradigm can elicit the most "normal" pattern. The purpose of the current study is to develop an analytical tool that can compare and quantify stroke survivors' EMG patterns to a normative profile. Data from 37 stroke survivors and 20 healthy individuals were



collected for 8 lower limb muscles during treadmill walking at self-selected speeds. Using "k-means" cluster analysis, periods of activity and inactivity of each muscle were identified from their linear envelope. We divided the gait cycle into six regions/bins based on: first double support, first and second halves of single-leg stance, second double support, and first and second halves of swing. We computed the active time period within a bin as percent of total bin time. We also computed the EMG amplitude during the active period of each bin as percent of EMG amplitude during the gait cycle. To compare amplitude and timing profiles of each muscle for corresponding bins between stroke survivors' paretic limb and healthy individuals, we computed z-scores: $Z\text{-SCORE} = (\text{STROKE DATA} - \text{MEAN}_{\text{Healthy}}) / \text{SD}_{\text{Healthy}}$. A z-score indicates how many standard deviations (SD) an element is from the population mean. Assuming that our sample of healthy individuals represents a normative pattern, we used means and SD of healthy subjects to compute z-scores for both healthy and stroke subjects. Healthy individuals revealed scores ranging mostly between ± 2.57 . Therefore, stroke subjects' data with z-scores within the same range indicate agreement with the normative profile. A negative z-score indicates that the muscle has smaller amplitude or shorter active period than the normal pattern and vice versa. This method weights each bin separately and penalizes the stroke subjects more for impaired activation in bins demonstrating a consistent profile (absolute active or inactive bins) than a variable profile across healthy controls. For example, Medial Gastrocnemius muscle is active throughout bin3 across healthy controls (mean=99.4%; $\text{SD} = \pm 1.7$), but activity in bin4 is much more variable (mean=40.4%; $\text{SD} = \pm 14.4$). Here stroke subjects are penalized more in bin3 for abnormal activity compared to bin4, therefore they score worse in bin3 (z-score mostly between ± 0.5 to -11) than bin4 (z-score between ± 2 to -1). Unlike previous methods, this method quantifies the EMG pattern for each gait cycle region independently accounting for inter-individual variability of healthy population. This approach may also contribute to development of a rationale for selecting training parameters based on specific gait cycle regions. Therefore, this novel method can serve as a tool for quantifying changes in EMG pattern post-stroke.

2-C-17 Fluctuation Analysis of Center of Pressure in Peripheral Neuropathy

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The control of balance can be impaired in persons with a peripheral neuropathy. Some of the factors contributing to the symptoms include the following: the nature of the underlying pathophysiology; whether sensory and/or motor nerves are affected; and the duration and rate of progression of the neuropathy (NINDS, Dec. 2014). The present study is part of an effort to quantify variability in the center of pressure (CoP) in persons with a peripheral neuropathy while the subject maintains a steady balance when standing on a forceplate. The general aim is to identify and characterize the short and long range correlation and self-similarity of fluctuations over time in the CoP using a multifractal, de-trended fluctuation analysis (Kantelhardt et al., 2002), MFDFA, of time series data. For this initial work the analysis was applied to CoP data during the following conditions: in the light while fixating on a distant, straight-ahead target; in darkness (eyes closed; no cognitive task); in darkness and engaged in an attention-demanding task (counting); in the light and engaged in an attention-demanding task (looking at a distant computer screen and identifying colored circles). The preliminary results suggest possible fractal properties of the postural control system dynamics,



interactions across temporal scales, and how that is manifested in peripheral neuropathy. This approach could provide further insight into some of the factors affecting the control of balance in peripheral neuropathy.

2-C-18 Stability and control of running on rough terrains

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Animals are adept at running over rough terrains. Running is repeatedly flying through the air, punctuated by stance that redirects the body's momentum. Here, we use simple models to characterize the relative contribution of open-loop, anticipatory and feedback strategies for running stably on rough terrains. We model the runner as a disc in the sagittal plane, with drag-free flight and an impulsive stance that redirects the body's momentum. A passive collision is followed by an active push-off during stance. The passive collision, defined by a normal and a tangential coefficient of restitution, approximates elastic energy storage in the leg, and leg retraction respectively. The active push-off is chosen to exactly compensate for the passive collision on a flat terrain. This same active push-off is applied on rough terrains, i.e. no step-to-step feedback corrections. The primary mode of failure in the context of this model is to tumble forward, or less often to lose forward velocity and no longer move forward. Tumbling falls are governed by the tangential collision, which leads to pitching moments about the center of mass. On rough terrains, these pitching moments change from step-to-step and cannot be compensated for by the push-off strategy. Using our model, we show that an anticipatory strategy of leg retraction stabilizes the tumbling falls on rough terrains, but open-loop runners always tumble. The anticipatory leg retraction strategy requires precise knowledge of the runner's mechanical state as well as the slope and height of the terrain patch where the runner is about to land. This is used to retract the leg such that the tangential velocity of the foot relative to the terrain is zero. Monte Carlo simulations on rough terrains show that imperfect implementation of the anticipatory leg retraction strategy leads to a sharp decline in stability. Runners with a perfectly implemented anticipatory leg retraction strategy avoid falling, but lose forward velocity and eventually stop running. Thus, slow time-scale feedback, acting over multiple steps, is required to keep running forward. For piecewise flat terrains, unlike natural trails but resembling some laboratory experiments, purely open-loop strategies are able to avoid falls. Therefore, an alternative anticipatory strategy to prevent falling is to aim for local maxima on rough terrains so that the foot lands on flat terrain patches. We conducted human-subject experiments with amateur long-distance runners on artificially constructed rough and flat terrains, in order to study their leg retraction and foot placement strategies. These data show that human runners tangentially scuff the ground with their feet, unlike the anticipatory leg retraction strategy predicted by the model. This choice may reflect a trade-off between precise estimation of the terrain slope versus aiming their feet to land on flat terrain patches. Ongoing data analyses will assess foot placement strategies.

2-C-19 INTER-JOINT COORDINATION AND MOVEMENT DECOMPOSITION DURING WALKING IN INDIVIDUALS WITH POST-STROKE HEMIPARESIS



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Post-stroke gait is characterized by impairments in intra-limb and inter-limb coordination. Measures of inter-joint coordination have been shown to be related with walking function and fall risk post-stroke. Here, our objective was to compare inter-joint coordination in the paretic versus non-paretic lower limb of individuals with post-stroke hemiparesis, and to determine whether inter-joint coordination is modified following gait retraining. Ten individuals with post-stroke hemiparesis and 10 able-bodied controls were recruited for the study. Gait analysis was performed during walking on an instrumented treadmill at a self-selected speed before and after a 30-minute session of gait training. Two dependent variables were used to evaluate inter-joint coordination. The average coefficient of correspondence (ACC) was used to quantify the consistency of coupling between adjacent joints during multiple gait cycles. ACCs can range from 0 to 1, with numbers closer to 1 describing perfect stride-to-stride consistency. The decomposition index (DCI) was computed as the percentage of the gait cycle when a distal joint (ankle or knee) moved without concurrent movement in the proximal joint (knee or hip), or vice versa. The DCI measures the 'smoothness' of trajectories and the degree of individuation or fractionation during lower limb movements. ACC and DCI values for ankle-knee and knee-hip angle-angle data-plots were compared between the paretic versus non-paretic limb post-stroke, between non-paretic limb versus able-bodied controls, and before versus after gait training. Our results to date show lower ACCs for the paretic versus non-paretic legs in individuals post-stroke for both ankle-knee coordination (0.87 for paretic and 0.94 for non-paretic) and knee-hip coordination (0.90 for paretic and 0.96 for non-paretic). Additionally, ACCs for both the non-paretic and paretic limbs were lower than ACCs demonstrated by able-bodied individuals (>0.98). Interestingly, analysis of DCI values revealed significantly increased DCI in the non-paretic limb compared to able-bodied controls, as well as differences between the paretic (17.7 ± 3.5 for ankle-knee and 13.2 ± 3.5 for knee-hip) and non-paretic (24.4 ± 5.1 for ankle-knee and 18.9 ± 4.6 for knee-hip) limbs. Additionally, ACCs increased after the session of gait retraining. This study demonstrates deficits in inter-joint coordination in both paretic and non-paretic lower limbs of stroke survivors during walking. To our knowledge, this is the first study to explore the use of joint decomposition (DCI), previously utilized to quantify coordination of upper limb movements in individuals with cerebellar ataxia, in post-stroke gait. Additionally, we show that a single session of gait retraining may result in improved stride-to-stride consistency of inter-joint coordination. This study takes a step toward understanding deficits in coordination during post-stroke gait, and how they are modified by rehabilitation.

2-D-20 The role of haptic feedback in eye-hand coordination when manipulating non-rigid objects

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Previous studies have shown that learning to manipulate efficiently a non rigid-object can be challenging (Dingwell et al, 2002), and that the provision of haptic feedback is critical for skilled



manual performance (Danion et al, 2012). Here we explored the role of haptic feedback in eye-hand coordination when an explicit requirement of the task is to track with the eyes the resulting motion of the object. Two hand-target mappings were used, either a rigid one in which hand and target motion matched perfectly, or a non-rigid one in which the target behaved as a mass attached to the hand by means a spring. Target animation was obtained by asking subjects to move an object attached to a lightweight robotic device that provided, or not, haptic feedback consistent with the target dynamics. Our results showed that eye tracking performance was more accurate under the rigid mapping than the non-rigid one. In the latter case, we found that haptic feedback improved eye tracking performance. Subsequently, we explored a continuation task in which the target was unexpectedly blanked for 7 seconds while subjects had to keep tracking the invisible target. When manoeuvring the non-rigid target the results showed that haptic feedback was critical in stabilizing eye-hand coordination during target blanking. Indeed the drift in eye-hand coordination was reduced when haptic feedback was provided. We conclude that haptic feedback enhances the ability to track with the eyes a self-moved target with complex dynamics. This study extends the view that haptic feedback is critical not only for manipulating non-rigid objects efficiently, but also to coordinate proficiently eye and hand actions when manipulating them. Acknowledgments This work was supported by a PICS from the CNRS and a French National Grant (REM ANR-13-APPR-0008)

2-D-21 Cutaneous and Proprioceptive Components of Motor Responses to Fingertip Loading

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The neural basis of grasp control includes tactile feedback that provides information about the object properties such as texture and friction. As well, muscle afferent feedback provides information about the grasp configuration. Previous work suggests that each sensory system can generate rapid motor responses following perturbations applied to held objects. However, their specific contribution to feedback control of grip force has not been clearly identified. Here we investigate this question in two experiments addressing motor responses to fingertip loading. In each experiment, participants applied a normal force of 5N with their right index fingertip on a horizontal platform. After a random delay, the platform moved horizontally, thereby applying a tangential force to the fingertip. In Experiment 1, participants (N=12) were instructed to increase the normal force to avoid slipping when they felt the perturbation. We varied the perturbation direction and magnitude, and used two conditions in which the finger lateral motion was restrained or not. We reasoned that in the restrained condition, the reduction in perturbation-related motion along with the increase in strain at the finger-object interface would enhance the contribution of cutaneous afferents. In Experiment 2, participants (N=9) were instructed to exceed a target force of 12N within 500ms or 200ms after they felt the perturbation. These time limits were used to characterize the dependency of the motor response on task instructions. We collected the activity of extrinsic (Flexor Digitorum Superficialis: FDS) and intrinsic (First Dorsal Interosseous: FDI) hand muscles involved in grip force control. In Experiment 1, when the finger was not restrained, we found that the best linear model for the activity of FDI included the baseline activity and the horizontal motion of the platform as predictors. The average activity in a sliding window of 30ms, starting at 60ms, revealed that the partial correlation of the baseline decreased and that of the



motion increased over time. Importantly, the partial correlation between the muscle response and the platform motion was markedly reduced when considering the extrinsic muscle, or when fitting the same model to the response collected in the restrained condition. In the second experiment, participants generated a significant increase in normal force within 200ms. Long-latency responses in the FDI were significantly influenced by the perturbation direction and the time limit, while FDS was only influenced by the time limit. The combined influence of the baseline activity and of the finger motion is consistent with a stretch response mediated by proprioceptive feedback. The response component that can be ascribed to cutaneous feedback (as for FDS or by restraining the finger motion) displayed lower response gain and reduced scaling with the stimulus intensity.

2-D-22 What is the role of primary motor cortex in Eye-Hand coordination? A TMS study

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The ability to track a moving target with the eye is substantially improved when the target is self-moved as compared to when it is moved by an external agent. To account for this result, previous literature has proposed that the oculomotor system has access to an estimate of the current hand position by means of a forward model that receives the arm efferent copy. However, direct neurophysiological evidence for this scheme is still lacking. The goal of the current study was to investigate the effect of TMS over the hand area of the primary motor cortex (M1) during a eye-hand coordination task. Subjects were asked to track with their eyes a visual target whose motion was driven by their grip force. When TMS was applied over M1 hand area, involuntary grip force pulse led to transient target jumps. We reasoned that if the output of M1 is used by the oculomotor system to keep track of the target, TMS on top of disturbing grip force, should also disrupt eye tracking performance. For comparison purposes, eye tracking was also monitored when these (perturbed) target trajectories were played back, as well as when TMS was applied while tracking an externally-moved target. Our preliminary data (4 subjects) suggest that eye tracking performance is poorly influenced by TMS over M1. First, we found no obvious effect of TMS on eye motion when tracking an externally-moved target. Second, during the self-moving task eye tracking performance within 200ms following TMS was similar to what was observed when playing back the same target trajectories. Overall the results of this TMS study suggests that the output of M1 has a limited contribution into Eye-Hand coordination. Acknowledgements This work was supported by Innovative Training Network 'Perception and Action in Complex Environment'(PACE) under the Marie Sklodowska-Curie grant agreement N°642961 and by a French National Grant (REM ANR-13-APPR-0008).

2-D-23 Broad and narrow spiking neurons in dorsal premotor cortex project to the superior colliculus

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It has become a standard procedure to separate broad and narrow spiking neurons recorded in various cortical areas in awake monkeys with the implication that broad spiking neurons are most likely pyramidal cells and narrow spiking neurons are interneurons. Supporting this idea, broad and narrow spiking neurons were often found to have different functional properties. Direct proof for the anatomical distinction is difficult to obtain in chronic recordings from awake monkeys but antidromic stimulation of corticofugal axons allows to identify at least classic pyramidal cells in layer 5 and 6. All pyramidal cells in prefrontal cortex projecting to the superior colliculus fall in the broad spike group (Johnston et al. 2009) whereas a substantial fraction of pyramidal neurons in M1 and area F5 projecting into the pyramidal tract exhibit narrow spikes (Vigneswaran et al. 2011). Interestingly, pyramidal cells with the shortest antidromic latencies had the narrowest spikes. These controversial results prompted us to do a similar analysis on our sample of neurons in dorsal premotor cortex projecting to the superior colliculus. We compared the widths of spikes from corticotectal neurons with spikes from PMd cells elicited orthodromically from the same stimulation sites in the colliculus. The total distribution of spikewidths showed a clear dip at <250 ms (Hardigan's dip test $p < 0.005$) similar to the results of Song & McPeck, 2009 and Churchland et al, 2010. Interestingly, 33 of 99 antidromic spikes fell into the narrow spiking group (<250 ms). However, this was a significantly smaller proportion than in neurons orthodromically activated from colliculus with 100 narrow versus 38 broad spiking neurons ($p < 0.0001$ in a Whitney-Mann U-test). Neurons with very narrow spike widths (<200 ms) were only found in the group orthodromically activated from SC. As in M1 and F5 we found a highly significant correlation between spike width and antidromic latency in the PMd neurons projecting to the colliculus ($r = 0.53$; $p < 0.0001$). These data taken together with published results (Vigneswaran et al. 2011) seem to suggest that layer 5 corticofugal pyramidal cells in motor and premotor cortices have a spike width distribution overlapping with the narrow and broad spiking populations recorded in the same cortical area. The unexpected narrow spikes in pyramidal cells belong to the cells with the fastest conducting axons and thereby probably to the very large somata characteristic to motor and premotor cortices but not frequently found in other frontal cortical areas.

2-D-25 Robot-assisted surgery as a platform to study natural behavior; a preliminary analysis of surgeon eye gaze and hand movements

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Studying human sensorimotor control during natural behaviors is appealing but challenging. On the one hand, it offers the potential to validate existing theories of sensorimotor control from basic experiments, to reveal new theories unobserved in basic experiments, and to help improve technologies aimed to enhance behavior, such as stroke rehabilitation and robot-assisted surgery (RAS). On the other hand, many of the simplified experimental conditions used to isolate properties of human sensorimotor in the laboratory cannot be applied to most natural behaviors and, therefore, it is difficult to make causal conclusions. Furthermore, subjects often need to be instrumented with additional sensors to measure relevant behavioral features which can negatively influence behavior and restrict measurements to focused experiments rather than large subject populations. In this work, we study one particular natural behavior - RAS - which partially overcomes



the challenge of unobtrusive sensing and that has a large subject pool of residents, fellows, and attending surgeons whose job it is to master surgery, a highly demanding sensorimotor behavior. Given its teleoperative architecture, RAS offers the ability to record many aspects of behavior during inanimate tasks, virtual reality simulations, animal training labs, and actual clinical cases on humans. In this study, we measured hand movements, instrument movements, stereoscopic video of the surgical scene, and eye gaze from novice (N=3) and expert (N=4) surgeons while they operated on porcine and cadaver models. Surgeons were free to behave naturally on the da Vinci Si Surgical System to complete specific training exercises that resembled clinical scenarios. Firstly, we confirm previous results from visuomotor research and show that eye gaze leads hand movement during certain tasks. Secondly, we show that the location of fixation on the field of view differs for experts and novices; experts' fixations are much more localized to the center of the screen. We have previously shown that viewpoint (camera) adjustments were much more frequent for experts than novices. We hypothesize that experts optimize their viewpoint and fixations to define an origin coordinate system to better make subsequent movements requiring high accuracy and precision. Finally, we show clear differences between the directionality of hand movements and eye gaze; eye gaze direction is more uniformly distributed whereas movements consist of horizontally dominant directions. We plan to conduct additional analyses to further characterize surgeon eye gaze and movements during complex surgical tasks. In conclusion, we present initial, descriptive results from RAS that align with findings from basic, laboratory experiments. We highlight the opportunity RAS offers to study human sensorimotor control and to dissect a natural behavior to reveal fundamental movement and sensory strategies.

2-D-26 Accounting for intersegmental limb dynamics when making single-joint movements.

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A hallmark of the nervous system is its ability to perform the same arm movement patterns in a wide variety of contexts. The mechanical interactions between limb segments makes this a complicated process because torque generated at one joint causes motion at other joints. For example, producing single-joint motion at the elbow requires generating torques not only at the elbow but also at the shoulder and wrist to counter interaction torques and prevent their movement. We are currently investigating how the nervous system accounts for intersegmental dynamics during reaching and when countering mechanical perturbations. In our first experiment, fifteen participants performed fast and accurate reaching movements to targets using a robotic exoskeleton (IMT Tech.) that permits rotations at the shoulder, elbow and wrist joints. Targets were drawn such that they could be reached with either 40 degrees of pure elbow flexion/extension (120 trials) or 40 degrees of pure wrist flexion/extension (120 trials). As required to counter the intersegmental interactions, we found activation of (a) the pectoralis muscle for pure elbow flexion trials, (b) posterior deltoid muscle for pure elbow extension trials, (c) biceps muscle for wrist flexion, (d) triceps lateral muscle for wrist extension trials. In our second experiment, we investigated whether the nervous system adapts to novel intersegmental dynamics by locking the wrist during pure elbow motion trials. The same fifteen participants performed fast reaching movements by generating pure elbow rotations of 40 degrees of either flexion or extension (baseline phase, 120 trials). We then mechanically locked



the wrist joint and participants repeated the same elbow rotation movements (adaptation phase, 120 trials). Importantly, locking the wrist joint cancels the interaction forces that arise at the wrist during elbow rotation. We then unlocked the wrist joint and participants again had to counter the intersegmental dynamics (post-adaptation phase, 120 trials). We found no reduction of wrist flexor and extensor activity when they acted as agonists. Our results suggest that the nervous system accounts for intersegmental interactions during single joint movement at both the elbow and wrist and does not adapt to novel intersegmental limb dynamics caused by wrist fixation on the timescale of this experiment.

2-D-27 Intracortical Microstimulation of Human Somatosensory Cortex as a Feedback Source for Brain-Computer Interface Users

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Somatosensory feedback is necessary for skilled movement. While brain-computer interfaces (BCI) have enabled users to achieve high degree-of-freedom control of a prosthesis, feedback of the limb has been limited to vision. In tasks such as object manipulation however, providing somatosensory feedback could be an important step to improving BCI limb control as vision provides less salient cues. One possible mode of delivering this feedback is by using intracortical microstimulation (ICMS) of the primary somatosensory cortex (S1). In this study, a twenty-seven year old participant with a chronic C5 motor and C6 sensory AIS B spinal cord injury was implanted with two intracortical microelectrode arrays in primary motor cortex and two arrays in S1. The S1 electrode arrays were targeted to the hand region of area 1 in the left hemisphere based on presurgical imaging. The goal was to elicit cutaneous percepts that project to the fingers of the right hand. Electrodes were stimulated at supraliminal intensities so that the participant could describe the locations and qualities of the percepts. The projected fields of the electrodes were located in digits 2-5 and at base of each of those fingers. Sensations were reported from 59 of 64 electrodes, and no painful sensations or paresthesias were reported. Detection thresholds for these electrodes were found to have a median value of 34.9 μ A, with upper and lower quartiles at 60.0 and 24.8 μ A, respectively, and were stable over time. Increasing the stimulation amplitude also resulted in a linear increase ($R^2 = 0.98$) in the perceived intensity of the stimulus for the 5 electrodes tested. We then evaluated the effect ICMS feedback had on BCI task performance. First, we verified that the subject could use the ICMS feedback to identify which of four fingers of an anthropomorphic robotic limb was being touched by converting finger torque to stimulus intensity using a linear relationship. The load-bearing finger was identified with 84.3% accuracy ($n = 54$ trials). The feedback was then used in a force matching task that required the subject to control the torque applied to various fingers on the robotic limb under BCI control. Preliminary data suggests ICMS feedback significantly improved the subject's ability to apply the instructed torque ($p < 0.005$). We found that percepts were evoked at somatotopically relevant locations, and that the perceived intensity of stimuli scaled linearly over a large range. These features enable us to relay both the location and intensity of object contact, two sources of information that would be helpful for BCI users to interact with objects. The ability to



provide artificial somatosensory feedback to BCI users could improve the user's control and experience with the prosthetic device.

2-D-28 Spatiotemporal Dynamics of Error Correction During Sensorimotor Coordination

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We report on electroencephalography (EEG) and transcranial magnetic stimulation (TMS) studies investigating error correction during sensorimotor synchronization. During both experiments participants coordinated finger tapping of their right hand with a rhythmic auditory stimulus presented at 1.66 Hz (.6 ms ISI). After approximately 12 trials (10-14 determined randomly) the auditory stimulus was perturbed by advancing (occurring earlier than expected) or delaying (occurring later than expected) presentation by either 3% or 10% of the ISI. Small perturbations are subliminal whereas large perturbations are generally liminal. We aligned EEG trials to the tap associated with the perturbed stimulus before applying a minimum norm approach to estimate the distributed cortical network underlying sensorimotor synchronization. We then performed time frequency decomposition of the cortical sources averaged within each region and computed the phase locking within discrete frequency bands across regions. We found three main results. First, there is an increase in theta activity in the supplementary motor cortex beginning at approximately 200 ms after the tap that was larger for the late large perturbation. This finding suggests that SMA responds relatively early, but only to the detection of large error in which the stimulus is later than expected. Second, when compared to the small perturbations, beta band rebound in the primary motor cortex (at approximately 300 ms post tap) was greater for the late large perturbation and smaller for the early large perturbation. This finding suggests that error correction may involve modulation of inhibitory processes in the motor cortex. Third, a functional link between SMA and M1 was implied by an increase in phase locking for the late large perturbation condition. A TMS study directly probed changes in motor excitability for early and late large perturbation. Preliminary results support our conclusions by showing a decrease in motor evoked potential amplitude at 300 ms prior to the corrected tap for the late large perturbation when compared to a non-perturbed control. Overall these results provide evidence that SMA may modulate motor cortex function by influencing activity in local inhibitory circuits.

2-D-29 Comparison of the reference frames for encoding self-motion in the rostral fastigial nucleus and posterior cerebellar vermis

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As we move, the brain combines sensory signals (vestibular, proprioceptive, visual) to create self-motion estimates that are essential for a wide range of motor tasks. Many of these behaviors (e.g., postural control, locomotion, reaching) rely on estimates of our body motion. Our vestibular sensors are among the most important sources of self-motion signals. However, they encode motion in head-centered coordinates. To contribute to behaviors requiring estimates of body motion these



signals must be transformed from a head- to a body-centered reference frame. Previous studies provided evidence for a partial transformation of vestibular signals towards body-centered coordinates in the rostral fastigial nucleus (rFN) (Shaikh et al., 2004; Kleine et al., 2004). However, these studies only examined cell tuning properties for a limited set of motions and head-re-body orientations in the horizontal plane. If true "body-motion encoding" cells exist in the rFN, they should also reflect such a transformation when the head is reoriented in the vertical plane (i.e., in 3D). Furthermore, the extent to which the rFN plays a role in performing these transformations versus encoding the result of computations performed upstream in the cerebellar cortex remains unclear. To address these issues, we examined the reference frames for encoding translational motion in the rFN and in regions of the posterior cerebellar vermis (nodulus and uvula, NU, lobules 9 and 10) that project to the rFN and have recently been shown to play an important role in estimating translation (Yakusheva et al., 2007; Laurens et al., 2013). We recorded rFN and NU Purkinje cells in 2 rhesus monkeys during translational motion (0.5 Hz, 2B/-9 cm) delivered along 13 directions in 3D space using a 6 DOF motion platform. Cell tuning was characterized with the head upright as well as after static reorientation of the head relative to the body in the vertical plane (i.e., in pitch or roll) and the horizontal plane (i.e., in yaw). Consistent with the requirements for a 3D transformation, significant tuning shifts toward body-centered coordinates were observed in 50% of rFN cells after both vertical- and horizontal-plane head reorientations. However, tuning properties were broadly distributed with different extents of transformation often observed for reorientation in each plane. Thus, while as a population rFN neurons reflected a 3D transformation of vestibular signals, only 12% of individual cells exhibited fully body-centered tuning in 3D. In contrast, the tuning of most NU cells (90%) was consistent with head-centered translation encoding. Thus, our NU results to date suggest that, in keeping with theoretical assumptions (e.g., Green et al, 2004), the NU computes a mainly head-centered representation of translation. The transformation towards body-centered coordinates is likely to take place either in the rFN itself or upstream in the anterior vermis (Manzoni et al, 1999).

2-G-30 Modular organization of hand control

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Human body has more biomechanical degrees of freedom (DoFs) than needed to perform any particular task. How the central nervous system (CNS) coordinates these DOFs to achieve a goal is still a central problem in motor control. The hand with its 60 DoFs and 36 muscles represents an optimal model to study the complexity of motor control. Different studies highlighted that the biomechanical DoFs in the hand are not controlled independently, but joint excursions and muscle activations are organized in covariation patterns: postural and muscle synergies, respectively. More recently, findings on primates showed that corticomotoneuronal cells in the primary motor cortex have monosynaptic connections with motoneurons and are functionally tuned to coordinate wrist agonist and antagonist muscles. Moreover, salient features of these coactivations seem to be encrypted both at the muscular and cortical level, corroborating the neural control of muscular synergistic patterns. In this work, we were interested in deepening the theory of synergistic control by evaluating the variability of postural and muscular synergies during human reaching and grasping



movements. Indeed, variability is a marker of optimal motor control since it allows distinguishing task relevant and irrelevant parameters. We recorded hand kinematics by using 26 reflective markers and the electromyographical activity (EMG) of 15 upper limb muscles in 8 young healthy subjects while they performed 7 times reaching, grasping, and holding of 12 objects accounting for four grasp types (ulnar, pulp, five finger pinch, and cylindrical grasps) and 3 sizes (big, medium, small). For each subject and object, we extracted postural synergies from the trajectory of the center of mass of each hand segment, and muscular synergies by using the non-negative matrix factorization algorithm. Then we computed the inter- and intra-subjects variability of the weight coefficients by using normalized scalar products and of the timing activations by using the Pearson correlation coefficient. For each object, both kinematics and muscle activity were decomposed in four modules accounting for more than 95 % of the variance. Across different grasp types and object sizes, the same muscle synergies structure was preserved reinforcing the hypothesis of a common organization behind the generation of muscle activity to grasp different objects. The inter- and intra-subjects variability was lower for the weight coefficients of muscle synergies compared to the one related to postural synergies. Moreover, low variability was observed for the timing activations of postural synergies. Our preliminary results reveal the low dimensional modular nature of hand motor control and they suggest a different control of the CNS for muscles and joints. In particular, it seems that the CNS controls the coordination and organization of muscles in order to achieve hand postures and the timing of these last to successfully achieve a task.

2-G-31 Learning posture through movement

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When someone acquires a new skill, be it locomotion or ballet, and expands their movement repertoire, their posture changes so to provide support for the variety of movements which they are practicing. Inversely when someone's movement repertoire becomes limited, as for example after an injury, they develop postural problems, adopting a posture which limits the movements that can be performed without pain. The purpose of this project is to understand the computational principles allowing for posture to adapt to the repertoire of movements being practiced. We consider a person standing on a platform which is translated backwards or forwards. When the support is wide, the perturbation is followed by a response at the ankle which restores balance ; however when the support is narrow, such a response at the ankle further upsets balance, and, after practice, it is replaced by a more appropriate response at the hip (Horak and Nashner 1986). Classical models of posture suppose that, in this task, head motion signals (such as provided by optic flow and the vestibular system) and proprioceptive signals (such as provided by muscle spindles) are used as error signals for the feedback control of balance. We suggest to distinguish between a 'movement' system which uses head motion error signals and classical feedback control to stabilise the head in space, and a 'postural' system which uses proprioceptive signals to perform anticipatory learning rather than feedback control. The postural system senses the effect of support perturbations on proprioception, but has only indirect access to the head motion error signal, through the effect on proprioception of the corrections provided by the movement system. We propose an anticipatory learning rule which allows the postural system to learn to anticipate on



these corrections and provide a fast and appropriate postural response following a proprioceptive perturbation. This response stabilises the head in space and therefore preempts the need for feedback control by the movement system. This anticipatory learning rule allows the postural system to learn both a response at the ankle when the support is wide and a response at the hip when the support is narrow. In this model, feedback control by the movement system is initially necessary for adapting the postural response to the support conditions, but not for performing the postural response once learning has occurred. Thus, the adequate postural response is learned through movement. In principle, this anticipatory postural learning rule may therefore allow the postural response to adapt to any repertoire of movement which is being repeatedly practiced, thus providing a unified computational principle which can account for the changes in posture following both skill learning and injury.

2-G-32 Mechanisms underlying the modulation of motor patterns during epidural electrical stimulation of the lumbar spinal cord

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Severe spinal cord injury (SCI) disrupts the communication between supraspinal centers and spinal circuits producing leg movement, usually located below the lesion. The interruption of descending pathways abolishes the sources of modulation and excitation that are essential to enable functional states of spinal circuits. Albeit intact, denervated lumbar circuits remain in a state that is not permissive for standing and walking. Electrical epidural stimulation (EES) of lumbar segments provides a strategy to reactivate these circuits, facilitating standing and walking in animal models and humans with spinal cord injury. However, the mechanisms through which EES enables the production of motor patterns remain enigmatic, even though this understanding is pivotal in the translation of this paradigm into a viable clinical application. In the last decade computer simulations and experimental studies provided evidence that EES primarily engages large myelinated fibers associated with proprioceptive and cutaneous feedback circuits. We used these results to develop a computational framework that predicts the interactions between EES and the dynamics of spinal sensorimotor circuits. In particular, we modeled, using NEURON, muscle spindle feedback pathways and integrated these circuits within the minimal neuronal network that is responsible for the reciprocal recruitment of agonist muscles. We then estimated the natural firing rates of the afferent fibers during stepping using an experimentally derived muscles spindle model driven by a validated musculoskeletal model of the rat hindlimb implemented in OpenSim. Finally, we modeled the effect of EES on afferent and efferent fibers and integrated this input together with the estimated sensory information. Using this computational model and behavioral experiments, we provide evidence that epidural electrical stimulation synergistically interacts with muscle spindle feedback circuits to modulate muscle activity during locomotion. Furthermore, the model allowed for the dissection of the role of muscle spindle feedback circuits in the spinal control of locomotion. Hypothesis-driven strategies emerging from simulations steered the design of stimulation protocols that adjust bilateral hindlimb kinematics throughout gait execution in rats after spinal cord injury. The conservation of muscle spindle feedback circuits across mammals suggests that the same



mechanisms may facilitate motor control in humans. However, we show that some limitations may apply to human translation due to the action potential propagation time along proprioceptive fibers. In particular, we show that the propagation time influences the occurrence probability of destructive interference between EES and sensory information impacting significantly on the mechanisms of action of EES. These results provide a conceptual framework to improve stimulation protocols for clinical applications.

2-G-33 Neural Control of Discrete and Rhythmic Movements

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Human dexterity exceeds that of modern robots, despite omnipresent noise and vastly slower neural processing. Several lines of research have accrued evidence that the complex biological system is hierarchically organized, with building blocks or motor primitives under only partial cortical supervision. This study continues research on the hypothesis that viable candidates for such motor primitives are discrete and rhythmic movements, defined as point and limit cycle attractors, generated in the neuromechanical network. The distinction between rhythmic and discrete primitives was supported by a previous neuroimaging study that showed strikingly different cortical and subcortical activation: while rhythmic movements were associated with mostly primary motor areas, contralateral M1 and ipsilateral cerebellum, discrete movements involved a significantly broader network of cortical areas, including bilateral parietal and prefrontal regions. Given the rapid advances in imaging technology and analysis, the present study aims to replicate and extend these results from more than 10 years ago. Using the same movements, we recorded fMRI data with simultaneous recording of behavior. Subjects performed flexions and extensions with their right dominant wrist during acquisition of whole-brain scans in a 3T scanner; kinematic data were acquired by a custom-made goniometric device. In Experiment 1, movements were self-paced, performed in continuously rhythmic fashion or as single flexions and extensions self-initiated at random intervals over the 36-sec run. Using a GLM analysis, results largely replicated those of the previous study: rhythmic movement primarily elicited contralateral motor cortical, supplemental motor cortical, and ipsilateral cerebellar activations, whereas the discrete condition implicated a broader network of parietal and prefrontal areas, in addition to primary motor areas. In order to probe whether self-initiated timing was responsible for the extensive activations, Experiment 2 compared rhythmic and discrete movements that were visually cued and the number of initiations and terminations were matched. Preliminary results were largely consistent with the earlier study, but also raised additional questions. To shed light on the functional meaning of the activated network, novel connectivity analyses will be conducted. In addition, more focused follow-up measurements will be done using 9.4T scanning that provide significant increases in spatial resolution. These studies will provide a first important replication of previous influential results, supporting that even non-visually guided discrete movements require an extensive set of cortical areas, while continuous rhythmic movements are generated with significantly less cortical substrate, but possibly rely on lower brainstem activation. This different neurophysiological substrate



underscores that these two movement types act as different building blocks at different levels of the neural axis.

2-G-34 The Computational and Behavioral Implications of Aim- and Reach-Based Generalization

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In sensorimotor learning, the pattern of generalization from experienced situations to novel ones is thought to reflect the neural representation of the motor system. Numerous studies have sought to understand the reference frame of this representation and the manner in which movement errors update it (Ghahramani et al., 1996; Thoroughman and Shadmehr, 2000; Berniker et al., 2014). Recent work (Castro et al., 2011; Yokoi et al., 2011) has shown that generalization is likely not, as previously believed, in a target-based reference frame, and target-based errors do not appear to drive implicit motor adaptation (Mazzoni and Krakauer, 2006; Taylor and Ivry, 2011). Instead, it appears that the relevant reference frame may be centered around the actual movement trajectory (Castro et al., 2011) and/or the explicit aiming strategy (Day et al., 2015). Furthermore, it has been shown that sensory prediction errors -- defined as the difference between the planned movement and observed feedback -- drive implicit adaptation (Mazzoni and Krakauer, 2006). In light of these new findings, we sought to reevaluate previous interpretations of generalization patterns, learning time courses, and aftereffects, and reconfigure the standard state-space learning model accordingly. First, we develop an updated version of the standard dual-rate state-space model (Smith et al., 2006) that incorporates both explicit aiming strategies (McDougle et al., 2015) and generalization. In addition, the state-space model's internal estimate of learning is updated based on sensory prediction error and not target error. Second, by having subjects perform a generalization task while reporting their intended aiming location, we derive a genuine implicit generalization function. Third, we apply this model and its experimentally derived parameters to several data sets and replicate basic findings of the aforementioned studies (Castro et al., 2011; Day et al., 2015), showing that target-based generalization is indeed insufficient to explain the generalization pattern of implicit adaptation during a visuomotor rotation task. Finally, based on a counter-intuitive prediction of our model, we show that when the size of a rotation is abruptly increased during learning (though its sign is maintained), adaptation actually decreases because of the reference frame of generalization. While the experiments here do not explicitly favor either movement- or aim-based generalization reference frames, they demonstrate the behavioral and computational consequences of non target-based generalization.

2-G-35 Efferent microneurography recordings during volitional movements: direct insight into how motoneurons control hand force and velocity

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Currently there are no reliable electroneurogram (ENG)-driven control algorithms for hand prostheses. The reason behind this is a lack of full comprehension of the discharging activity of motoneurons during the volitional control of movements. It is important, though, to access the human peripheral nerves in order to investigate the ability to decode features of neural control of the hand motion. We conducted microneurography (MNG) sessions on three healthy volunteers and acquired efferent signals from their median nerve along with the electrical activity of the hand muscles (EMG) innervated by it. In particular, a neurologist placed the electrode in the fascicles that presented ENG correlated with the hand EMGs but not with muscles stretch or skin touch. This expert overview was necessary to minimize and eventually avoid the acquisition of tactile or proprioceptive signals. Then, the subjects were asked to execute several hand grasps/movement, at different forces and velocities. We found that the neurons firing rate has a strong relation with the force exerted during the grasps. This relation has been modeled mathematically. Finally, we observed that when identical tasks are executed at increasing velocities, the average (positive) derivative of the neurons firing rate has a significant increase. Successively, we investigated whether the information could be used to predict grasping forces and muscle contraction velocities from ENG data, in real-time. Hence, we developed two decoders, based on a feature set chosen after the encoding model just determined. In particular, the exponential of the average motoneurons firing (AFR) rate was used to detect forces while the increasing slope of AFR was used to detect velocities. Other features have been introduced to identify subjects' rest and activity in the AFR. We found that the two decoders were able to reliably predict rest with respect to hand motion and to distinguish between 3 forces and two velocities with an accuracy of 60% and 68% respectively. Finally, in order to investigate the impact of supraspinal and peripheral inputs onto the generation of the observed dynamic behavior of alpha motoneurons, we developed a simplified model of a local neuromuscular circuit. Overall, the simulation results for tasks in which force and velocity were modulated showed that during voluntary hand movements, the firing of motoneurons is mostly conditioned by the driving input from central nervous system and by their intrinsic properties such as adaptation rather than by the feedback brought by proprioceptive fibers, supporting the applicability of the presented results also to people with no sensory feedback (as amputees). This work represents an important neurophysiological insight into the way the PNS encodes the control of the force and velocity of hand movements, supporting the idea that MNG could represent a method to deeply investigate the way the motoneurons control the volitional limbs motion.

2-G-36 Recording neural commands from peripheral nerves: physical origin of the signal and optimization of neural interface by computational model

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Reliable and stable recording of neural signals from peripheral nerves (PN) is important, both for the understanding of mechanisms underlying the control of movement, as for the construction of the future brain machine interfaces, which could be used in case of upper or lower limb amputations. Several groups have shown the feasibility of sporadic recording of electroneurogram data (ENG) from the peripheral nerves of humans. However, these recordings were instable, and of difficult interpretation. Among the main reasons for that is the missing understanding about the interface-



tissue interaction and the origin of recorded signals, which would enable the construction of optimized devices, amenable for selective and long-term recording of useful signals. In order to fill this gap we developed the detailed hybrid Finite Elements (FEM)-Neuron computational model of a peripheral nerve, with different neural interfaces implanted inside and studied their recording capabilities. The realistic nerve histology was segmented, and then extruded within the FEM solver, while on the biophysics side the realistic population of axons has been implemented within NEURON. Model was validated with respect to the experimental recordings, which we performed, showing the results that were statistically not different. Several types of interfaces were studied: epineural, intraneural shaft and wire electrodes, and for all of them we systematically evaluated the area of recording, spatial selectivity, type and distance of recorded fibers. For the intraneural electrodes we were able to design the optimal distance between active sites and show the minor importance of the dimension of active sites for the signal recorded. For wire electrodes, we assessed the sensitivity of the recording respect to the solid angle of wire tip, showing its importance. Overall, the nature and shape of signals obtained for three electrodes were studied, resulting in intraneural wire as the most sensitive device and less selective the epineural ones, being unable to record any activity except the one from the superficial fascicles, with the smallest signal to noise ratio among all. Finally, the big issue for long-term recording consisting in fibrosis was addressed. Experimentally found fibrotic tissues dimensions were introduced into the model, resulting in loss of sensitivity for small-medium fibers, together with the problems related to distance from cells to device, introduced by means of fibrosis. Our results indicate that this is the most probably origin of the recording failure over the long-time, and suggest that the work should be done on drugs release or appropriate materials disposition over active sites, in order to make this tissue response more mild. Present work represents an important step toward the deep investigation of the nature of recorded neural signals from the PN, and indicates the optimal way to interface it, in the most informative and stable manner.

2-G-37 Dissociating the role of sensory prediction error from performance errors in strategy-based motor adaptation

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In theory, no goal is needed for motor adaptation: the sensory prediction error (SPE), i.e., the error between actual and predicted hand location, is sufficient to update the motor command. In most studies, however, performance-related signals such as performance errors (PE) and rewards, which are known to play significant roles in motor adaptation, are typically present. Is there any effective strategy to dissociate the roles of SPE from PE? In the visuomotor adaptation studies by Mazzoni and Krakauer (2006) and Taylor and Ivry (2011), subjects were instructed to aim explicitly to a neighboring target of the main target to cancel the initial PE with respect to the main target due to the perturbation. In subsequent trials, subjects exhibited gradual over-compensation, which has been suggested to be the signature of internal forward model update by SPE. Here, we hypothesize that adaptation in this paradigm is due to three different types of errors: PE between the visual cursor and the main target (PE1), PE between the visual cursor and the neighboring target (PE2), and SPE between the visual cursor and the visual prediction of the hand. To test this idea, we performed



a visuomotor adaptation experiment with 45 degrees perturbation that extends that of Taylor and Ivry (2011) with 4 conditions. Visuomotor rotation was introduced for 200 trials. After the second trial following the perturbation, subjects were instructed to shoot to the neighboring targets located at 45 degrees from the main targets. A localization test of 10 trials was then given, followed by 80 washout trials. Final cursor feedback was always available except during localization trials. In condition 1, the two targets remained on the screen during the trial. Thus, PE1, PE2, and SPE were available. In condition 2, the main target disappeared as soon as the movement was initiated, leaving PE2 and SPE. In contrast, in condition 3, the neighboring target disappeared, leaving PE1 and SPE. In condition 4, both targets disappeared, leaving SPE only. Preliminary results indicate that the overcompensation following strategy was largest in condition 2 (PE2+SPE), then in condition 1 (PE1+PE2+SPE) and in condition 4 (SPE), and least in condition 3 (PE1+SPE), in which the initial overcompensation returned to near zero (as found in Taylor and Ivry, 2011). A large overcompensation similar to that observed in Mazzoni and Krakauer (2006) was only observed in condition 2 (PE2+SPE). In addition, increase in localization errors were observed in all four groups. These results complement our previous results (Oh et al, NCM 2014) that no target is needed for adaptation. In summary, our study suggests that 1) PE2 plays a role in producing the over-compensation observed in Mazzoni and Krakauer (2006), 2) PEs and SPE influence motor adaptation by generating adaptive responses with different time courses, and 3) SPE is always present and is sufficient for motor adaptation.

2-G-38 A cerebellar model for Bayesian estimation of time intervals

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Humans estimate time intervals by combining noisy measurements with the distribution from which the intervals are drawn (prior), as predicted by a Bayesian integration strategy (Jazayeri & Shadlen 2010). While normative Bayesian models capture human estimates remarkably well, the neural mechanisms that give rise to such Bayesian behavior remain unknown. We hypothesized that the cerebellum, by virtue of its involvement in timing (Buonomano & Mauk 1994, Ivry 1996) and the adaptive nature of its learning mechanisms (Fujita 1982), might serve as a suitable substrate for learning the temporal statistics of sensory events, thus providing the means for encoding the prior used in Bayesian interval estimation. We tested this idea by constructing a simple model of the cerebellum in which excitatory inputs from granule cells (GCs) and climbing fibers (CFs) sculpt the activity of Purkinje cells (PC) via long-term depression (LTD). Interval information is imparted to the model via cues that signal the beginning and end of the interval. The cue signaling the beginning of the interval triggers rich and reproducible firing patterns in the GC population that serve as a basis for learning temporal structures. The cue signaling the end, on the other hand, activates CFs and causes temporally specific LTD, thereby reducing the synaptic efficacy of GC inputs that are active near the end of the interval. To ensure that the learning reflects recent history, the model incorporates a weak and slow restoring potentiation that allows synapses to recover in the absence of CF input. The cumulative action of LTD across trials imprints a negative image of the history of the observed intervals upon the PC firing rate dynamics. This decrease in PC activity disinhibits neurons in the deep nuclei leading to commensurate prior-dependent increases in the cerebellar output. The



model instantiates the final Bayesian estimate by integrating the cerebellar output over time. We hypothesize that this integration is likely to occur outside the cerebellum, in cortical regions that receive transthalamic input from cerebellar deep nuclei (Prevosto et al. 2010), which is consistent with recent recordings in the parietal cortex of monkeys performing a time interval reproduction task (Jazayeri & Shadlen 2015). Furthermore, by introducing stochasticity into the GC population activity and thereby reducing temporal precision of LTD for longer intervals, the model can accommodate the observation that estimates of longer intervals are more biased towards the mean of the prior than shorter intervals. Finally, the behavior of the model is robust to parametric variations of the GC dynamics and LTD, and can account for Bayesian integration with different prior distributions. The model thus offers a plausible neural mechanism for the acquisition and updating of prior beliefs and underscores the cerebellum's potential in supporting Bayesian behavior for interval estimation.

2-G-39 Sprint to the Finish: How Time and Effort Interact in Motor Decisions

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In both decision making and motor control, it has been shown that reward is temporally discounted. Animals prefer an immediate reward to the same reward later. They also make faster movements to more rewarding targets. Every rewarding action is discounted by the effort it requires, but the interaction between time and effort is not well understood. Previous models only temporally discount reward and simply subtract effort, while others discount the net reward (with effort subtracted) by time. Logically, one could argue both scenarios. Here, we sought to clarify the role of time with respect to effort in determining the utility of an action. If effort does interact with time, then an individual would care about when they invested a given amount of effort. Subjects generated 14 different effort profiles by isometrically pushing against a force transducer. They sat in front of a computer screen, and were asked to trace a line presented to them using a cursor on the screen. The cursor moved horizontally at a fixed rate, while subjects controlled the vertical position with their pushing force. All profiles were 17 seconds in duration, and were normalized to each subject's maximum voluntary contraction (MVC). Each profile was composed of periods of low effort (10% MVC) and high effort (50% MVC). The duration of high effort was varied between 1, 3 and 5 seconds, and the onset times varied from 2.5 to 12.5 seconds from the beginning of the trial in 2 second intervals. Importantly, for a given high-effort duration, the total time-integral of force was constant across trials no matter the high-effort onset time. After a familiarization period, subjects were presented with a two-alternative forced choice task, in which they chose the effort profile they would rather complete. Each of the 91 possible combinations was presented five times, and half of the combinations were realized pseudorandomly throughout the experiment. Initial results (n=9) suggest that subjects have a temporal preference for where effort occurs within a movement. Eight of the subjects showed a preference for generating higher effort later in the trial rather than earlier, akin to the hyperbolic discounting model used to discount reward, while a single subject exhibited a preference for the opposite. These results suggest that effort, like reward, may be discounted with time. Ultimately, this would significantly revise our understanding of effort in the field of motor control and decision making.



3-D-1 The influence of activating versus relaxing music on repetitive finger movement and associated motor cortical activity

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Music is a therapeutic strategy proposed to improve movement performance in people with neurological impairments. Research examining the brain activity associated with movement and music is lacking. It has recently been shown in healthy adults that the style of music can differentially affect movement performance. The purpose of this study was to examine movement performance and associated motor cortical activity while moving to different styles of music at two different rates in young healthy adults. Thirty-two participants were asked to perform an unconstrained finger flexion-extension movement in time with a tone only, and in time with two music conditions, relaxing music and activating music. Two rates (70 beats per minute and 140 beats per minute) were presented for each condition. A metronome click was included in the music conditions to ensure participants were tapping at the correct rate. Finger movement was measured using a 2 mm sensor (Ascension trakSTAR) placed on the dorsum of the middle phalanx of the index finger, and bipolar surface electromyography (EMG) was recorded from the first dorsal interosseous and the extensor digitorum communis (Delsys Trigno). Position signals were collected for movement in the vertical plane only. Electroencephalography (EEG) signals were recorded from a montage of 64 scalp-surface electrodes encompassing the surface of the scalp (BioSemi Active Two System) during movement conditions and during rest. Kinematic and kinetic data was obtained from the sensor and EMG data. Movement onsets were also manually obtained and EEG signals were epoched relative to movement onset. Epochs were then collated for all trials across each tone rate and each condition (i.e. 70 Tone, 70 Active, 70 Relaxing), resulting in approximately 120 epochs for each tone rate in each condition per subject. A fast Fourier transform was applied. The power spectrum was normalized so that total power in the spectrum was equal to 1 and then summed for each participant. To obtain the mean spectrum across participants, all epochs were averaged resulting in a chi-square distribution. To compare spectra between conditions, the mean spectrum of one condition was divided by the mean spectrum of the second condition resulting in an F distribution. This allowed for statistical comparison of spectrum between groups by obtaining the 95th percentile confidence limits from an F table using the total number of epochs in each group as the degrees of freedom. Any value below or above these limits was designated a significant difference between spectrums. Results revealed that the amplitude of repetitive finger movement was did not differ between conditions. However, associated power in the alpha and beta band was significantly increased for activating music. These results suggest that the type of music used to facilitate movement may effect associated brain activity in the sensorimotor cortex.

3-D-2 Ageing related changes of sensorimotor noise and mechanisms of falls in the elderly

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Falls are the prominent causes of unintentional injuries in the elderly and thus pose a major hazard to our ageing societies (Rubenstein, 2006). Studies using epidemiological (Rubenstein, 2006), anecdotal (Campbell et al, 1990) and kinematic measurements (Khandoker et al, 2008) have made significant progress in understanding the risk factors of falls in the elderly. While, falls and lower limb motor control are often treated as biomechanical problems, less is known about the underlying motor neuroscience and systematic changes to the neural mechanisms that lead to increased falls in the elderly. We aim to provide a link between pathological changes in ageing sensorimotor system to behavioural changes using motor control theory. We hypothesize that both inherent perceptual and motor uncertainty (i.e. noise) (Faisal, Selen & Wolpert 2008) is likely to increase with age and may lead to imprecise foot placements causing trip overs, the major triggers of falls (Robinovitch et al, 2013). To test our hypothesis, we designed a controlled robotic environment for the estimation of sensorimotor noise and integration in the lower extremities. We devised the foot height positioning (FOHEPO) task to measure sensorimotor noise. In FOHEPO task, participants were asked to align the inferior surface of their feet to the edge of a movable obstacle (height 50-150 mm). This task mimics obstacle clearing without risk for participants being in contact with, or being tripped by the obstacle. In the same robotic environment, sensory psychophysics was performed to measure sensory uncertainty when participants compared foot and obstacle heights using vision and proprioception. Twenty-three healthy young (22-36 years, 6 females) and 24 elderly (65-81 years, 9 females) volunteers took part. Our preliminary findings are as follows: The elderly group had statistically significantly higher sensorimotor noise compared to their younger counterparts (estimated sensorimotor noise young = 11.4 mm elderly = 14.7 mm; $F(1,43)=6.95$ $p=0.01$). Sensorimotor noise in foot height placement increased proportionally with age. Judging obstacle height visually was not significantly affected by ageing (estimated object visual noise: young = 4.81 mm, elderly = 4.63 mm). Elderly performed significantly worse when they had to discriminate the difference between their own foot height and obstacle height, whether with or without visual information. This is likely to be related to proprioceptive degeneration along the course of ageing (estimated proprioceptive noise: young = 1.43 mm, elderly = 8.71 mm). Our preliminary findings provide a new insight into computational mechanisms of falls in the elderly, namely, increased sensorimotor and proprioceptive uncertainty. The findings can be integrated as complementary knowledge to physiological and biomechanical studies so as to advance fall monitoring and prevention.

3-G-3 Haptic SLAM: ideal observer models and methods to study haptic object recognition

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Even without visual feedback, humans can accurately determine the shape and manipulation possibilities of objects solely on the basis of haptic feedback. The study of human haptic perception and object recognition as well as manipulation is complicated by the challenges of measuring rich contact dynamics in our fingers and palm when manipulating objects, without occluding the tactile surfaces with chunky sensors. To this end we adopt a mixed in vivo-in silico approach, we use data gloves to track hand movements and optical motion tracking of the manipulated object. We then accurately reconstruct the hand and object kinematics in a physics simulation engine to obtain contact point (and eventually forces). This enables us to formulate a Bayesian ideal observer of



haptic object representations. We present a computational model for haptic exploration and shape reconstruction derived from mobile robotics: simultaneous localisation and mapping (SLAM). Our method solely relies on the knowledge of object contacts on the end-points, noisy sensory readings and motor control signals. We present a proof-of-principle reconstruction of object shape (e.g. sphere) from mechanically realistic multi-finger exploration simulated using a physics engine. Our model provides a framework for principled study of natural human haptic exploration and context-aware prosthetics and can be used as a platform for direct comparison of computational algorithms for haptic exploration and human strategies for the same task.

3-G-4 Sparse coding of natural movement statistics provides a parsimonious description of motor control

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A central question in motor control is to understand how the brain controls the multiple degrees of freedom of our body (Bernstein 1967). Attempts to answer this question fall broadly into two categories: (1) optimization of a cost function and (2) dimensionality reduction. We offer here an analysis of natural human hand movement data combining the two ideas: 1. optimization of a cost function on neural activity to encode movements and 2. dimensionality reduction in the kinematic space so that motor control takes place in a low-dimensional subspace of possible joint configurations, through the notion of sparse coding of movement. We build upon previous work by analysing natural hand movement of both the dominant and non-dominant hand in natural settings, allowing us to examine not only low-dimensional control structures within each hand but to compare the synergies across hands and investigate the existence of bimanual synergies. The spatial structure of movements and evidence for low-dimensional control manifolds has typically been investigated using principal component analysis (PCA). We presented here a new algorithm for a sparse dictionary approach that extract time-scale and amplitude invariant patterns from kinematic time-series of arbitrary dimensionality. Three aspects set our approach apart from previous work: (1) data efficiency, (2) consideration of spatiotemporal instead of only spatial structure and (3) automatic estimate of the latent dimensionality. Our method can be understood as both an extension and an improvement on the techniques promoted in sensory neurosciences by Olshausen and Field (1997), Aharon et al. (2006) and Mairal et al. (2010). The hypothesis of sparse encoding of motor output has been mentioned before as interesting possibility (e.g. Tresch and Jarc 2009; Ingram et al. 2008; Johnson & Ballard, 2014) but has not been investigated further to the best of our knowledge. We find that our sparse coding outperforms PCA and other projections. We hypothesise that sparse encoding of movement may account for observed grasp-type specificity in neurons of the monkey F5 (equivalent to human PMv) area (Rizzolatti and Gentilucci 1988; Raos et al. 2006) and may help understand the neural mechanisms of learning by observation (Di Pellegrino et al. 1992).

3-B-5 First draft of the Human Ethome

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Studying motor behaviour in a laboratory setting has given us many important insights into sensorimotor learning and control. However, laboratory tasks are, by their very nature, limited in their ecological validity. In the following, we present a first draft of our work on the collection of human behavioural data in unconstrained settings – the Human Ethome project – which aims at collecting the majority of sensory input and motor output of human behavior. A total of 62 healthy subjects (18 female, age 19–34) were recorded in various experiments. We recorded subjects in three different settings emulating their natural life in a studio flat in our lab, including (1) a kitchen/breakfast area, (2) a bedroom area and (3) an office area. The data from the subjects' left and right hand were recorded using a CyberGlove I and III respectively (CyberGlove LLC, San Diego, CA, USA). The movement from their entire body (excluding fingers) were recorded using an IGS-150 or IGS-180 motion capture suits (Animazoo UK Ltd, Brighton, UK). In a subset of subjects eye movements and head-mounted RGB videos were integrated using ET2 eye tracking glasses (SMI, Teltow, Germany). The working area of the subjects was monitored externally using a standard video recorder. We report here the natural statistics of human joint angles and velocities of eyes, head, body and fingers and their relationships. We identify prominent features of this ethomics data that are preserved across subjects or were found to be characteristically individual. We then test well known laboratory assumptions (e.g. planarity of movements) and scaling laws of human movement on their validity in natural behavior. Our results enable us to quantify key statistics of natural behaviour which would normally not be measurable and put into question previous findings of experiments performed in restricted laboratory settings.

3-B-6 Interactions between grasp and transport components during reach-to-grasp actions

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Relatively little is known about how coordination of grasp is achieved. One theory suggests that grasp end-effectors (digits) are individually controlled. A competing hypothesis is that the hand is coordinated as a singular grasping apparatus. We used a mechanical finger perturbation to test these predictions. A secondary aim was to study the interactions between grasping and transport components of reach-to-grasp, by analyzing the effects that a perturbation of grasp would have on transport. Ten subjects wore a force-producing exoskeleton over their right hand. An optical system tracked the tip of the thumb, index finger, and wrist. Subjects started with their hand in an open grasp formation, thumb depressing a start button and the index finger over a marker 120mm away. Subjects were instructed to reach-to-grasp-to-lift a small glow-in-the-dark block located 250mm away following an auditory signal. Lights were shut off during motion, forcing subjects to rely on somatosensation to guide movement adjustments during perturbed trials. Perturbed and non-perturbed trials were pseudorandomly interspersed with a 1:3 ratio. For the perturbation, a 0.5N extension force was applied to the index finger by the exoskeleton at the time when grasp aperture fell below 100mm. The force was sustained for the duration of the trial resulting in a lateral displacement of the index finger. We were particularly interested in analyzing two perturbation effects: (1) the kinematic changes of the thumb (non-perturbed digit) following the perturbation to



the index finger. We hypothesized that if the fingers are independently controlled during grasp, then the compensatory response should be relatively isolated to the perturbed finger, whereas if grasping is achieved in a unified manner, then we may expect to see a compensatory response in the thumb; (2) whether the transport component, thought to be controlled independently of grasp, would too show compensatory changes as a result of perturbed grasp. The perturbation resulted in kinematic changes in both digits: a clear deviation of the index finger from its original spatial trajectory (as expected) and a parallel deviation of the unperturbed thumb, also into extension. Moreover, the unperturbed transport component showed evidence of two compensatory responses. First, the transport component in perturbed trials had longer movement times and lower peak velocities, and earlier time to peak velocity and peak deceleration. Most interestingly, however, the perturbation did not have any effect on the hand's spatial path, leaving the direction of the reach toward the object preserved. The finding that unperturbed effectors can rapidly compensate for a perturbation of a single finger suggests that grasp and transport during reach-to-grasp actions are likely coordinated through a unified control process, rather than independent channels.

3-B-7 Interplay between cortico-muscular organization and robot-aided rehabilitation training strategies

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Stroke is the leading cause of adult disability in western countries. Impairments in reaching and grasping movements are among the most common consequences of a cardiovascular accident. Systematic reviews suggested that the efficacy of post-stroke rehabilitation is related to the degree to which the neuromuscular system is challenged by repetitive movements. Robot-aided rehabilitation often complements the standard rehabilitation because it increases the intensity and the repeatability of the treatment. In their optimal use, robotic devices should assist the movement of the limb so that, when the patients are able to perform the movement, they remain transparent (active training), and, when the patients are not able to initiate or execute the movement, they assist them (passive training). The adoption of suitable control strategies for passive movements is crucial; indeed, the robot should induce a cortico-muscular activity similar to the one present during active movements, in order to avoid a negative effect on the neural plasticity. Currently, control strategies are based on limited knowledge of motor learning and recovery following active and passive training. Therefore, effectiveness of robot-aided rehabilitation can further benefit from new insights into the interplay between passive strategies and cortico-muscular organization. Here, we investigated how the choice of different passive strategies affects the induced cortico-muscular organization in fifteen healthy young subjects. We employed a recently developed exoskeleton, and we proposed point-to-point reaching movements achieved with: i) linear trajectories executed at constant speed; ii) linear trajectories executed according to a minimum jerk speed profile; and iii) pre-recorded trajectories from healthy subjects. We compared across passive conditions the elicited muscle activity, in terms of level of muscle synergies composition, and the induced cortical activity, in terms of whole-brain activity. In particular, we used electroencephalography (EEG) topographical analysis (a.k.a. microstates) that we recently demonstrated being able to disentangle the temporal organization of the whole-brain activity during volitional tasks. Preliminary results suggested that the



level of complexity of the muscle activity was simplified in the induced movements compared to the active ones. In particular, trajectories executed according to a minimum jerk speed profile seemed to elicit a muscle organization more similar to the active condition. EEG microstates analysis, instead, revealed that passive movements, and particularly trajectories executed at constant speed, elicited global brain states similar to those present during active movements. Our results suggest that the choice of the control strategy should be carefully considered in the design of passive robot-aided rehabilitative training since it may impact the elicited cortico-muscular organization and, thus, the driven neural plasticity.

3-B-8 Sub-threshold TMS applied over primary motor cortex does not facilitate startle reaction time even when controlling for timing of TMS application

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Presentation of a startling acoustic stimulus (SAS) in a simple reaction time (RT) task leads to the involuntary release of a prepared movement and significant reductions in RT, yet despite an abundance of research the neural mechanism underlying this phenomenon is still widely debated. One proposal is that a SAS involuntarily increases initiation-related activation processes via an ascending sub-cortically mediated pathway, triggering the release of a cortically stored motor program while bypassing usual cortical processing. Indirect support for this hypothesis comes from research showing that the startle-induced shortening of RT is due to an additive effect of startle and voluntary initiation-related activation processes, with startle processes beginning earlier. Another method for transiently increasing cortical activation is through the use of sub-threshold TMS applied to the primary motor cortex (M1), which increases cortical excitability for 6-30 ms through a process termed intracortical facilitation, and significantly reduces simple RT when applied early in the RT interval. Based on this, a previous study conducted in our laboratory used a simple RT paradigm and applied sub-threshold TMS 30 ms following the go-signal and 15 ms following the SAS in control and startle trials, respectively. TMS significantly reduced RT in control trials, but there was no effect of TMS in startle trials. This result suggests that the cortex may in fact play only a limited role in the startle-induced facilitation of RT (i.e. StartReact effect); however, these results may alternatively be due to the different timing of TMS application employed between the two groups. As such, the purpose of the present experiment was to extend the previous investigation to determine if the application of sub-threshold TMS over M1 30 ms following a SAS would lead to facilitation of startle RT in the same manner as for control RT. Participants completed a simple RT task requiring ballistic wrist extension in response to an auditory go signal, which was randomly replaced by a 120 dB SAS on 25% of trials. On a subset of trials sub-threshold TMS or sham TMS was applied over the motor hotspot corresponding to the wrist extensors in M1 30 ms following the imperative stimulus (go-signal or SAS). Similar to our previous study, both sham TMS and TMS significantly facilitated RT in control trials, with TMS having a larger effect (~20ms), but neither sham TMS nor TMS affected RT on startle trials. These results indicate that the results of our previous study are not due to the differences in timing of TMS application. While these results further suggest that the cortex has limited involvement in startle-induced reductions in RT, startle may lead to a floor effect on simple RT such that sub-threshold TMS cannot lead to any additional RT facilitation.



3-B-9 "Mirror neuron" activity reflects timing of actions more than object and grasp type

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Neurons whose activity changes not only during action execution but also during action observation have been described in premotor and primary motor cortices. So far, little is known about the informational content of this activity, partly because grip types and objects have not been disambiguated in previous studies. In a previous experiment (Vargas-Irwin et al. 2015a), we recorded single unit activity simultaneously from PMv, PMd, and MI using BlackRock arrays while non-human primates performed a cued grasping task with instructed delay (CGID). First, monkeys were presented with one of two objects which could be grasped in two ways (precision/power and key/power grips). Then, a cue was presented instructing the monkey to either perform the power or the other grasp. After a delay, a "go" cue told the monkey to reach and lift the object using the indicated grasp. Here, we also included observation trials during which the "go" cue was replaced by a "no-go" cue and the experimenter performed the indicated action instead. We previously found that on an ensemble level, neural activity shows object specific patterns (for method, cf. Vargas-Irwin et al. 2015b) as soon as the object is shown, and further separation of neural states as grip type is cued and the action is performed. We extended our analysis to investigate whether individual units contain information about objects or grasp types in their firing patterns during action observation and execution. We found that during action execution a large proportion of recorded neurons shows selectivity for grasp type and object but only few units show selectivity during observation. In accordance with other studies, we find a large proportion of units whose activity changes relative to baseline during execution and observation trials ("mirror neurons"). Although changes in firing rate were time-locked to the observed movement, most firing patterns lack the object or grip related information detected during movement execution. Neurons also do not seem to fall into clear categories regarding timing and informational content. In conclusion, we find that "mirror neurons" may carry more information about the timing of actions rather than the goal of the action or the grasp employed. Even though mirror activity includes object and grip related information, it is sparsely encoded by far smaller numbers of neurons than those engaged during action execution. Whether object and grasp information carried by individual neurons is independent of other factors such as relative position or orientation is subject to future investigation. Vargas-Irwin CE et al. (2015a). Linking Objects to Actions: Encoding of Target Object and Grasping Strategy in Primate Ventral Premotor Cortex. *Journal of Neuroscience*. 35(30):10888-97. Vargas-Irwin CE et al. (2015b). Spike Train SIMilarity Space (SSIMS): A Framework for Single Neuron and Ensemble Data Analysis. *Neural Computation*. 27(1):1-31.

3-B-10 Using signal dependent noise to train desired movement patterns

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In everyday life, the human motor system must organize a high number of degrees of freedom to complete low dimensional tasks. Accordingly, for many of our movements, there are infinite



"equivalent" ways the body can coordinate joint angles to successfully complete some task. However, for well-practiced skills such as reaching and eye movements, people make stereotypical movements. While it is not quite clear what factors cause people to make these specific movements, they have been shown to be those that minimize task variability in the face of signal dependent motor noise. Here, we test the hypothesis that by strategically designing artificial signal dependent noise, we can elicit desired motor behaviors. Specifically, we inserted noise into a novel motor task, where ($N = 16$) subjects used 4-dimensional hand movements to control a 2-dimensional computer cursor. The roll and pitch of two inertial measurement units, one in each hand, were linearly mapped to the location of a cursor on a computer monitor. For this task, there are infinite (actually ∞^2) hand postures that result in a single cursor location. Signal dependent noise was artificially inserted such that the variance of the cursor at each location was dependent on the hand posture. The noise was designed such that the desired policy was the collection of hand postures that minimized cursor variance. We found that this paradigm was effective at biasing subjects towards the desired policy. Subjects who trained with the noise paradigm learned to control the computer cursor using coordination patterns that were significantly closer to the desired policy than subjects who trained with no additional noise. Interestingly, we also found that adding signal dependent noise in the visual feedback led to significantly improved task performance when visual feedback was removed. Together, these results confirm that people plan movements in an attempt to minimize task specific variability. Additionally, they validate the concept that designing signal dependent noise can be an effective means to elicit desired motor behaviors. These results have broad implications from designing more effective rehabilitation paradigms to improving the performance of brain- and human-machine interfaces.

3-B-11 Force field generalization is local: new evidence for the local representation of knowledge

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How the central nervous system stores and represents a newly learned motor task with an internal model is a central question in movement science. Much is known about this internal model: it acts as a repository for the learned behavior, allowing us to perform the task well, both now and in the future, and it provides the ability to transfer, or generalize that knowledge to new tasks. However, the variables used to encode this model, and how they are represented, remain unknown. To address this question, many studies use generalization tasks to better understand the corresponding internal model. Typically this is done by having subjects adapt to a force field in a one region of their workspace, and then testing their ability to make reaches in the same force field but in a new region of their limb's workspace. This basic approach has been used to study internal models, such as how information generalizes across the workspace, across limbs, or even across time. However, rather than converge on a set of coordinates, these many studies have found contrasting, and even contradictory evidence. New studies, however, may help to explain these inconsistencies. It has recently been shown that the ability to generalize is far more limited than previously supposed. This implies that prior studies may have been testing generalization beyond the limits of the internal model's representation; that is, outside the region where the internal model could effectively contribute to generating movements. To verify this, we performed an experiment that probes the



ability to generalize on a granular scale. Subjects adapt to a force field while reaching to a single target, and then are tested on reaches to other targets. These test targets are rotated relative to the learned target in increments of 45°. Error clamp trials, which measure a subject's reaching forces, are used to measure the ability to predict the force field. Generalization across changes in reaching direction is then quantified by comparing the error clamp forces in the test target forces with their naïve baseline forces. We find that the ability to generalize is indeed very limited and local. When reaching to targets only 45 degrees away, the ability to predict the force field, or generalize, is approximately halved. Even larger angular deviations in reaching direction suggest the ability to generalize is essentially non-existent, and there is no benefit from training. These findings have important implications. First, prior studies may have inadvertently elicited a non-specific motor response not reflective of the learned internal model, by testing generalization on behaviors too dissimilar from the trained behavior. Second, this implies that internal models, and motor knowledge in general, may be strictly local. Future work will continue to quantify the range over which generalization is valid, and in turn probe the coordinates used to encode motor information.

3-B-12 A developmental trajectory of motor learning using a novel virtual task

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How does the ability to learn new motor skills change across the lifespan - from children to older adults? Answering this question using real-world motor tasks has been problematic since development not only results in changes to the nervous system, but to the body itself. As a result, when differences in learning a motor task are observed, these are also confounded by physical differences in body size and body composition. Therefore, we sought to minimize these confounds by creating a body-machine interface and investigated how the ability to learn this novel virtual task changed across the lifespan. Participants (n = 50) between 9-75 years of age volunteered for the study and were divided into one of 4 groups - 9-year olds, 12-year olds, young adults (18-25), and older adults (45-75). The task for the participants was to control a cursor on the screen using movements of the upper body. We attached 4 inertial measurement units to the upper body and mapped the signals from the inertial measurement units to the position of the cursor. To ensure that the task difficulty was similar for all groups, we first had participants go through a calibration phase where they were encouraged to freely explore different movements of the upper body. We then used PCA to determine the two principal components of this exploration data, which was used to construct the map. This procedure allowed us to ensure that each participant could do the task with their own movement abilities. Once the map between the upper body motions and cursor motion was determined, participants were instructed to move the cursor to different targets on the screen as quickly as possible. Practice consisted of a single session of practice (160 trials) and we evaluated learning by examining how performance changed with practice. Results showed that task performance at the end of learning resembled an inverted-U shape with the young adults showing the best performance (i.e. lowest movement time). Children and elderly tended to have longer movement times (~2x longer) compared to young adults. The analysis of trajectories showed that the longer movement times in children were associated with less straight paths indicating that children and elderly had less ability to control the cursor (and not simply due to lower peak



velocities). In addition, there was greater variability between individuals, which was manifested in the large within group variance. Overall, these differences suggest that young adults are better at learning a new motor task compared to both children and older adults, and this may reflect the time course of development of neural mechanisms for learning.

3-B-13 Older adults show increased chunking behavior with extended practice

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Older adults seem to have a reduced ability to chunk keying sequences. However, it remains unclear whether they are unable to use chunking strategies or whether they are just slower in developing them. Using a discrete sequence production (DSP) task with extended practice, we here provide evidence supporting slower development. Across 3 to 4 hours of practice, older adults appeared to improve on multiple measures that are thought to be indicative of chunking behavior. A group of healthy older adults (n = 18, age 74 - 85) visited the lab on two days. For subject characterization we administered the Montreal Cognitive Assessment, a digit symbol substitution task and a visual working memory task. The DSP task was performed using a standard computer and keyboard. A sequence of 3 and a sequence of 6 elements were both practiced 432 times. The two sequences were presented in random order with a short break after every sequence. After the practice phase, an explicit knowledge questionnaire was administered. Then, a test phase with a block of 24 random trials and a block with 24 trials of learned sequences was performed. Chunking behavior is associated with a prolonged movement time for the first element of a sequence and shorter movement times for subsequential elements. The difference between the first and the average of the following movement times can be used as an index for the extent of chunking behavior. Our results show that this simple chunking index continued to increase over the extended practice period, with a steeper curve for the 3- than for the 6-element sequence. To control for general task learning, we also compared the magnitude of this chunking index between the random and learned sequences of the test phase. Based on this comparison, we find that our participants show more chunking behavior than participants in previous studies with less practice. Again, this effect was stronger in the 3- than in the 6-element sequence. As an additional test of chunking behavior in elderly, we analyzed our data using a Bayesian chunk inference algorithm that was recently published. First, we randomly shuffled the movement times within trials for all participants; this should remove most indications of chunking behavior while other properties like the mean, standard deviation and general learning effects remain. Then, we fitted the model to the original data and to the shuffled data for each participant. We found that the model fits the original data better than the shuffled data, indicating that chunking behavior at least partly explains the variance in reaction times in our data. Participants in our study continued to increase chunking behavior until the last phase of an extended practice period showing no ceiling effect. Hence, our results support the idea that reduced chunking behavior in older adults results, at least partly, from slower chunk development.

3-B-14 Shared mechanisms in the estimation of self-generated actions and the prediction of other's actions



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The ability to estimate and predict outcomes of self-generated actions and actions observed in others is fundamental for our social life. Previous theoretical studies have suggested that the brain uses parts of the forward model (used to estimate sensory outcomes of self-generated actions) to predict outcomes of observed actions (Wolpert et al., 2003). However, this hypothesis has remained controversial due to the lack of direct experimental evidence. In this study, we examine if a same forward model is involved in both, outcome prediction of observed actions and outcome estimation of self-generated actions by humans. To address this question, we utilized the understanding learning paradigm (Ikegami & Ganesh, 2014) and computational modelling to examine how outcome prediction of observed actions affects one's ability to estimate one's own actions. As sports professionals are known to have an acute outcome estimation of their own actions as well as prediction of actions observed in others (Aglioti et al., 2008), we recruited darts professionals in our experiment. We first show that learning to predict the outcomes of observed throws deteriorates a professional's ability to estimate the outcome of his own throws. Next, we introduce a state-space model to show that learning to predict observed actions affects one's forward model, introducing errors in the outcome estimates of self-generated actions, but interestingly not in one's ability to make action corrections corresponding to the (erroneous) self-estimation, usually attributed to the inverse model. Our results suggest that parts of the same forward model are utilized to both, estimate outcomes of self-generated actions and predict outcomes of observed actions.

3-B-15 A spike timing mechanism for respiratory motor control

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The nervous system controls the body using patterns of action potentials (spikes) to activate the muscles. However, it is poorly understood how spike patterns are used to encode motor output. Neurons could drive subsequent activity using spike rate, the precise timing of spikes, or a combination of both. Nearly all prior studies of motor function in vertebrates have assumed that muscles are controlled via a rate code. Recently, we demonstrated in individual neurons in the songbird vocal motor cortex that the precise timing of action potentials, down to the timescale of milliseconds, predicts behavioral output far better than does the spike rate (Tang et al., PLoS Biol 2014). This finding suggests an intriguing hypothesis - that small differences in spike timing in the cortex drive similarly precise timing patterns in muscle tissue, that these temporally precise motor commands cause significant differences in muscle force production, and that these differences in force output in turn cause measurable variations in behavior. To evaluate this hypothesis, we first performed single motor unit EMG recordings on a respiratory muscle in anesthetized Bengalese finches while simultaneously recording air sac pressure. We found that consecutive inter-spike intervals had more mutual information than would be expected with a nonhomogeneous Poisson spike train approximation. Spike trains with the same rate, but spike timing varying by as little as 1



ms were found to have significantly different pressure trajectories. Moreover, there was significant mutual information between spike timing and the associated pressure patterns after controlling for information found in the spike rate. While these results indicate that motor timing correlates with differences in respiratory behavior, the causality of the relationship is not clear. Therefore, to further investigate the causal role of motor timing, we next stimulated the muscle during anesthetized respiration using stimulation patterns that varied in timing but not rate while simultaneously recording air sac pressure. We found a significant difference in air sac pressure from varying a single spike's timing by 2 ms, regardless of whether that spike occurred early, late, or in the middle of the spike train. Because the transformation from muscle output to air sac pressure is a complex one, we wanted to ensure the muscle was, in fact, mediating the millisecond-scale effects we had observed. To achieve this, we extracted the muscle and stimulated it in vitro while recording force output. As in our in vivo results, varying stimulation timing by 2 ms in vitro resulted in significant differences in force output, suggesting that the pressure effects calculated from the in vivo data were indeed driven by the muscle output. Together, these findings suggest that not only are muscles capable of interpreting millisecond-scale timing in the incoming neural code, but the brain generates such signals to control muscles.

3-B-16 Neural substrates of priming of pop-out during eye and hand movements

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Target selection is strongly influenced by recent experience. For example, responses are facilitated when target features, such as color, are repeated (priming of pop-out; POP). Previous research indicates that POP leads to repetition suppression of the BOLD signal in regions associated with top-down attention, including the frontal eye fields (FEF) and intraparietal sulcus (IPS), as well as the lateral occipital cortex and fusiform gyrus. During a perceptual task, activation in these regions decreased when target colors were repeated compared to when they switched (Kristjansson et al., 2007). The authors interpreted this result in terms of perceptual reorienting, such that additional resources are required to switch attentional states when the search display changes. Importantly, however, many everyday tasks often involve multiple types of actions with different effectors (e.g., eye and hand). For instance, cooking dinner requires looking for and performing suitable actions toward specific ingredients. Here, we investigated whether the brain networks involved in this target selection bias are specific to the response used (effector-dependent) or if any of these regions impact target selection generally, regardless of the response mode (effector-independent). Using event-related fMRI paired with a color-odddity search task, we investigated the neural basis POP when participants were required make a saccade or reach to the odd colored target. The saccade and reach tasks were scanned in separate runs and participants maintained fixation with the effector not used for that run. We found that repeating target colors produced repetition suppression in brain areas involved in color processing (i.e., fusiform gyrus) and bottom-up attentional capture (i.e., right insula), and this was independent of the effector used. In addition to this effector-independent repetition suppression, we also identified a brain area involved in the effector-independent repetition enhancement. We observed that in the right superior parietal lobule, an area implicated in visuomotor coordination, showed increased activity when target colors were repeated for both



saccades and reaches. We suggest that increased activity within this motor area might be driven by facilitated motor planning led by color priming. Furthermore, we found an interaction driven by repetition enhancement for saccades, but not reaches, in the right inferior parietal lobule, which has been shown to increase in activity with saccadic accuracy. In sum, we find that areas associated with attentional capture and color processing exhibit repetition suppression effects of color priming, independent of effector. Moreover, we demonstrate that POP produces both effector-specific and effector-independent repetition enhancement in regions related to motor control. Thus, our results suggest that the neural correlates of POP differ for perception and goal-directed action and can also be modulated by the effector used.

3-B-17 Reaction time can be up to 100ms shorter if motor commands can be refined for accuracy demands after movement onset.

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Motor planning is the process of selecting the appropriate motor commands in order to achieve a goal. This process has been largely considered as part of a single building block that specifies the entirety of the motor program for the upcoming movement. The features of this process are reflected in the reaction time. Over the years, it has been shown that movement complexity, movement distance and accuracy demand modulate movement reaction time. For instance, Henry and Rogers (1960) showed that simpler movements had a shorter reaction time than more complex movements. Accuracy requirements have also a clear impact on movement reaction time as reaction time is up to 100ms shorter for non-goal directed movement (absence of accuracy demands) than for goal directed movements with strict accuracy demands (Laszlo & Livesey, 1977). To investigate the influence of movement accuracy on reaction time and movement planning, we asked thirty subjects to perform a virtual line bisection task with a robotic manipulandum. Subjects had to bisect a line in two segments of equal length. The lines were placed either 10cm in front of the starting position and 17,5cm on the side (far target) or 10cm in front of the starting position and straight ahead. Subjects were instructed to bisect the line with a continuous and smooth movement. Movements to the near target were essentially straight while movements to the far target were often curved (i.e. more complex). That is, for the far target, participants moved their hand laterally first before moving towards the target. Interestingly, we observed that movements to the far targets had shorter reaction times than movements to the near target (mean difference: 32ms, SE: 5ms, max: 104ms) despite being more complex. Interestingly, this is not a black or white process but the kinematic features of the movement played an important role in determining reaction time. That is, change in movement curvature from the near to the far target was correlated with the change in reaction time ($R=-0.56$, $p=0.001$). In other words, the earlier accuracy demands were taken into account (straighter movements), the longer the reaction time was. In summary, accuracy demand imposes a reaction time penalty if it is integrated in the movement planning before movement onset. This penalty is reduced if the start of the movement can consist of a transport phase and therefore the accuracy demand can be incorporated in the motor commands later in the movement, hence reducing the cost of accuracy demand on reaction time (up to 100ms). That is, in contrast with



current theories (Wong, Haith and Krakauer 2015), tuning motor commands in function of accuracy demand can occur beyond movement planning (i.e. after movement onset).

3-F-18 Corticomuscular coherence reflects modulation of sensory feedback gain during motor adaptation

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Corticomuscular coherence (CMC), which is used as an index of synchronization between cortical motor areas and muscles, is observed in the beta-band around 20 Hz during static force tasks (e.g. Baker et al. 1997). CMC is considered to contribute to sensorimotor binding necessary for facilitating rapid online feedback corrections during motor control or learning (Kilner et al. 2000; Perez et al. 2006). From the computational view, such online maintenance of movement is achieved by modulating the gain of the feedback controller, a part of whose function is likely to be implemented in primary motor cortex (M1; Shadmehr and Krakauer 2008). Thus, it can be hypothesized that CMC reflects modulation of feedback gains. In addition, in the course of motor adaptation feedback gains were upregulated at first and decreased through the end of adaptation (Franklin et al. 2012). Assuming from their results, the gain would have decreased because the acquisition of internal model reduced uncertainty in the body states. Therefore, we predicted a correlation between an efficacy of trial-by-trial adaptation (i.e., error sensitivity) and decrease in feedback gains. We tested the above-mentioned hypothesis in twenty healthy individuals by using a hand-reaching task under the viscous force counteracting their movements. The participants' open hand was fixed on a custom-made rotary brace, which was connected to a robotic device. The fingertip position sampled by the device was visually fed back to the participants with a cursor on a computer monitor placed horizontally above their arms. They made reaching movements toward a target on the monitor by extending their wrist while the resistive force was provided. To measure CMC during isometric contraction, they were asked to hold the hand at the target after the movement for about 8 s. To assess feedback gains, a brief mechanical perturbation was applied to the hand at random times during movement preparation in every trial, and stretch-dependent rapid motor response was evaluated. In addition, we estimated trial-by-trial error sensitivity using a computational model of motor adaptation. The maximal peak of CMC within the beta-band and magnitude of long latency rapid motor response calculated for the entire period of training were positively correlated across participants, suggesting that CMC is associated with modulation of feedback gains. Furthermore, CMC significantly decreased from the early to the late adaptation period, and the greater the decrease in CMC, the higher the trial-by-trial error sensitivity during adaptation. These results imply that individual who had a higher error sensitivity acquired the internal model faster, and thus resulted in a greater decrease in the feedback gain since the uncertainty of the body states was solved. The current study provides a novel insight into the functional role of CMC, and bridges the gap between computational and physiological understanding of motor learning.

3-F-19 Congruent visual motion cues speed dynamic motor adaptation

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Motor adaptation to novel dynamics occurs rapidly using sensed errors to update the current motor memory. This adaptation is strongly driven by proprioceptive input (1), although studies have also shown the importance of visual feedback (2). The importance of additional visual cues in reducing interference in learning two opposing force fields was recently shown (3). Here we examine whether additional visual cues increase the speed of adaptation in a single force field, specifically when the cue is visual motion congruent with the novel dynamics. Six groups of ten subjects performed alternating reaching movements in two directions while grasping the handle of a robotic manipulandum. Their hand position was indicated on a screen with a yellow cursor. Connected to the cursor via a thin line was a red object, located 2 cm in advance of the cursor (the visual cue). After initial null field movements, either a unidirectional (3 groups) or a bidirectional (3 groups) velocity-dependent force field was applied. For each group, the movement of the red object relative to the cursor was either congruent with the force field dynamics, incongruent with the force field dynamics or constant (fixed at 2 cm distance). The visual feedback was counter-balanced across force field types. Specifically, the incongruent visual movement in the unidirectional force field was identical to the congruent visual movement received in the bidirectional force field. Similarly, the incongruent visual movement in the bidirectional force field was identical to the congruent visual movement received in the unidirectional force field. Throughout the experiment, adaptation was assessed using maximum perpendicular error on the free moving trials and force compensation on channel trials. The unidirectional force field groups had higher final adaptation compared to the bidirectional force field groups. However, for both the unidirectional and bidirectional force fields, the groups in which the visual cues matched the type of force field (congruent visual cue) exhibited both faster learning and higher adaptation at the end of learning. On the other hand, there was little difference between the incongruent and constant visual cue groups. Although all groups received visual feedback of the cursor motion (providing visual information regarding the errors), additional congruent visual motion cues assist with the formation of the motor memory of the external dynamics. (1). DiZio, P. & Lackner, J. R. Congenitally blind individuals rapidly adapt to coriolis force perturbations of their reaching movements. *J Neurophysiol* 84, 2175-2180 (2000). (2). Sarlegna, F. R., Malfait, N., Bringoux, L., Bourdin, C. & Vercher, J.-L. Force-field adaptation without proprioception: can vision be used to model limb dynamics? *Neuropsychologia* 48, 60-67 (2010). (3). Howard, I. S., Wolpert, D. M. & Franklin, D. W. The effect of contextual cues on the encoding of motor memories. *J Neurophysiol* 109, 2632-2644 (2013).

3-F-20 Examining the contribution of explicit knowledge to structural learning in a visuomotor adaptation task

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Structural learning is a meta-learning phenomenon evidenced by an accelerated learning rate for novel tasks of the same structure as the training task. Exposure to pseudorandomly varying visuomotor perturbations of a fixed structure (i.e., rotations) facilitates the rate at which novel, yet isostructural, perturbations are learned (Braun et al., 2009). Previous investigations suggest that this



effect is driven by extraction of invariant features of the task, thereby reducing the dimensionality of the solution space. However, given that recent experiments have unveiled multiple processes (e.g., aiming strategies, implicit adaptation of a forward model) which contribute to learning in visuomotor adaptation tasks, the form of this meta-learning process is unclear. We sought to examine the level of knowledge at which structural learning operates and how it might contribute to performance in a visuomotor adaptation task. Extending the study conducted by Braun and colleagues, we exposed separate groups of participants to pseudorandom perturbations drawn from either a rotational structure or a random structure (exposure phase) prior to a consistent rotation at the end of training (test phase). We also included a control condition in which participants did not experience any perturbations prior to the test phase. To probe participants' explicit knowledge of the task conditions, they were instructed to report their intended aiming direction via a touchscreen monitor prior to reaching. In contrast to previous results, we found that both the rotation and random structure groups learned the consistent rotation in the test phase more quickly than the control group. This benefit was not the result of an internal model and, for the rotation group, explicit aiming strategies appeared to account for the majority of this effect. To better analyze the development of structural learning in the exposure phase, we examined reported aiming locations and found that participants in the rotational structure group aimed in a rotation-appropriate way while the random structure group did not approximate the solution space as well. Given these results, we suspect that there may be two forms of meta-learning operating in a visuomotor adaptation task: one that may be able to extract structural information from exposure to a variable perturbation sequence, which is possible in the rotational structure condition, and another that may be more consistent with a generalized aiming strategy or heuristic capable of countering multiple perturbation types.

3-F-21 Dissociating error-based and reinforcement-based learning.

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Error-based and reinforcement-based learning both lead to motor adaptation [1, 2]. Despite having the same final kinematics in a visuomotor task [1], the proposed adaptive mechanisms for these two forms of learning are quite different [2]. For error-based learning, it is suggested that adaptation occurs by minimizing error to update an internal model. For reinforcement-based learning, it has been proposed that adaptation occurs by sampling motor outputs to find a set that maximizes success (hitting the target). For both these forms of learning to occur implies that the nervous system uses two loss functions to update control policies--one that minimizes error and another that maximizes success. The goal of this study was to characterize these two loss functions in the context of a motor adaptation task involving error and reinforcement feedback. A commonly used paradigm to experimentally estimate loss functions involves providing participants with feedback about their movements that is corrupted by random noise [3,4]. The loss functions associated with minimizing (squared) error or maximizing success predict that subjects will adapt their movements based on the mean and mode of the noise distribution, respectively. Here we used a skewed noise distribution that, unlike a symmetrical distribution, separates the mean and mode. This makes it possible to dissociate the predictions of error-based and reinforcement-based loss functions. We predicted that



participants receiving error feedback would learn a compensatory adjustment in a direction opposite to their estimate of the skewed noise (the mean), and participants receiving reinforcement feedback would learn to compensate based on the mode. Participants grasped the handle of a robotic arm and reached to a virtual target. Vision of the arm was occluded. Feedback was provided only at the target and indicated true hand position plus a lateral shift drawn from a skewed distribution. This feedback was either an error signal or a reinforcement signal. The error group was presented with a single white dot at the location where the (displaced) cursor passed the target. The reinforcement group was presented with a binary signal indicating whether they hit the target. The reinforcement signal was comprised of visual, auditory and monetary components. With practice the error group learned to compensate for their estimate of the skewed mean. Participants in the reinforcement group followed a different pattern, one where their compensation approached their estimate of the skewed mode. These results show that for motor learning, the nervous system uses at least two loss functions that are driven by different forms of feedback. [1] Izawa et al. (2011) PloS Comput Biol. 7(2), e1002012. [2] Huang et al. (2011) Neuron. 70 (4), 787-801. [3] Kording et al. (2004) Nature. 427(6971), 244-7. [4] Kording et al. (2004) PNAS. 101(26), 9839-42.

3-F-22 Bilateral interactions between choice learning and motor learning during human movement learning

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In order to improve performance in most real world tasks, humans have to learn both, to make the correct choice among possible strategies that enable the task, and to execute the chosen strategy while considering the dynamics of the environment and their own limbs. Traditionally, choice learning and dynamics or motor learning have been extensively examined but as distinct processes enabled by distinct neural mechanisms and it has remained unclear whether and how they interact with each other. In this study we addressed this issue with a novel virtual penalty shoot task that required simultaneous choice and motor learning in an environment which, similar to many real life tasks, provides subjects with multiple choice- execution options to maximize their reward. We observed complex bilateral interactions between choice learning and motor learning by humans. Choice learning is predominantly driven by rewards but is also modulated by motor execution errors. Motor learning is implicit and independent of the reward; motor learning continues even when not required for attaining the task goal and reward. However, the motor learning gain is modulated by reward and the motor savings seem to be spatially modulated by the learnt choice. These results provide an insight into the movement learning in the real world and highlight the need for future studies to examine choice learning and motor learning together, as interacting components of a single hierarchical learning architecture.

3-F-23 Multi-Session Transcranial Direct Current Stimulation Concurrent with Discrete Sequence Production Task in Young and Older Adults

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The discrete sequence production (DSP) task is an explicit motor sequence learning task that can be used to measure chunking, or a grouping together of once discrete individual elements. The DSP task used here involves two, 6-item sequences presented at one time. Over many trials, participants learn the two, 6-item sequences and execute the sequences as 2 or more segments, or chunks. Right and left dorsolateral prefrontal cortex (DLPFC) have been demonstrated to be involved in early explicit sequence learning as well as early adaptation. Primary motor cortex (M1) has been shown to be involved in explicit sequence learning and retention. Further, pre-SMA has been shown to be involved in chunk loading in sequence learning. Here, we use transcranial direct current stimulation (tDCS), a non-invasive form of brain stimulation, in an effort to facilitate chunking in young and older adults in a modified version of the DSP task. Forty young (range 18-28 years) and 16 older (range 65-85 years), right-handed, adults completed a modified version of the DSP task while receiving anodal or sham tDCS to either right DLPFC, left DLPFC, M1, or pre-SMA over two sessions. Using a model developed by Acuna et al. (2014) to quantify chunking, preliminary results suggest that tDCS stimulation to pre-SMA facilitates at least one component of chunking in both young and older adults, whereas tDCS stimulation to m1 is more beneficial to only young adults. Specifically, the pause at the beginning of a chunk was significantly faster for young and older adults in the pre-SMA group relative to the sham group ($p = .037$) providing further support for the notion that this region plays a role in chunk loading. There were no significant differences between m1, right, and left DLPFC groups relative to sham.

3-F-24 Feedback delay modulates implicit and explicit visuomotor adaptation

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Previous studies of adaptation to novel visuomotor transformations suggest that the timing of performance feedback modulates overall visuomotor adaptation. However, visuomotor adaptation is not a unitary process, but comprises explicit as well as implicit knowledge that together contribute to overall adaptation. By implicit knowledge, we refer to the development of separate internal models that approximate the respective transformations and give rise to aftereffects. By explicit knowledge, we refer to conscious awareness of characteristics of the transformations, which, in conjunction with contingent contextual cues, can serve as a basis for conscious and intentional strategic corrections. In the present study, we examined the effects of delayed terminal visual feedback about the outcome of a pointing movement on the relative contribution of explicit and implicit components of adaptation to a visuomotor rotation. Participants practiced a 30° rotation while receiving terminal visual feedback with either a short (20ms) or a long (1.5s) delay. Explicit and implicit components of overall adaptation were then dissociated by using a comprehensive set of visual open-loop tests. In those tests, a color cue indicates the presence or absence of the visuomotor rotation in order to obtain a measure of aftereffects that is unconfounded by strategic corrections. Because of the possibility that internal models are implicitly conditioned to the respective color cue and thus the transformations are switched on or off depending on the color cue, a test of explicit knowledge is included in which explicit judgments of the movement orientation believed to be appropriate to reach the visual targets in the presence of the visuomotor transformations are collected. Results show that the short-delay group displayed larger aftereffects



(Cohen's $d=1.45[.65, 2.26]$, $p<.001$), but smaller amounts of explicit knowledge of the transformation ($d=-.84[-1.59, -.1]$, $p=.044$) than the long-delay group. This finding of feedback delay differentially affecting model-based adaptation as indexed by aftereffects and conscious strategic corrections based on explicit knowledge of the transformation suggests that both processes are driven by separate error signals. Here, it will be argued that these different signals pertain to (a) a sensory prediction error driving implicit adaptation, which is apparently tied to the presence of motor outflow and suffers from delayed terminal feedback, and (b) an intersensory conflict signal, which reflects the discrepancy between visual coordinates of the controlled cursor and proprioceptive coordinates of the hand and is strengthened with delayed visual feedback. Finally, the present findings also substantiate the importance of distinguishing implicit and explicit components of adaptation even with rotations of smaller size and emphasizes the need to consider setup-dependent time delays when interpreting adaptation to a visuomotor transformation.

3-F-25 Can an artificial 'feel of North' change the perception of space? Evidence for vestibular recalibration via auditory sensorimotor contingencies signalling magnetic north using a novel device: the hearSpace app.

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Sensorimotor theory (SMT) stresses how perception involves active control of (cross-modal) laws that determine how stimuli change contingent on actions. Sensory adaptation, substitution and augmentation strive to alter or enhance perception by introducing novel sensorimotor contingencies (SMC's) to the sensory apparatus. However, evidence for sub-cognitive perceptual integration is sparse and has recently been questioned. Here, we present hearSpace, a novel sensory enhancement paradigm. The hearSpace app uses an electronic compass to provide an auditory head-related transfer function (HRTF) signal to the user that signals the head's orientation to magnetic North. This artificial sensorimotor contingency affords aligning the head-based reference frame to a globally stable spatial reference. The signal is continuous and has very low latency, yielding the immediacy needed for sub-cognitive sensory integration processes that lead to perceptual presence. We tested for sub-cognitive integration in a rotation experiment. Blindfolded subjects performed short-term (45 minutes) training involving active and passive rotations on a turning chair. To induce a measurable effect on spatial perception, we introduced a conflict by applying a gain of 0.5 between real rotations and the auditory signal providing the direction of North. Before and after training, we tested subjects' perception of self-rotation in response to passive vestibular-only rotations. We find that rotation estimates decrease after exposure to the conflicting novel orientation signal even when the signal is absent. Our results indicate a persistent sub-cognitive change in the perception of self-rotations caused by our artificial auditory signal indicating the direction of North. Since the change persists in absence of the signal, it can not be explained by cognitive evaluation of the signal itself. Instead it is more likely caused by auditory recalibration of the vestibular system, indicating a sub-cognitive integration of the novel information in perception. Such sub-cognitive perceptual integration highlights the potential for the compensation of perceptual disabilities via sensory augmentation devices. An interactive demonstration of the



novel device will be available at the conference. Acknowledgement: The authors are supported by ERC Advanced Grant 323674 "FEEL" to J. Kevin O'Regan.

3-F-26 Distinct adaptation to abrupt and gradual torque perturbations with a multi-joint exoskeleton robot

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In motor learning and rehabilitation research, it has been of great interest whether training results in overwriting of an existing motor program, or the creation of a novel context-dependently learned program. Recent studies showed that training parameters such as magnitude and schedule of perturbation could lead to different generalization, aftereffects, and relearning [Oh and Schweighofer, NCM 2015; Torres-Oviedo and Bastian, 2012; Morehead et al., 2015]. However, most reaching adaptation studies have been performed in planar two-dimensional settings. Our previous study and other studies suggested that subjects could exploit spatial redundancy in joint-space to control task-space [Mistry et al., 2005; Crocher et al., 2012; Brokaw et al., 2013]. Here, we further investigate how abruptly and gradually applied force fields differently drive adaptation in task- and joint-spaces. Subjects performed 3-dimensional point-to-point reaching movement with a 7-DOF exoskeleton arm (Sarcos Master Arm). In the adaptation phase, the robot applied elbow joint torques from a gain and sum of the shoulder joint velocities (flexion/extension and abduction/adduction). In the Abrupt group (N=11), the gain increased abruptly from 0 to a maximum value, whereas in the Gradual group (N=10), the gain increased gradually over trials to the same maximum. In both groups, a subsequent abrupt washout phase was followed by an abrupt relearning phase. We observed partial adaptation in both groups, but with distinct patterns. The abrupt group exhibited a sharp increase followed by gradual decrease in movement duration and hand-path distance at the initial learning phase. Washout and relearning were very quick such that performance returned to the baseline immediately. On the other hand, the gradual group maintained close-to-the-baseline performance throughout the initial learning and washout phases, but needed more trials to return to the baseline in the relearning phase. The Abrupt group showed overall higher levels of distance in joint-space with large trial-by-trial variability. In contrast, the Gradual group maintained the lower distances in joint-space with smooth and gradual changes. These findings suggest that subjects adapt using different strategies in abruptly and gradually changing environments when allowed redundant arm control. Subjects exploited redundancy of the joint-space to control the task-space performance [Mistry et al., 2005]. However, in the gradually changing environment, subjects maintained similar inter-joint coordination to the baseline. These results also concur with the idea that errors due to rapid environmental changes generate new internal models assigned for the specific context [Torres-Oviedo and Bastian, 2012; Berniker and Kording, 2011], whereas gradual environmental changes update existing internal models. Our study extends this idea to movement with spatial redundancy, observing distinct changes in both task- and joint-spaces.

3-F-27 Synergistic changes in muscle coordination post-stroke during split-belt walking



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BACKGROUND AND AIM: Promising studies have shown that patients post-stroke can re-learn to step symmetrically after walking on a split-belt treadmill, which moves their legs at different speeds (Reisman et al. 2013). While this is encouraging, little is known about the underlying changes in muscle activity. The latter is important to understand the actual plasticity of neural mechanisms in these patients. **METHODS:** We investigated changes in muscle coordination of 16 chronic post-stroke subjects and 16 sex- and age-matched controls during split-belt walking. All patients were in their chronic stage (>6 months after stroke) and had diverse motor impairments as quantified by their Fugl-Meyer scores ranging from 21 to 33. Patients experienced a typical adaptation paradigm consisting of a baseline, adaptation, and post-adaptation conditions. In the baseline and post-adaptation conditions both legs moved at the same speed, whereas in the adaptation condition legs moved at different speeds (i.e., the paretic leg moved twice as slow as the non-paretic one). We measured electromyographic activity in 15 muscles on each leg and evaluated changes in activity between the adapted vs. both the baseline and the post-adaptation conditions using Skillings-Mack test. Bonferroni correction was used to account for multiple comparisons. In addition, a measure of independence in muscle activity was obtained using principal component factorization analysis. This was done to determine if abnormal muscle synergies post-stroke were disrupted when experiencing the split-belt condition (Fig. 1A). **RESULTS:** We found consistent changes in muscle coordination bilaterally and not only in the sound limb. Interestingly, we observed partial spatial and temporal symmetry in these changes. In other words, increased activity on one side was mostly matched by decreased activity on the other side (spatial symmetry) and changes in muscle activity for each leg occurred during the same phase of the ipsi-lateral gait cycle (temporal symmetry). Similar adaptation of muscle activity was observed in age-matched controls. Importantly, our analysis of muscle independence indicated that paretic muscles increased its independent activity during the adaptation condition compared to baseline (Fig. 1B). This suggests that patients can modulate paretic muscles independently when learning a new walking pattern on the split-belt treadmill. **CONCLUSIONS:** Our results indicate that walking in a novel condition, such as split-belt walking, induces changes in the paretic limb beyond the expected compensatory changes in the non-paretic limb. Moreover, our proxy for muscle control independence suggests that co-activation of paretic muscles can be reduced during split-belt walking. Taken together, these are promising findings indicating that chronic post-stroke patients may still have the flexibility to change their muscle coordination to improve their walking despite of their cortical lesions.

3-F-28 Pushing the limits: neural representations of motor sequencing task difficulty in older adults

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Execution of motor sequences of varying motoric demand is integral to daily human functioning. Previous research has shown consistent effects of task difficulty on neural activation and behavioral



performance in several cognitive domains. The findings suggest that as task difficulty increases, neural activation also increases; however, at a certain difficulty level, a resource ceiling is reached, at which point both neural activation and behavioral performance decline. Importantly, this pattern has been observed in both young and older adults (although at different ceiling levels). While converging evidence supports the notion that additional, but limited, resources can be allocated under cognitively challenging conditions, the effects of demand driven resource recruitment during motor sequence execution are not well understood. To this end, the present study investigates neural representations of motor sequencing difficulty in older adults. While undergoing fMRI scanning, older adult participants (63-75) perform a motor sequencing task with difficulty levels that vary by parametrically manipulating the number of fingers as well as the number of transitions between fingers required to complete a sequence. Harrington et al. (2000) found that increasing the number of fingers was associated with increasing activation in the cerebellum and superior parietal cortex, whereas increasing the number of transitions was associated with increasing activation in the dorsal premotor cortex and superior temporal--middle frontal gyrus networks. Behavioral pilot data show that increasing sequence difficulty while sequence length is held constant results in increased sequence completion time (SCT). Confirming the effectiveness of the difficulty manipulation, both young and older adults responded to increasing sequencing demand, although these preliminary results suggest the effect of increasing difficulty is greater in older than younger adults. These results support the suitability of our task for investigating neural representations of motor sequencing difficulty, including whether demand-driven increases neural activation result in a similar resource ceiling observed in cognitive tasks. Within subjects comparisons of difficulty effects in the cognitive and motor domains will be presented. This study aims to advance our broader understanding of neural resource allocation and its limitations, as well as the functional implications of reduced neural resources in older adults. Implications for understanding neural representations of cognitively and motorically challenging tasks will also be discussed.

3-F-29 Modulation of intracortical inhibition following a bimanual interference task

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Recent studies have shown that visual perturbation of one hand during a bimanual movement task induces interference in the contralateral, kinesthetically controlled hand. Interference differed between participants - some showed interference in the same direction as the perturbation, and some in the opposite direction. One possible mechanism for the dichotomy could be differences in intracortical inhibition of motor cortical networks. The goal of our study was to compare inhibition in both hemispheres before and after a bimanual movement task, using transcranial magnetic stimulation (TMS), and measuring short-interval intracortical inhibition (SICI). Twenty-three right-handed participants (mean age: 21.9) performed a bimanual center-out task, moving two KINARM end-point robots from two home positions to peripheral targets at 90° or 270° (distance: 10cm); vision of the hands was occluded. Participants performed a visual baseline condition, with both cursors visible, and a kinesthetic baseline where visual feedback was only present for the right hand, but not the left. Twelve participants were then exposed to 120 trials with a 40° rotation of visual feedback in the right hand, and were instructed to continue moving straight with the nonvisible left



hand. Control participants received veridical visual feedback for the right hand throughout the experiment. Initial directional error (IDE) was used to determine the feed-forward directional control component of the movements as a measure of adaptation. For TMS, resting and active motor thresholds for the extensor digitorum were determined over each hemisphere and recorded with surface electromyography (EMG). Cortical excitability and inhibition were determined prior to the adaptation task, using a single pulse paradigm to elicit a 1mV peak-to-peak amplitude motor evoked potential (MEP), and a paired-pulse paradigm for SICI at 2.5ms interstimulus interval. Inhibition was calculated as a percentage of the single pulse MEP (1mV) amplitude. MEPs were obtained again at the same stimulator output immediately after adaptation, and were compared to those acquired pre-adaptation. The behavioral results showed an IDE reduction for the right hand over the adaptation trials, indicating that all participants adapted to the kinematic perturbation, whereas the nonvisible left hand showed small, yet consistent directional interference effects. In eight of the 'rotated' participants interference was in the same direction as the perturbed right hand (ISO), and in four it was in the opposite direction (ANISO). The TMS results showed that SICI was modulated differentially for the ISO group, which showed increased inhibition in both hemispheres post adaptation, compared to the controls; results for the ANISO participants were less consistent. These preliminary results suggest that isodirectional interference during discrete bimanual movements may involve inhibitory processes in both dominant and non-dominant hemispheres.

3-F-30 Extended Single Session Adaptation to Clamped Visual Errors

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Many current models of visuomotor adaptation posit a single, monolithic error signal. It has, however, been posited theoretically (Jordan & Rumelhart, 1992) and shown empirically (Mazzoni & Krakauer, 2006; Nikooyan & Ahmed, 2015) that both task performance error and sensory prediction errors can independently drive changes in behavior during adaptation tasks. In this study, we attempted to isolate sensorimotor prediction errors, so that adaptive changes driven by these errors could be specifically studied. To accomplish this, participants reached to eight targets spaced in 45° increments around a central start location while being exposed to a visual error clamp that offset cursor motion from the target direction by a fixed angle, either 7.5° or 30° (10 participants each). Participants were informed in advance about how the cursor motion was manipulated and they were asked to ignore this cursor motion, and to instead focus on moving their unseen hand to the target on each trial. Previous work with this manipulation (Morehead et al., 2014) showed an adaptation function that was invariant to the imposed sensory-prediction error size and appeared to saturate at approximately 12° of change in reach heading angle. We extended this work by addressing three limitations of the previous experiments: a relatively large temporal lag for the visual feedback relative to the hand position (~90ms), a small number (40) of reaches to each target with perturbed visual feedback, and an incomplete experimental balancing of perturbation direction (clockwise & counter-clockwise). The present experiments featured a much smaller visual feedback delay of ~25ms, 1920 perturbation trials (240 per target), and the sign of the induced error clamps was properly balanced. First, we observed an adaptive response that was invariant to the size of the error clamp offset, similar to previous work. However, we found that this adaptive response was



larger on the new low-latency display setup relative to previous data (~90ms), resulting in significantly larger per-trial changes in hand angle and greater hand angle at asymptote (~25°). Second, we found that learning reached asymptote after roughly 70 reaches to each target. Finally, differences in response to the angular sign of the perturbation was revealed by proper counterbalancing. In particular, the clockwise subgroup showed more total change in hand angle, resulting in greater asymptotic performance. We hypothesize that these differences may come about because of anisotropies in proprioceptive sensitivity around the workspace. In summary, we show that previous work employing this manipulation did not fully describe the extent of behavioral change that can be induced by irrelevant clamped feedback. However, we did again observe an adaptive response that was invariant to sensory prediction error size, which may be useful for differentiating between adaptation resulting from performance errors or sensory prediction errors.

3-F-31 Sensorimotor adaptation in unrelated effector systems: common or distinct learning mechanisms?

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For reaching movements, adaptation to kinematic errors (e.g., a visuo-motor rotation) and dynamic errors (e.g., a viscous force field) are not correlated across subjects and depend on mostly segregated cerebellar areas. Nevertheless, sequential adaptation to either kinematic or dynamic errors can result in mutual interference effects, suggesting partial overlap of neural substrates or mechanisms. Despite this interest in possibly common principles underlying different forms of adaptation within an effector system, it remains entirely unknown whether a common learning ability underlies similar forms of adaptation (e.g., to kinematic errors) in unrelated effector systems (e.g., the upper limb for reaching and orofacial structures for speech). In speech experiments, real-time manipulations of auditory feedback cause a mismatch between predicted and perceived formant frequencies (vocal tract resonances). Given that vocal tract shape is determined by the positions of movable articulators, such auditory perturbations induce kinematic errors, analogous to visual perturbations implemented during reaching movements. Here, we used this similarity in the paradigms to start exploring a possible relationship between individual subjects' extent and rate of visuo-motor reach learning vs auditory-motor speech learning. Sixteen right-handed female subjects participated in two sessions with one reaching task and one speaking task per session. During a given session, feedback was manipulated incrementally for one task and instantaneously for the other task. Assignment of tasks to sessions and order of tasks within sessions were counterbalanced. In reach tasks, subjects reached to three radially-oriented targets while seeing visual feedback as a real-time cursor on a back-projection screen that blocked vision of the hand. A perturbation was implemented by rotating the cursor location counter-clockwise around the start position (up to 30 degrees). In speech tasks, subjects spoke three monosyllabic words while hearing auditory feedback through insert earphones that blocked normal air-conducted feedback. The perturbation consisted of an upward shift (up to 250 cents) of all formants. Number of trials and duration were identical across tasks. For each task, we calculated each subject's rate and extent of adaptation. When collapsing data across target words and across reach directions, there were no statistically significant correlations between initial movement direction adaptation in the reach task and formant



adaptation in the speech task. Interestingly, the extent of adaptation to incremental and instantaneous perturbations for the same task showed a statistically significant positive correlation for reaching but not for speaking. More complex results emerged when the speech data were separated by word and the reach data were separated by direction. Results suggest that largely independent learning abilities underlie sensorimotor adaptation in these effector systems.

3-G-32 Speech motor control taking into account feedback: an implementation using a biomechanical model

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Human speech is a complex motor action the control of which requires a correspondingly complex control mechanism. This mechanism must be able to take into account feedback of multiple sensory modalities, namely proprioceptive, tactile and auditory, with their respective time delays. It must also be able to make use of this feedback for purposes as different as online error correction, offline replanning and learning. Several control frameworks allowing for such complexity have been proposed in the context of motor control and in speech motor control in particular. None, however, have been implemented in order to control a biomechanical model speech production to actually produce speech gestures and speech sounds. We have built a controller taking into account feedback in the planning and replanning of the production of speech sounds by a biomechanical simulation of the vocal tract. For this we constructed a 2nd-order model of the forward dynamics, incorporated multimodal, multiscale feedback delays based on studies of the corresponding neural circuits and derived a Kalman gain function to optimally estimate the state of the model. Additionally we propose a hierarchical, multimodal representation of task goals. All this together allows us to optimally control the biomechanical model in the production of a series of target sounds. Lastly we analyze some example productions produced by the combined system. Our work demonstrates the feasibility of integrating feedback in the control of a physical model of the vocal tract. This work provides a particularly interesting testbed for theories of control of movement and a starting point for investigations into more complex aspects of speech motor planning and motor planning in general.

3-G-33 Corticospinal Integration and Coordination of Movement Commands

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Movements are achieved by cerebral commands that are executed via the corticospinal and neuromuscular systems. However, our understanding about the important corticospinal mechanisms is sketchy due to the lack of in vivo data. In this report, we use evidence supported computational analysis for both normal and abnormal movements to gain insights into the corticospinal processing of motor commands. It is well known that resting tremor in patients with Parkinson's disease (PD) is caused by involuntary cerebral oscillations at tremor and double tremor frequencies. We conducted a series of studies using computational modeling combined with EMG coherence analysis to reveal



tremor signal transmission and processing in the corticomuscular systems. We identified a particular group of pre-motoneurons, the propriospinal neurons (PN) in the C3-C4 spinal cord, that may be the converging center for descending cerebral signals. We hypothesized that the PN plays a pivotal role to integrate the two cerebral signals, and to divide the double tremor frequency oscillation into two alternating bursting signals of single tremor frequency for flexor and extensor muscles at a joint. This hypothesis was first verified using a computational model consisting of a PN network and a virtual arm (VA). It was then further corroborated with inter-muscular coherence analysis using EMGs obtained in a set of upper extremity muscles in PD subjects. Finally, we designed new experiments to obtain direct evidence that supports the hypothesis of corticomuscular mechanism of tremor genesis. We will present these experimental results from PD subjects that demonstrated an effective inhibition of tremor activities by cutaneous afferent reflex evoked by stimulating dorsal skin of hand. This result is the first illustration of PN's role in transmitting and processing cortical descending signals involving motor functions. Based on these studies, we further hypothesize that descending commands for normal and abnormal movements are channeled to peripheral muscles and spindles via a dual pathway, the multi-synaptic PN network and the mono-synaptic corticospinal connections. The role of PN network in integrating and coordinating cortical motor commands was analyzed using the same computational model of PN network and virtual arm (VA). We fitted model outputs to movement and EMG data obtained from normal subjects, and then manipulated model outputs by deafferenting and deafferenting the model. The results revealed that model behaviors in intact and altered states were all consistent with experimental data in literature about deafferented and deafferented movements in animals and humans. Our studies provide solid evidence to support the conclusion that the propriospinal neurons (PNs) are the key corticospinal center for integrating and coordinating descending motor commands in both normal and disorder movements.

[3-G-34 A framework for explaining serial processing and sequence execution strategies.](#)

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Behavioral research produced many task-specific cognitive models that do not say much about the underlying information processing architecture. Such an architecture is badly needed to understand better how cognitive neuroscience can benefit from existing cognitive models. This problem is especially pertinent in the domain of sequential behavior where behavioral research suggests a diversity of cognitive processes, processing modes and representations. Inspired by decades of reaction time (RT) research with the Additive Factors Method, the Psychological Refractory Period paradigm, and the Discrete Sequence Production task, we propose the Cognitive framework for Sequential Motor Behavior (C-SMB). We argue that C-SMB accounts for cognitive models developed for a range of sequential motor tasks (like those proposed by Keele et al., 2003; Rosenbaum et al., 1983, 1986, 1995; Schmidt, 1975; Sternberg et al., 1978, 1988). C-SMB postulates that sequence execution is controlled by a central processor using central-symbolic representations, and a motor processor using sequence-specific motor representations. On the basis of this framework we present a classification of the strategies to produce movement sequences. We complete this presentation by proposing the neural underpinnings of this framework.



3-G-35 Dynamic Stability in Human Control of Complex Objects

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From swinging a hammer to drinking a cup of coffee, interaction with objects—tool use—is a skill that has provided humans with an evolutionary advantage. When guiding a cup of coffee to one's mouth, the actor not only exerts forces on the cup and indirectly onto the coffee inside, but the sloshing coffee also exerts forces on your hand. It requires precise control to preempt and compensate those complex interaction forces to avoid spilling. To date, motor neuroscience has primarily focused on simple movements like reaching to a target, or grasping static objects rather than manipulating them. However, findings from simple actions are difficult to extrapolate to tasks with complex dynamics. Slow neural transmission and neuromotor noise make error correction insufficient and prediction based on internal models implausible for such nonlinear interactions. Previous work on rhythmic interactions showed that humans increased predictability of object dynamics to facilitate control. This study examined discrete movements and hypothesized that actors make the interaction dynamically stable to preempt and compensate for noise and perturbations. As traditional Lyapunov analysis is confined to stable attractors, contraction analysis was applied to evaluate convergence, or stability, of the trajectories. We expected that with practice subjects increased the stability of cup and ball dynamics, specifically in the presence of external perturbations. Using a virtual set-up, we implemented a simple 2D model for the task of carrying a cup of coffee: using the cart-and-pendulum system, the pendulum bob represented the liquid moving inside a cup defined by the bob's semicircular path. Participants moved a robotic manipulandum to control the virtual cup with the ball "rolling" inside; the goal was to move the cup to a target as fast as possible without letting the ball escape. A small perturbation assisting or resisting the motion was presented at a fixed location along the path. Participants performed one block of assistive and resistive trials. Hypotheses: 1) With assistive perturbations, trajectories should become less stable, exploiting the energy from the perturbation. 2) With resistive perturbations, trajectories preceding the perturbation should become more stable, reducing the chance of the ball escaping. Contraction exponents analytically determined for all phase space states of the cup-ball system served to quantify the contraction properties of the experimental trajectories. Results showed that: 1) for assistive perturbations, subjects adapted time and location of perturbation onset to be in a divergent location of phase space to exploit the assisting forces; 2) for resistive perturbations, trajectories met the perturbation in a convergent location to compensate external forces. These results demonstrate that humans are sensitive to stability properties of the task and simplify the interactive dynamics to make model-based prediction possible.

3-G-36 Linking Objects to Actions: Incorporating novel objects into existing neural templates

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Primate ventral premotor cortex (PMv) is a key node in a parieto-frontal cortical network involved in guiding grasping movements using visual inputs. In a previous experiment (Vargas-Irwin et al. 2015A)



we examined the time course of neural ensemble activity in PMv during a cued grasping task with instructed delay (CGID). The target objects in the CGID task could be grasped in two ways: power/key grip (object A) or power/precision grip (object B). Ensemble spiking patterns were compared using spike train similarity analysis (SSIMS, Vargas-Irwin et al, 2015B). Our results showed that PMv ensembles displayed object-specific states when as soon as the objects were visible, further differentiating into states reflecting both object and grip information once the grip type was cued. The present experiment examines the changes in neural activity associated with the introduction a novel objects to the CGID task. The new objects featured familiar components arranged in a combination the monkeys had not interacted with before: key/precision grip. The two novel objects differed in the vertical positioning of the components; the precision grip component was presented on the lower section of object C and the upper section of object D (the position of the key grip component remained constant). Based on previous results, we expected the novel objects to elicit a distinct ensemble state during visual presentation. However, our analysis revealed only two object-related clusters of activity patterns during this phase. Each cluster included one novel and one familiar object that elicited statistically indistinguishable spiking patterns. Despite the initial overlap in the neural representations of the objects, ensemble activity shifted during the instructed delay and movement execution periods, resulting in a set of activity patterns reflecting each of the eight possible object+grip combinations. The differentiation of activity patterns observed in later task stages may reflect subtle differences in the motor strategies used in for each grip. In agreement with previous results, familiar objects elicited different neural activity patterns in PMv. Novel objects elicited patterns matching those of familiar objects. Pairing novel objects with familiar ones may reflect a learning strategy to deal with unfamiliar situations. Future experiments will examine the stability of object representations following more extensive task experience. SSIMS mapping reveals that during this task phase, objects are not grouped according to grip affordances, but can be separated according to orientation. Our findings suggest that the overall visual appearance (outline) of the objects may be the main distinguishing feature during the initial phase of the task. Broadening the task to include a greater number of objects will be necessary to test this hypothesis. References: Vargas-Irwin et. al. J Neurosci. 2015A Jul 29;35(30):10888-97 Vargas-Irwin et al. Neural Comput. 2015B Jan;27(1):1-

3-G-37 Characterization of the learning process while operating a body-machine interface

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Studies of motor learning have established that movements' adaptation to patterns of deterministic forces takes place through the gradual formation of an internal representation, or internal model of the force field. Moreover the evolution of the state variable of a dynamic system has been proposed to represent the evolution of the internal model. Here, we extend this idea to the learning process that occurs in subjects that operate an external device through a body-machine interface (BMI). The interface establishes a linear mapping from the body sensor signals to the lower dimensional control signals of the device. The mapping is set by embedding the operational space, i.e. the plane where a cursor moves, within the higher dimensional space of body motions, spanned by the signals generated by the motion sensors. In this work we want to adopt a computational approach to



characterize human learning in a BMI as a dynamical process through which the user acquires an inverse model of the BMI mapping. The internal model is an inverse kinematic model of the redundant forward map implemented by the interface; for this reason the inverse kinematics problem is ill-posed because it has multiple solutions. In our analysis the forward map transforms a configuration of body signals into control signals in the operational space $p=H q$, where H is a rectangular $N \times 2$ matrix ($N > 2$). As the forward map is many-to-one, there is a null-space of inverse solutions for each value of its output, corresponding to different patterns of body signals that result in the same output. To be successful during a reaching task, the participants must learn an inverse mapping from target cursor location to body vectors. Assuming that it is a linear mapping $q=G p$ this mapping must be a right-inverse of H and it must satisfy the condition $H G= I_2$, where I_2 is a 2-dimensional identity matrix. Since there are infinite such candidate mappings, we consider if subjects with practice learn a particular inverse. We address this question experimentally by a least squares procedure over the body-signal and target data. We also consider a state based-computational model where the evolution of the inverse mapping depends upon its initial value and upon the experienced pattern of reaching errors. As users are engaged in using a BMI, the observed errors guide the learning process. In fact error-based learning is considered one of the main mechanisms through which we normally acquire and refine motor skills. Here, the history of errors is used to develop and evaluate the process through which subjects acquire effective inverse models of the interface through which they act. We have also estimated the development of an internal model and the time history of reaching errors in unimpaired subjects executing a sequence of movements through a BMI. These data are qualitatively consistent with the first order learning dynamics postulated in this work.

4-A-1 Unconscious Effects of Pre-Search Cues on Visual Search Scanning Behaviors

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Several studies have found that when a visual search stimulus image is repeated across multiple trials, participants are faster to identify the targets in those images. This contextual cueing effect occurs even when participants do not explicitly recognize this image repetition (e.g., Chun and Jiang, 1998). Our current experiments built on this foundation, and found that participants can implicitly learn a relation between a pre-search fixation cue and search target location. Participants viewed a fixation stimulus for two seconds, after which a search display appeared. Participants identified the orientation of a T-shaped target stimulus embedded among 12 similar L-shaped distractors as quickly as possible. The size of the fixation stimulus predicted the horizontal position of the target, e.g., when the fixation disk was small, the target was located in the left part of the image; when the fixation disk was large, the target was located in the right part of the image. Participants moved their eyes to the target faster after approximately 100 learning trials of this type. Questions administered after the study demonstrated that these changes in eye movement behavior were not accompanied by explicit knowledge of the size-position relation. Following a learning phase, we tested whether the size aspect of this size-position relation could be influenced by two pictorial illusions of size--the Ebbinghaus illusion and the horizontal-vertical illusion. In several conditions we found that changing



the composition of the stimulus display disrupted the implicit learning. The learning, while rapid and unconscious, was remarkably context specific.

4-F-2 Can hand-loss impair motor control and bilateral sensorimotor representation of the other hand?

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In daily life, individuals born with one hand (congenital one-handers) rely on their residual limb to perform typically bimanual tasks, and do not solely depend on their intact hand. This is in stark contrast to individuals with acquired limb loss (amputees), who predominantly rely on their intact hand. These compensatory strategies map onto divergent patterns of brain activity where acquired (but not congenital) one-handers show increased ipsilateral sensorimotor activity during simple hand movements. Here we investigated these dissociated behavioural preferences, and their neural underpinnings. We tested motor control of the intact hand in congenital and acquired one-handers, and examined how this corresponds to activity in bilateral sensorimotor cortex. We used a highly demanding motor task, as demanding tasks have been suggested to associate with increased ipsilateral processing. We therefore predicted that if congenital one-handers are unable to recruit their ipsilateral cortex during a demanding motor task then this might result in motor impairments of their intact hand. Acquired and congenital one-handers and two-handed controls performed a complex finger synergy task (piano chords) both outside and inside the MRI scanner. Behavioural performance was measured as the mean deviation from the optimal trajectory from trial start to endpoint throughout the trial. Outside the scanner, congenital one-handers showed initial deficits in motor performance compared to the two other groups. After brief training, performance was similar across groups, indicating increased learning gains in the congenital one-handers. Individuals from the congenital group that relied more on their intact hand in daily life (as indexed by questionnaire measures) showed greater learning gains, suggesting that habitual compensatory strategies are rooted in basic capacity for motor control and learning. Next we examined activity levels in the ipsilateral primary sensorimotor cortex during the finger synergy task. Acquired one-handers showed increased ipsilateral activity, compared with the other two groups, as previously reported during non-demanding motor tasks. Congenital one-handers showed similar ipsilateral activity levels to controls. This suggests that congenital one-handers, unlike acquired one-handers, are unable to recruit additional resources of the ipsilateral cortex to support intact hand motor control. In summary, congenital absence of one hand might result in impairment in motor control of the intact hand. This could relate to congenital one-handers' inability to recruit additional resources from the ipsilateral sensorimotor cortex during increased motor demands, although we note that their ipsilateral activity levels did not differ from controls. Additional analysis, designed to index the information stored in the multivoxel patterns (e.g. representational similarity analysis) will be performed to investigate this relationship further.

4-E-3 Defining the dystonic fingerprint of musicians' dystonia



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Musicians' dystonia (MD) is a task-specific disorder of motor control in which intended patterns of finger movements are disrupted primarily during musical performance. The widely accepted hypothesis for the pathophysiology underlying MD is that aberrant plasticity in the sensory-motor cortex induces an increased overlap of the cortical finger representations, which in turn causes involuntary co-contraction during task-specific activity. Typically, the proposed overlap in these representations is quantified as the spatial distance between the centres-of-gravity (CoG) of cortical finger activity patterns, with individuals with MD sometimes showing smaller distances in comparison to healthy controls. However, in a previous paper we found that the exact spatial arrangement of the finger patches is highly variable across subjects, demonstrating that the spatial distances between CoGs are a poor metric for capturing the structure of finger activity patterns in the sensorimotor cortices. Here, we use the more robust analytical framework of representational similarity analysis (RSA) to test the hypothesis that MD results in an overlap of finger representations. Furthermore, we quantified the ability of subjects to individuate the fingers outside of the context of musical performance. 17 professional pianists and guitarists, 9 that had developed MD, were tested on a finger individuation task. Participants produced varying levels of force with single fingers while keeping the other fingers as stable as possible. The participants ability to individuate a finger was measured by the magnitude of involuntary co-contracted passive finger movements of the active (enslaving) and passive hand (mirroring). Musicians with dystonia demonstrated increased enslaving ($t(16) = -3.15, p=0.006$) and mirroring ($t(16) = -2.978, p=0.009$) compared to healthy musicians, both on their affected hand, as well as on their unaffected hand. Thus, in contrast to the specific dystonic symptoms, the deficit in the ability to individuate fingers was much more generalized and not solely task specific. During high-resolution functional magnetic resonance imaging, participants made isometric key presses ('motor' condition) with individual fingers at low force levels or had single fingers passively lifted ('sensory' condition) by a robotic device. Even using our sensitive measures of pattern overlap, we found no significant difference in the arrangement of digit activation patterns between groups. This was true for both the primary somatosensory and motor cortex, and for both motor and sensory task conditions. The increase in enslaving and mirroring suggests a general deficit of finger individuation in the affected and unaffected hand in MD. However the cause of this loss of independent finger movement remains to be established as our results challenge the notion that MD is a result of the merging of digit representations in primary sensory cortex.

4-B-4 Studying the representational structure of simple and complex hand movements in the human motor cortex

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Hand movements elicit complex activity patterns in primary motor cortex. While the fine spatial organisation of the activity patterns is largely idiosyncratic to each individual, the representational structure - i.e. the relative dissimilarities between the activity patterns of pairs of movements - is highly preserved across subjects and provides important insights into the neural organisation of movement control (Ejaz et al., 2015). These findings open the door to study the representation of complex movements in the intact human brain. As a technical foundation, we need to establish how activity patterns of simple finger movements change when the overall activity in the area increases. This is important as complex movements are usually associated with a higher mean activity level than simple movements, and this alone could distort the overall representational structure of movements. Here we report the results of a control experiment, in which we increased the overall level of activity by increasing the movement frequency of single finger presses close to the performance limit. In the study, participants produced short isometric finger presses with one of the five fingers of the right hand. Within a 6 sec interval, a visual metronome instructed subject to press the finger 2, 4, 8, or 16 times. Functional imaging data was acquired on a 7T scanner with a repetition time of 1s and an isotropic resolution of 2mm. For each trial, the functional signal over the full 6s of activity for each voxel was averaged. As previously reported, the average activity in primary motor cortex increased approximately with the log of the tapping frequency. We then calculated a crossvalidated Mahalanobis distance as a dissimilarity measure between all pairs of the 20 conditions (5 fingers x 4 speeds), allowing us to analyse the data in a single representational space. We found that the overall dissimilarities between fingers increased with movement speed, but that their relationship remained stable. This was caused by a multiplicative scaling of the finger-specific pattern relative to rest with increasing movement speed. Additionally, we also found a general background activation pattern that increased with speed for any finger movement. This speed-dependent background pattern was independent of the patterns that encode finger movements, and could therefore be cleanly separated. Overall, these results indicate a reassuring stability of the representational structure over a considerable range of movement frequencies and activation levels. We now use these insights to analyse the exact relationship between the activity patterns for single finger presses and short movement sequences, allowing us to determine if the motor cortex encodes specific transitions between fingers, or whether the activity patterns of sequences are simply a weighted combination of the activity patterns for simple movements.

4-D-5 Distinct cortical movement representations during unimanual and bimanual wrist movements in humans

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To understand how the brain achieves finely coordinated movements of the two hands is one of the long-standing questions in human neuroscience. We have previously shown that during bimanual reaching movement both arm movements are integrated by multiplicative gain-field which helps each arm movement to adapt to complicated dynamic environment changing with both arms' motion (Yokoi et al., 2011). Furthermore, using fMRI to study bimanual finger movements, we have shown evidence for nonlinear encoding of left and right movements in premotor cortex (PM) and in the intra-parietal sulcus (IPS) (Diedrichsen et al., 2013). We now extend this experimental approach



to bimanual goal-directed reaching movements. Particularly, we ask the question whether a bilateral representation of unimanual movement directions are in intrinsic or extrinsic coordinates and how the two individual movements combine into a bimanual movement representation. We first developed a MRI-compatible 2DoF device to record bilateral wrist movements. We then scanned seven human subjects while they performed either unimanual or bimanual wrist pointing movements. Extension/flexion and ulnar/radial deviation angles were monitored by the device and projected into 2D motion of visual cursors on the screen. For each hand, six potential visual targets were located around center position. In unimanual trials, subjects were asked to make out-and-back wrist movement toward one of these targets for either hand. For bimanual trials, movements of both hands were required to be simultaneous. The order of movement conditions was randomized, each condition was repeated twice during a session, and the session was repeated for 10 times with short breaks. Rather than analyzing univariate activations, we calculated the dissimilarity across multivariate activation patterns for different movement conditions (Kriegeskorte et al., 2008) and analyzed these dissimilarity structures. Specifically we compared the observed dissimilarity structure with that predicted from a directional tuning model to see whether and how wrist movements were represented in certain brain region. Consistent with previous studies, we found strong directional selectivity for the contralateral wrist motion in the primary motor cortex (M1), the dorsal premotor cortex (PMd), and IPS. There were also substantial ipsilateral movement representations in right M1, PMd, and bilateral IPS. We further found significant bimanual movement representation in right M1, and bilateral PMd and IPS. Further analyses show that while both the multiplicative and additive integration models explain more variance than a null model, the multiplicative tuning model explained significantly larger amount of data in IPS bilaterally ($P < 0.05$). Taken together with previous finding (Diedrichsen et al., 2013), these results suggest that bilateral IPS might be key regions to nonlinearly integrate bilateral movement information for flexible bimanual coordination.

4-D-6 Can transient loss of afferent input promote sensory learning?

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Animal research has established that sensory input loss from one finger (e.g. through amputation) results in increased cortical representation of its neighbouring fingers. The implications of cortical reorganisation of digit topography on perceptual abilities are, however, still debated. In humans, relatively minor blocking of sensory input (e.g. through skin numbing or ischemic block) can enhance tactile and motor abilities on an adjacent or homologous body part. At the current time, it is unknown whether this enhancement is directly caused by deafferentation (e.g. through cortical magnification), or indirectly through a boost in sensory learning (e.g. by changing neurochemical balance of excitation/inhibition). To examine these competing explanations, we compared tactile acuity gains following 3 separate interventions: (i) deafferentation alone; (ii) deafferentation coupled with a paradigm of minimal tactile training to the neighbouring finger; and (iii) sham deafferentation (using saline), coupled with the same tactile training paradigm. Temporary deafferentation (45min-1.5hours) was delivered via pharmacological block to the base of the right index finger (2-4mL Lidocaine 1-2%) in 2 sessions over consecutive days (groups i and ii). The tactile training (approximately 1 hour) was conducted on the right middle finger, concurrent with the block



(groups ii and iii). In all groups, longitudinal tests of tactile acuity were performed on the index, middle and ring fingers of both hands (pre- and post-training, 1- and 5-day follow up). Tactile acuity was measured using a grating orientation task and thresholds were estimated by fitting psychometric functions to accuracy data. In the deafferentation alone group (i), we found no improvement in acuity over time and acuity was consistent between fingers over time. This suggests temporary deafferentation alone was not sufficient to modulate tactile acuity. In the sham %2B training group (ii), general improvements in acuity were documented across all fingers, suggesting a non-specific benefit from the tactile training paradigm. The deafferentation %2B training group (iii), however, not only demonstrated a significant improvement over time, but this improvement varied significantly between fingers, indicating a finger-specific learning effect. Interestingly, unlike in previous studies of tactile learning, the finger benefiting most from tactile exposure during temporary deafferentation was neither adjacent nor homologous to the trained finger, a suggesting relatively large-scale modulation of somatosensory topography. We demonstrate that while temporary deafferentation does not produce tactile improvement by itself, it can enhance sensory training, potentially by inducing widespread somatotopic plasticity. These findings emphasise the potential scope of temporary deafferentation protocols for enhancing the efficacy of sensory and motor rehabilitation after insult or injury.

4-F-7 Cortical sensorimotor reorganisation following congenital hand absence

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Congenital input absence is a major trigger for brain reorganisation, freeing up the deprived cortex for remapping. We previously showed that compensatory arm usage in individuals born with one hand (hereafter, one-handers) impacts both representation and functional connectivity in the cortical hand region. Here we used multiple neuroimaging techniques to study brain reorganisation in one-handers and its potential relationship with habitual behaviour involving multiple body parts. We first examined task-based fMRI activation in the sensorimotor cortex normally representing the (here missing) hand. Movements of the residual arm, lips, and legs all activate the missing-hand cortex more in one-handers (n=16) than in controls (n=24). Reorganisation was also evident in one-handers during rest, indicated by increased functional connectivity between the missing hand territory and both the lips and legs territories (ROI analysis). A possible explanation for the enhanced representation of other body parts in the missing-hand cortex is that the congenital input absence may cause reduced inhibition in the hand region, thus decreasing connectional selectivity (e.g. unmasking of silenced inputs). Indeed, MR spectroscopy revealed lower absolute GABA levels in the missing-hand cortex compared to the intact-hand cortex of one-handers. Decreased functional selectivity of the missing hand area was also evident from increased resting state connectivity of this region with the averaged time-course across all gray matter voxels (known as the global signal) in one-handers compared to controls. Finally, we assessed whether the observed reorganisation associates with compensatory usage strategies of different body parts, by examining behaviour in everyday tasks that normally require bimanual coordination. Compared to controls, one-handers were more likely to use the residual arm, consistent with our previous reports. While the one-



handlers also showed increased usage of their legs, they did not take greater advantage of their lower face (mouth, chin) while performing the behavioural tasks. To conclude, although extensive cortical reorganisation is found in individuals with congenital limb absence, this may not map consistently onto behaviour. We previously showed that remapping of the upper limbs to the missing hand cortex reflects compensatory usage of the upper limbs following congenital and acquired hand-loss (adaptive reorganisation). Others proposed that reorganisation of the sensorimotor homunculus, and specifically the remapping of lips into the missing hand area may be maladaptive and cause phantom limb pain. As one-handers do not experience phantom pain, the observed lips remapping demonstrates that reorganisation in the homunculus is not sufficient to cause phantom pain. As increased brain activity or connectivity may not necessarily support changed behaviour, other examples of reorganisation should be interpreted with caution and should be validated causally

4-B-8 EMG-EMG coherence reveals increased reticulospinal contributions to upper limb postural adjustments.

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EMG-EMG coherence reveals increased reticulospinal contributions to upper limb postural adjustments Alexandra Leguerrier¹, Dana Maslovat², & Anthony N. Carlsen¹ ¹School of Human Kinetics, University of Ottawa, Ottawa, Canada ²School of Kinesiology, University of British Columbia, Vancouver, Canada Movement is produced using different neural networks based on the nature of the task. Balance and posture are thought to largely involve subcortical brainstem structures, while voluntary movement and movements of distal effectors are thought to be primarily corticospinally mediated. Studies using a startling acoustic stimulus (SAS) in a simple reaction time task have demonstrated the involuntary and rapid release of pre-planned movements (StartReact effect), a phenomenon hypothesized to arise from the release of the planned action from subcortical structures. Conversely, results from experiments using transcranial magnetic stimulation have provided evidence that the motor cortex (M1) also contributes to the StartReact effect. The current study investigated the relative contributions of the neural pathways involved in different types of movements using EMG coherence analysis between homologous muscles. EMG-EMG coherence provides information about the origin of oscillatory neural drive associated with a movement by determining the extent of the correlation of the power in each frequency between limbs. Coherence in the 15-20 Hz range is associated with reticulospinal drive, while that in the 25-30 Hz range is associated with corticospinal activation. In this study, 12 participants completed two simple RT tasks in sequential blocks. Each block consisted of 10 practice and 80 experimental trials, with block order counterbalanced. The first task involved simultaneous bimanual wrist extension with elbows remaining flexed at 90°; this task paired a focal movement of the extensor carpi radialis longus (ECRL) with a postural adjustment of the triceps brachii (TB) to maintain the elbow angle. The second task involved focal bimanual elbow extension with wrists held posturally fixed at neutral. Participants were to react as fast as possible to an auditory go-signal, which was unexpectedly replaced by a SAS (120 dB) in 20% of experimental trials. Surface EMG was collected from both sternocleidomastoid muscles and bilaterally from the ECRL and TB. Results of the coherence analysis



reveal increased coherence in the 13-20 Hz range in the TB and ECRL when acting posturally versus focally for both control and startle conditions. An additional contribution of startle to this increase in coherence is seen, as evidenced by larger coherence in the 15-20 Hz range compared to control for both movements. These results suggest there is a larger contribution from subcortical structures to muscles when acting as postural stabilizers. In addition, there is an increase in subcortical drive in both movements when they are triggered by the startle. Supported by NSERC and the OMRI

4-B-9 The Tuning of Reflexes to Environmental Risk

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In order to characterize and emphasize the influence of risk in the environment on human movement, we have designed a series of experiments. In a previous study, we provided evidence that not only do humans consider risk when initially planning a movement, but also that they are constantly evaluating the environmental loss function in a continuous task. Many studies have demonstrated that humans have the ability to modulate the long latency stretch reflex based on the goal of a task, such as in a go-don't-go paradigm. It is our hypothesis that awareness to risk is so fundamental, that humans also maintain reflexes tuned specifically to the risk of the environment, even when the goal of the task remains constant. In the experiment, subjects were positioned in front of a monitor with their dominant arm strapped to a manipulandum designed to apply torque at the elbow joint while maintaining all other arm joints immobile. The subject's hand gripped a rigid joystick attached to the arm of the manipulandum that controlled a cursor horizontally on the screen. The monitor displayed three equidistant rectangles, two cost regions on either side of a center reward region. Subjects were instructed to maximize points by keeping the cursor within the center reward region while avoiding the cost regions that would result in a loss of points. Nine cost functions were evaluated, all combinations of no penalty, low penalty, and high penalty, in order to evaluate the effect of both symmetric and asymmetric risk. Thus the goal of the task was always to remain in the center target, but the risk of hitting the penalty regions was varied. The robot generated a constant 1 N force (activating the bicep) and randomized 3 N perturbations in both directions (in addition to baseline force) at a mean rate of 5 seconds. Surface electromyography from the bicep and triceps were recorded and filtered. Only trials in the direction that provoked the bicep stretch reflex were analyzed. Reflex response was categorized into standard epochs for baseline, short latency, long latency, and voluntary response. The filtered EMG within each epoch was averaged to a single value per trial for analysis. Results demonstrate a difference in the long latency stretch reflex dependent on the risk of the environment. However, results were only clear for the symmetric cost conditions; subjects did not demonstrate a consistent ability to set separate reflex responses for different directions when the direction of perturbation was unplanned. Therefore, results suggest that humans do plan for error by tuning reflexes to the risk of the environment and that they do this independent of the goal of the task.

4-B-10 Motor and muscular patterns during simulated human flight

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Behavioral studies on animals and humans showed that motor and muscle synergies extracted from the factorization analysis of kinematics and electromyographic (EMG) signals suggest a reduction of dimensionality for the control of the musculoskeletal system, and reveal underlying patterns in joint angles, limb trajectories or muscle activity that may reflect different levels of neural functions. In particular, the observation that the activity of multiple muscles can be linearly decomposed in a small number of synergies under different biomechanical conditions, including variations of load, posture, speed, or movement direction, their evolution with the development, and the preservation of this scheme across species led to the assumption that such low-dimensional modules represent or directly reflect neural control signals. Investigations of the modular organization of motor performance and muscle activity covered a large variety of movements performed in everyday life. In the study presented here, we evaluated whether the principles discovered for natural and well-practiced tasks are expressed in a similar manner during unfamiliar movements. For this purpose, we designed an experiment in which 11 naïve young participants were presented an immersive flight simulation comprising a set of distinct maneuvers and were asked to follow the motion of the aircraft from different postures (standing, sitting, lying) by actively moving their upper body as if they were flying themselves. The upper-body kinematics as well as the EMG activity of 32 muscles of the upper limbs and the torso were recorded. A qualitative evaluation revealed that a majority of the subjects selected common motor strategies similar to the ones found in well-practiced tasks. Factorization analysis on the trajectories of the center of mass of each upper body segment and on the EMG signals suggests that the modular nature of motor control is respected in the case of nonspontaneous gestures, and that the invariance to postural conditions is preserved. These results support the concept of an innate modular organization of motor control that is independent from motor learning processes. References 1. Mussa-Ivaldi, F.A., S.F. Giszter, and E. Bizzi, Linear combinations of primitives in vertebrate motor control. *Proc Natl Acad Sci U S A*, 1994. 91(16): p. 7534-8. 2. d'Avella, A., et al., Control of fast-reaching movements by muscle synergy combinations. *J Neurosci*, 2006. 26(30): p. 7791-810. 3. Bizzi, E. and V.C. Cheung, The neural origin of muscle synergies. *Front Comput Neurosci*, 2013. 7: p. 51.

4-B-11 Human Mu Rhythm Activity During Observation of and Linguistic Description of Action

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The so-called mirror neuron system (MNS), originally detected in the monkey, appears to lie at the seat of self/other considerations. Cells in the MNS fire when an individual completes a movement such as a reach but the cells also fire when the individual observes another completing the same kind of action. The MNS may provide a root of social engagement and understanding. In a sense, this is the place where the cells may work for us to be able to say "I understand what you are doing". The goal of the present study was to extend the study of the MNS by comparing the neural response during a visual observation of an action with the neural response found during a linguistic description of an action. Specifically, we compare neural responses to ballet moves observed as well as verbally described. Moreover, the neural response is examined in two distinct populations, expert



ballet dancers and non-dancers. Previous studies have established that the MNS's 8-12 Hz activity called mu rhythm associated with it decreases during action observation and execution. Here, this pattern of MNS activation is associated with expert ballet dancers for both the visual observation and the verbal description. Weaker MNS activation is present in the non-dancers to the visual observation with even less or no MNS activation during the verbal description. This is the first study examining MNS responses to linguistic descriptions of action contexts across expert and novice populations.

4-B-12 Intrinsic functional organization of the human motor cortex

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Introduction: The Human Connectome Project (HCP www.humanconnectome.org) provides acquisitions of whole brain functional MRI data at high resolution and high speed. The higher resolution and short repetition time (TR) greatly enhances our ability to capture the spatial and temporal variation of brain activity and connections. This let us explore, with high anatomical accuracy and specificity, detailed interactions within a specific brain area - the motor cortex. Method: HCP developed protocol capable of acquiring the whole brain volume at 2x2x2 mm resolution within a TR of 720 ms. The resting state blood oxygenation level dependent (BOLD) time series, after proper prewhitening, were cross-correlated with varying lags. For left and right motor cortex we computed all possible pairwise crosscorrelation functions (CCF with 30 positive and negative lags) between prewhitened BOLD time series of ~2000 vertices (~2 million CCFs). For each CCF we located the highest absolute CC (CCmax), noted its value, sign and the lag where it occurred, and the intervertex distance. We then evaluated key spatiotemporal functions, including dependencies of the signed absolute CCmax on intervertex distance, absolute lag on intervertex distance, and signed absolute CCmax on absolute lag. Results: We found that these key functions were very robust across hemispheres and participants, indicating invariant functional interaction properties of the cortical circuitry. The frequency distribution of the signed absolute CCmax revealed a bimodal pattern consisting of separate negative and positive CCs. We found that the percentage of negative absolute CCmax was practically identical between the left and right motor cortex for a given participant but varied substantially among participants (range: 8.4 - 46.6%), which we term inhibitory drive. We found that the prevalence of inhibition was positively correlated with the motor dexterity and negatively correlated with the motor strength of the participant. Conclusions: The overall inhibitory drive is correlated with the individual's motor behavior and is the neural signature of motor capacities for a particular brain. These results are in accord with our recently advanced hypothesis that the level of motor cortical inhibitory drive is intimately related to accuracy and speed of motor performance (Mahan & Georgopoulos, *Front Neural Circuits* 7:92, 2013; Georgopoulos, *Exp Brain Res* 232:2391-2405, 2014; Georgopoulos & Carpenter, *Curr Opin Neurobiol* 33:34-39, 2015).

4-B-13 Differential contributions to response preparation depending on movement goal

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Over the past decade many studies have investigated response preparation through the use of a startling acoustic stimulus (SAS) presented during reaction time (RT) tasks. A common finding is that RTs are dramatically facilitated when a startle reflex is induced, often resulting a mean premotor RTs of <70 ms. One hypothesis explaining this "StartReact" response is that details of the motor plan are stored in brainstem centres (e.g. reticular formation) and triggered by startle reflex activation in these structures. However, in two studies using single pulse transcranial magnetic stimulation (TMS) to disrupt cortical processing by inducing a cortical silent period, it was shown that RTs were delayed in both non-SAS and SAS-triggered trials. This result was taken as evidence that at least some aspect of the preparatory and response initiation drive in SAS-triggered trials involves primary motor cortex contributions. However, it does not necessarily rule out brainstem contributions to the prepared action. The purpose of the present investigation was to determine if the RT delay resulting from a TMS induced cortical silent period might be modulated by anatomical requirements of the task or stimulus condition. It was hypothesized that actions with greater reticulospinal involvement would be less affected by the cortical silent period and thus the RT delay caused by the TMS would be shorter for these actions. Two experiments were conducted where participants performed a simple RT task requiring either targeted wrist flexion or wrist extension (counterbalanced blocked order). In Experiment 1 (192 RT trials) a SAS was unexpectedly delivered 200 ms prior to the go-signal in 10% of trials. Suprathreshold TMS (140% RMT) was delivered over the motor hotspot for the wrist flexors/extensors 80 ms following the go-signal in 10% of trials and TMS was delivered 30 ms following presentation of the SAS in 10% of trials. In Experiment 2 (144 trials) a SAS was unexpectedly delivered 200 ms prior to the go-signal in 11% of trials. Suprathreshold TMS calibrated individually to produce a cortical silent period of 90-130 ms was delivered over the motor hotspot for the wrist flexors/extensors 70 ms prior to each individual's median premotor control RT in 11% of trials. Along with a SAS presented 200 ms prior to the go-signal, calibrated TMS was also delivered 70 ms prior to the individual's median SAS RT in 11% of trials. Results from Experiment 1 showed a significant differential effect of the TMS induced silent period between control and SAS trials, as well as between flexion and extension movements. Experiment 2 showed similar results, driven by the finding that TMS had a smaller effect on SAS-triggered movements. Together, these results suggest a differential contribution of brainstem activation in the preparation and initiation of movements with different functional requirements. Supported by NSERC and the Ontario Ministry of Research and Innovation

4-B-14 Effects of gravity on human motor control

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To adequately control movements, the central nervous system needs to deal with gravitational forces. Typically, the influence of gravity on human motor behavior is studied by comparing movements that are performed either with or against gravity. Straightforward comparison of such movements is not without difficulties because they not only differ with respect to the field of gravity, but i) are typically performed with different muscles and/or with muscles that operate



differently (e.g. eccentric vs concentric contractions) depending on initial and target orientation, and ii) have different visual inputs to the motor system. These differences in movements may explain the inconsistencies found in the literature about the (magnitude of) the gravity dependent movement curvature and movement symmetry. The goal of this study was to investigate the effect of gravity on the kinematics of movements in identical movement tasks. To study the effects of gravity only, we developed an experimental setup with a chair that could be inclined backwards from a horizontal position (0°) to a complete vertical position (90°) in steps of 15° . Attached to the frame of the chair was a surface with two markers, placed 10 and 40 cm in front of the sternum. Participants had to move their index finger from one marker to another within 400 (± 100)ms. Auditory feedback was given about their timing. The 7 inclination angles were randomized, and per inclination angle participants made 50 outward and 50 inward movements. For outward movements, increasing the inclination angle led to an increase in gravity 'opposing' the movement, whereas for inward movements it led to an increase in gravity 'assisting' the movement. The preliminary experimental results indicate that the percentage of successful movements were not affected by the inclination angle of the chair. Average movement curvature (maximal perpendicular deviation from a straight line from start to target) for outward movements increased little with increasing inclination angle (on average about 2.5 mm). Inward movements were more curved than outward movements and increased about 5mm from 0° to 90° . As may be expected from the required movement time, the maximal speeds in the were not dependent on inclination angle nor on movement direction. Surprisingly, relative time to peak velocity was not affected by the inclination angle, but was on average different for outward compared to inward movements. These results suggest that some of the findings in the literature on difference in characteristics of movements performed against or with gravity may therefore be explained by differences in movement tasks, and not due to gravity per se.

4-B-15 A startling acoustic stimulus reveals advance preparation of intentional bimanual pattern switches

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During continuous bimanual coordination, participants can move the limbs in different oscillatory patterns with respect to one another. For example, during in-phase coordination the limbs are moved in a mirror symmetric manner (e.g., homologous muscle activation, typically more stable) versus anti-phase coordination in which the limbs are moved in the same direction (e.g., non-homologous muscle activation, typically less stable). In tasks where participants are asked to intentionally switch between coordination modes following an imperative stimulus, the time required to switch typically correlates with pattern stability. However, it is unknown whether this switching occurs due to advance preparation of the pattern switch, or due to the intrinsic dynamics of the relative coordination patterns. One way to investigate whether a motor response has been prepared in advance is to present a loud (>120 dB) startling acoustic stimulus (SAS) in place of the imperative stimulus during a reaction time (RT) task, which has been shown to involuntarily trigger a sufficiently prepared action at shortened response latencies. In the present experiment, a SAS was used to investigate if participants prepared the motor commands associated with a switch in the



required coordination pattern. Participants performed cyclical bimanual extension-flexion movements about the elbow joint paced at 1.5 Hz during the first half of each 18 s trial using a visual metronome and visual feedback. Trials began in either the in-phase or anti-phase pattern (30 trials each and randomly ordered) and when signaled by an auditory switch cue (80 dB, 1000 Hz), participants were required to voluntarily switch into the opposite coordination pattern as quickly as possible and to maintain that pattern for the remainder of the trial. In 50% of trials, the 80 dB switch cue was replaced by a SAS (120 dB, white noise). SAS trials were separated based on the presence/absence of a short latency EMG burst in the sternocleidomastoid (SCM) muscle (indicative of a startle reflex) in order to investigate the effect of the startle on motor preparation. Results indicated that switch onset (i.e., RT) was significantly faster (101 ms difference) following the SAS compared to the control tone ($p = .003$, $\eta^2p = .853$). Importantly, secondary analysis of switch onset times between trials with a reflexive startle response (SCM%2B) and those without (SCM-) suggest this result is not simply a stimulus intensity effect as switch onset times were significantly faster (77 ms difference) in trials with SCM activity trials compared to those without ($p = .010$, $\eta^2p = .766$). These findings suggest that an intentional bimanual switch can be sufficiently prepared during the ongoing production of a cyclic bimanual coordination pattern. Supported by NSERC and the Ontario Ministry of Research and Innovation

4-E-16 Synergy-based myocontrol of multiple degrees of freedom in children with secondary dystonia

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Myoelectric control can significantly improve human-robot interaction and intensive research has worked on the attempt of providing the user with intuitive control of multiple Degrees of Freedom (DOFs). However, no work has focused on patients with severe dyskinetic cerebral palsy (CP) who are unable to achieve effective voluntary movements. Research aimed at developing intuitive and flexible control interface strategies has the potential to provide these patients with significantly improved mobility. Indeed, in CP patients, there is no disconnect between the brain and the spinal cord, so that the electromyographic (EMG) signal provides a direct read-out of the movement-related activity in motor cortex. On the other hand, a major obstacle to the use of myoelectric control in patients with CP and arm dystonia is that the EMG signal is corrupted by co-contraction, variability, and noise. To address this problem, a synergy-based myoelectric approach should be tested. Indeed, when extracting synergies from multi-muscle EMG, a set of incoming EMG signals is converted into repeatable descriptors, while discarding irrelevant information, thus making muscle synergies more robust to possible noisy activity. In addition, previous studies showed that, although children with dystonia present aberrant EMG activity compared to control subjects, muscle synergies extracted from the two groups are very similar in terms of number and structure. In a previous work, we developed and successfully tested, on healthy subjects, a semi-supervised method to achieve online, simultaneous, continuous control of 2 DOFs of a robotic arm, using muscle synergies extracted from 8 upper limb muscles while performing reaching movements of the elbow and shoulder joints in the horizontal plane. Here, we tested this synergy-based myoelectric interface on 5 children with secondary dystonia due to CP. Our goal was to evaluate the feasibility and the



efficacy of the synergy-based control method, compared to the muscle-pair method typically used in commercial applications, using EMG signals recorded during both unconstrained movements (Dynamic Condition) and isometric contractions (Isometric Condition). For the Dynamic Condition, the control performance was assessed by computing the Root-mean-square Error and the Pearson's Correlation coefficient between the subject's and the robot's angles. For the Isometric Condition, we designed a graphical interface with a cursor that tracked the position of the robot's end-effector and specific targets to be reached. The performance was evaluated using the time needed to accomplish the task and the number of targets reached. Results show that our method is able to provide online, simultaneous, and accurate control of 2 DOFs of a robotic arm in children with secondary dystonia due to CP. The current study is a first step toward application of synergy-based myocontrol for patients with dyskinetic CP and other disorders of the control of muscles.

4-E-17 EMG-based augmented sensory feedback provides motor pattern changes in children with movement disorders

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Childhood dystonia and cerebral palsy (CP) are often affected with both motor and sensory deficits. There is still an unmet clinical need to understand the effect of sensory deficits on learning of upper-extremity and lower-extremity movement tasks in these children. The use of EMG-biofeedback has been effectively used in rehabilitation to learn fine control of muscle activity. The aim of the study was to test whether EMG augmented sensory feedback could lead to changes of motor patterns in children with dystonia and CP. Nine children with dystonia were asked to draw a 'figure 8' on a touchscreen tablet while recording arm kinematics and EMG of eight muscles of the arm. Subjects performed drawing movements first without biofeedback then receiving the EMG biofeedback via tactile vibration proportional to the activation of the wrist and shoulder muscles. We compared the task-correlated and task-uncorrelated muscle activity during the performance with and without the biofeedback. Eleven children with CP were recruited to test the effects of augmented sensory feedback in the lower extremities. Subjects were asked to make a series of three visits, each one month apart. Between the initial visit and the second visit no augmented sensory feedback was provided. During the second visit the subjects were asked to take the two EMG biofeedback devices home for a 1-month trial and instructed to wear them on two muscles for 5 hours a day, 7 days a week. As in the upper extremities study, the modality of the EMG biofeedback was via tactile vibration proportional to the muscle activation. Interjoint coordination of the hip and knee during the stance and swing phases of gait and hip, knee and ankle joint angles were used to test the effects of 1-month use of augmented sensory feedback. Results of the upper extremities study in children with dystonia showed a significant change of the task-correlated and task-uncorrelated muscle activity during the drawing task while the subjects were receiving the sensory feedback. The change in the muscle activity pattern was observed despite unchanged motor performance on drawing the 'figure 8'. Motor pattern changes were also observed in the gait for children with CP. Results of within-subject analysis showed changes of the peaks value of the relative phase interjoint



coordination pattern induced after a month using the biofeedback devices with respect to the month without biofeedback. Moreover, changes of hip, knee, and ankle joint angles have been seen after the use of biofeedback. The results suggest that enhanced sensory information using EMG biofeedback increases attention and enhances sensation of muscle contraction mimicking proprioception that results in changes of motor pattern. These preliminary results are promising and will help to refocus the current therapeutic paradigms by using the biofeedback technique as an exploration tool where sensory deficits can prevent the development of motor skills.

4-E-18 Changes in the control of posture and gait in pre-clinical stages of degenerative cerebellar ataxia

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Background: It is well-known from many neurodegenerative movement disorders, that subtle movement changes occur often years before clinical manifestation. This pre-clinical state offers the opportunity for a more detailed understanding of the course of dysfunctional motor control mechanisms and compensation strategies. Here, we examined measures that allow the identification of ataxia-specific dysfunctions already in the earliest stage of degenerative ataxia. We hypothesized that an increasing complexity of balance and gait tasks might reveal dysfunctions in pre-clinical stages of the disease. Methods: We assessed (i) stance in different complexities including closed eyes and on an elastic mat as well as (ii) walking and tandem walking on hard and soft ground. Ataxia-specific changes including spatial and temporal variability [1] and body sway were assessed by quantitative movement analysis. Assessments were performed in three groups: 1.) EARLY: 9 patients with early stage ataxia (SARA[2] score: 3-8 points); 2.) PRE: 14 mutation carriers for spinocerebellar ataxia (SCA) types 1,2,3 or 6; [SARA<3 points]; 3.) CON: 23 age-matched healthy controls. For SCA mutation carriers in the PRE group, movement parameters were related to the genetically estimated clinical disease onset[3]. Results: A difference in body sway was observed in all Romberg conditions between the groups EARLY and CON ($p<0.001$) as well as between EARLY and PRE ($p<0.02$). Differences between PRE and CON have been identified in classical Romberg, with closed eyes, and on the mat with closed eyes ($p<0.002$). Body sway was correlated with estimated disease onset³, indicating a continuous development of changes in the preclinical phase. For straight walking, the EARLY group showed an increased step length variability compared to PRE ($p=0.02$) and CON ($p=0.01$), but no differences were observed between PRE and CON ($p=0.25$). In contrast, for tandem walking and tandem walking on a mattress PRE showed significant increased variability in step length and in step cycle time compared to CON ($p<0.006$). Multivariate regression analysis categorized preclinical mutation carriers on a single-subject level with 100% accuracy within a range of 10 years to estimated onset. Movement features in stance and gait correlated significantly with genetically estimated time to onset, indicating a gradual increase of motor changes with increasing proximity to disease manifestation. Discussion: We identified features in stance and gait, which differentiate controls not only from early ataxia subjects, but also from pre-clinical ataxia subjects without clinical ataxia signs. These features show a correlation to the time of estimated disease onset, thus describing a continuum of change already within the pre-clinical phase. References 1. Ilg W



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4-E-19 Task-congruent visualizations increase muscle awareness in subjects with dystonia during a one-dimensional myocontrol task

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Previous studies on use of vibratory feedback in children with secondary dystonia showed that there were significant changes in overall muscle use with vibration that was scaled to muscle use. We then wanted to understand why vibration behaved in this manner, and decided to approach this problem differently. We spoke with coaches in various sports at the University of Southern California, and found that they all used visualizations to improve motor skills in their athletes. We hypothesized that visualization can be used in our subject group to increase muscle awareness, and thus show that scaled vibration behaves somewhat similarly to the kind of visualization utilized in sports. We designed a 3-block, unilateral myocontrol experiment in which subjects (4 patients, 5 controls) manipulated their arm to control a cursor on the computer. The brachioradialis and FDI muscles contributed to the horizontal motion of the cursor. Subjects were asked to move the cursor into a target as quickly as possible, and to stay in that target. Blocks 1 and 3 were baseline measurement blocks where we conducted 20 sets of trials lasting approximately 15s each. In block 2, we provided a visualization of their muscles (correlated to their activity), and asked them to continue the task using this new information, with the expectation that their performance and muscle use would change significantly with this visualization added. Results show that visualization can change muscle patterns both during and immediately after the task. Patients tended to increase the use of their brachioradialis, while controls increased use of their FDI. There was no significant change in time to reach the target. Subjects reported consciously changing their behaviors post visualization. We also conducted another experiment in which we provided a "wrong?" visualization, and we expect results to show that task performance was negatively affected by this kind of visualization. We believe use of visualization can be a very helpful tool for learning how to perform complex motor patterns over time, and we hope it would eventually prove to be useful in the clinical environment. We believe that scaled vibration can work in conjunction with visualization to provide increased performance on a motor skill, similar to that seen in coaching.

4-E-20 Disrupted motor memory in Parkinson's disease as demonstrated by altered interference effects

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Recent studies have suggested that people with Parkinson's disease (PD) are not as efficient as age-matched controls in the retention of certain kinds of motor memory. We chose to investigate this phenomenon by testing for interference effects in motor adaptation. Motor adaptation is the process responsible for maintaining motor accuracy in response to consistent altered sensory input,



e.g. prism adaptation. If a participant learns an adapted state and then is asked to learn a second adaptation (one that is not compatible with the first state), the ability to learn the second state is worse compared to the first. This is thought to occur because the memory trace of the first adaptation interferes with learning the second adaptation. Importantly interference depends on the strength of the initial memory. We hypothesized that if people with PD retain motor memories less well (i.e. their motor-memories are less robust), they should display smaller interference effects. People with PD and healthy age-matched controls were tested for adaptation and interference using a force-field adaptation task performed with the upper-limb. Initially, both groups adapted to a clockwise force-field (10 N/m/s) by making reaching movements to a target while holding the handle of a velocity-dependent force-controlled manipulandum. After a break and a period of washout (required to return participants performance back to baseline levels) the participants were asked to learn to reach through an identical but opposite (counter clockwise) force-field. Differences in learning rates in the second force-field condition allowed us to measure how much the memory of the first force-field interfered with learning the counter clockwise force-field. The break was either 1-hour or 24-hours to additionally measure the effect of sleep consolidation on motor memory. Preliminary results indicate a disrupted motor memory in people with PD - compared to the controls - as those in the 1-hour group (PD, n=12) show similar performance during the counter field as during the initial field. This finding is in contrast to the age-matched control group (n=12) who show worse performance, which is in line with the expected interference effect. The difference between the groups is reflected both in the hand displacement due to the force-field as well as in their force production. These findings suggest that people with PD display lower interference effects than age matched controls. This supports our hypothesis that motor memories are less robust in people with PD. We suggest this is evidence for a role for the basal ganglia in motor memory. Where its dysfunction in PD results in a decline in motor memory, possibly through problems with formation, retrieval or context-dependent switching of motor-memory. The results also indicate that the basal ganglia does not play a crucial role in the adaptation process itself, as performance in the initial adaptation phase seems not affected in people with PD.

4-E-21 Targeted high-throughput screening of olivocerebellar motor circuitry genes in essential tremor

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Background: Essential Tremor (ET) is a prevalent neurological disorder of unknown etiology that is characterized by the presence of action tremors occurring during voluntary motion and affecting primarily the upper limbs. The worldwide prevalence of ET is 0.9% in the general population and 4.6% in individuals ≥ 65 years old. Twin studies revealed variable concordance in ET but are nonetheless suggesting that genetic risk factors likely contribute to the pathology. To date, no gene was reproducibly reported to cause ET across unrelated cohorts which is likely due to the genetic heterogeneity of the disorder. Moreover, the precise pathophysiological origin of ET is still the subject of debate and common misdiagnoses are adding to the general confusion pertaining this pathology. However, mounting evidence currently suggests dysfunctions affecting the



olivocerebellar motor circuitry as the primary source of tremors; with the inferior olive, Purkinje cells and deep cerebellar nuclei being the main affected brain regions. Hypothesis: Genes that are phylogenetically conserved for their expressions in the olivocerebellar circuitry are susceptible to present genetic variations that would be ET risk factors. Methods: A preliminary list of 11 candidate genes that were selected based on their high level of expression in the olivocerebellar circuitry in both human and mouse has been generated using publicly available data from the Allen Brain Atlas. The 11 genes from this list, which noticeably appear to encode several proteins involved in calcium and glutamate signaling pathways, will be screened for the presence of genetic variations in a cohort of cases and controls. Calcium related genes are plausible candidates since previous evidence supports calcium dependent pathways to play a role in the generation of neuronal oscillations, resonance and pacemaker activities. Glutamate signaling related genes are also good candidates since NMDAR agonists are known to alleviate harmaline induced tremors. The mutation screen was done using a Molecular Inversion Probes (MIPs) capture methodology. For this particular project, a total of 991 MIPs were designed to screen 269 cases and 288 matching control individuals. The primary focus of our genetic analysis will be on the identification of nonsense and missense mutations as these are the most deleterious. Further examination will use a statistical burden method that will collapse all the rare variants located in the different candidate genes into a single value, which is then tested for association with the phenotype. Outcome: The list of 11 candidates contains genes functionally related to three defined pathways; the calcium signaling pathway, the metabotropic glutamate receptor group III pathway, and the ionotropic glutamate receptor pathway. Hence, if proven true, this approach has not only the potential in identifying novel ET risk factors but could also link this pathology to a particular signaling pathway.

4-E-22 Motor Control Training Enhances Reactive Driving Performance in Stroke

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In the US, there are up to 5 million stroke survivors who drive. Over 50% of these individuals require driving rehabilitation. Despite this, there is little research on rehabilitation approaches to enhance driving following stroke. Past work on driving in older adults has focused on reactive driving, a key component of car following task that requires visuomotor tracking and responding to a sudden visual stimuli with fast and precise movements. Evidence suggests that impaired reactive driving in older adults is related to motor control but not strength deficits. Given that declines in strength and motor control are a common consequence of stroke, the goal of this study was to compare the effect of strength training and motor control training in improving reactive driving following stroke. Here, we compare reactive driving performance in participants that were randomly assigned to either a) strength (N = 5, age = 66.3 ± 18.5 yrs.; time since stroke = 12.8 ± 5.2 yrs., Fugl-meyer lower extremity score = 23.4 ± 5.7) or b) motor control (N = 5, age = 64.6 ± 6.3 yrs.; time since stroke = 8.4 ± 5.2 yrs., Fugl-meyer lower extremity score = 19 ± 8.1) training groups. Both groups received a total of 12 hours of training over 2 weeks in 4 sessions with increasing intensity. Participants trained on isometric dorsiflexion and plantarflexion contractions with both the paretic and non-paretic ankles. The strength training group practiced fast motor contractions at 65%, 70%, 75% and 80% of their maximal voluntary capacity (MVC). The motor control group practiced sinusoidal tracking task at



0.05, 0.1, 0.2 and 0.1%2B0.2 Hz of frequency at 15% MVC. Before and after the training, we tested reactive driving performance in a simulated driving environment. We quantified motor output variability of the gas pedal tracking movement and the brake pedal force with coefficient of variation. We also quantified the total response time, premotor response time, and motor response time. The motor control training group showed greater improvements in reactive driving as compared with the strength training group. Specifically, the motor control group showed significant decrease in gas and brake pedal variability ($p < 0.05$) following training. In addition, the motor control group exhibited faster total, premotor, and motor response times ($p < 0.05$) as compared with the strength training group. Taken together, motor control training improved reactive driving by reducing the motor output variability on the gas and brake pedal and by decreasing the response times. In conclusion, we provide novel evidence that motor control but not strength training improves reactive driving following stroke. Driving rehabilitation in stroke will benefit from motor control training that targets reduction in motor output variability.

[4-E-23 Full Day Kinematic Differences in Leg Movements between Infants with Typical Development and At Risk of Developmental Delay](#)

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Background: Movement disorders in infants are not completely understood and there is a lack of accurate early detection of movement impairment. A portable, automated quantitative analysis method for measuring full-day infant movement will support objective assessments and a better understanding of infant neuromotor development. Our overall goal is to use inertial sensors to collect full-day leg movement data and differentiate infants with typical, delayed or impaired neuromotor development. Here we compare leg movements produced across a full day by infants at risk of developmental delay to infants with typical development. Methods: Inertial sensor data were collected from 12 infants with typical development (TD), (1-12 months), and 24 infants at risk of developmental delay (AR), (3-19 months, corrected age), for 8-13 hours per day. There were 2 months between visits and a total of 3 visits per infant. An inertial sensor was attached to each leg, and recorded simultaneous tri-axial accelerometer and gyroscope measurements at 20Hz. In previous work, we developed and validated a threshold-based algorithm where each pause or change of direction of the limb is counted as a discrete movement. Furthermore, duration, average acceleration, and peak acceleration of each movement were determined. We used a repeated measures linear mixed model with a diagonal covariance structure to test for group differences in each infants' average per visit: movements per hour of awake time, duration, acceleration and peak acceleration values for the left leg at $\alpha = 0.05$. We chose to analyze only the left leg here as the values for the right and left legs were similar: movements per hour of awake time ($r=0.95$), duration ($r=0.90$), average acceleration ($r=0.95$), and peak acceleration ($r=0.95$). Results: Significant differences were found between groups for average movements per hour of awake time, (TD: mean (M)=1841, Standard Error (SE) = 91; AR: M= 1377, SE = 66, $F[1,83.3]=17.17$, $p = > 0.01$), for average duration (s, TD: M=0.275, SE = 0.004; AR : M=0.261, SE= 0.003, $F[1,92.6]=9.33$, $p = 0.003$), for average acceleration (m/s^2 , TD: M=2.583, SE=0.73; AR: M=2.330, SE=0.053, $F[1,98.9]=7.85$, $p = 0.006$), and for average peak acceleration (m/s^2 , TD: M=5.188, SE=0.173; AR: M=4.605, SE= 0.124,



$F[1,100.23]=7.51$, $p = 0.01$). Conclusion: Our results show significant group differences in number of movements and kinematic characteristics. Infants AR moved less and, on average, produced movements that were shorter in duration with smaller average and peak accelerations than infants with TD. Currently, we do not know the 24-month neuromotor outcomes of the infants in the AR group. Once we have them, we will explore early differences between infants AR with good neuromotor outcomes and infants AR with poor neuromotor outcomes.

4-E-24 Enriched cortical motor synergies through subthreshold optogenetic stimulation in spinal complete adult rats.

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After complete T9/T10 spinal cord injury (SCI) in rats, motor compensations occur. The sensorimotor cortex reorganizes, and representations of novel trunk muscle synergies emerge (see Oza 2014, 2015). We have previously explored relationships between cortex muscle synergy formation and recovery. Rats transected as neonates (NTX) were trained to walk on a treadmill 20min/day for five weeks with robotic weight support (NTX-r N=8) leading to eventual weight supported stepping, or without (NTX-tm N=8). All rats underwent intracortical microstimulation (ICMS) mapping of the motor cortex, while recording trunk electromyograms (EMG). Borrowing from information theory, we quantified trunk synergy formation using entropy calculations. EMG from trunk segments located below the site of injury, and trunk EMG elicited from cortical regions below bregma showed more information in NTX-r rats than in NTX-tm rats. NTX-r rats had significantly higher cumulative pairwise mutual information compared to the NTX-tm group. Specific multi-muscle synergies were thus represented more consistently in the NTX-r group. Improved function of NTX-r rats coupled with formation of muscle synergies in cortex. We hypothesized that we could improve synergies and recovery in rats transected as adults (ATX) by increasing plasticity in the trunk motor cortex below bregma using subthreshold optogenetic stimulation. Using viral delivery below bregma, we introduced Channelrhodopsin (ChR2) or a control fluorophore (EYFP) targeted to pyramidal cells of the sensorimotor cortex. With robotic assistance, ATX rats were trained to walk on a treadmill, as described above, while also receiving continuous 470nm light stimulation. Three groups of robot trained rats were prepared: ATX with ChR2 (N=4), ATX-ChR2 rats with AAV5-BDNF injections into lumbar spinal cord inducing hindlimb alternation (N=4), and a control ATX-YFP group (N=4). A cage rest ChR2 group (N=4) received constant light stimulation 20mins/day for five weeks. All rats were then mapped with ICMS. A significant caudal shift in trunk representation center of gravity was observed in robot trained ChR2 rats but not in cage rest rats ($p < 0.05$ Wilcoxon rank-sum test). Both ChR2 robot trained groups showed more information in regions of cortex below bregma compared to controls. A significant increase in lumbar trunk representation was observed in all ChR2 treated rats compared to the control group ($p < 0.05$ Wilcoxon rank-sum test). The ChR2-BDNF group also showed more information from muscles located below the site of injury, and had higher cumulative pairwise mutual information than other groups. Optogenetic subthreshold excitation can thus enrich cortex trunk representations below bregma. These results, paired with the NTX results, also show the roles of both robot lumbar weight support and spinal stepping in the formation of richer trunk muscle synergies in cortex after SCI. This work is supported by NIH (NINDS) N054894, and NS072651.



4-E-25 Neural activation of muscle during maximal contractions in myotonic dystrophy

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Myotonic dystrophy type 1 (DM1) has a worldwide prevalence of 1:8000. It is the most common muscular dystrophy that is multisystemic and can induce several physiological and functional disturbances. The main clinical features at the muscle level are delayed relaxation (myotonia) and involuntary trains of actions potentials (percussion) after a strong contraction. These effects reduce with repetitive muscle activity (warm-up). Although classically myotonia is attributed to an abnormality in the muscle chloride ion channel, the disease clearly affects the central nervous system. Nonetheless, little is known about whether disturbances in the voluntary drive to the muscle contribute to myotonic contractions. Here, we compare the neural activation of muscle for myotonic (slow relaxation phase) and non-myotonic (fast relaxation phase) maximal contractions. Three individuals diagnosed and genetically confirmed with DM1 (39 ± 14.4 years) performed maximal isometric dorsiflexions with the left ankle joint. We examined the maximal force profile and neural activation of the agonist muscle before percussion. Specifically, we quantified the peak force, rate of force increase and release, electromechanical delay, and power in the wavelet spectrum from 10-60 Hz of the TA interference EMG. The force profile of maximal contractions was different for myotonic and non-myotonic trials. As expected, myotonic contractions took 6.3-38 s longer to relax than non-myotonic contractions. The peak force was similar for the two sets of trials (51.8 ± 38.25 N). Interestingly, myotonic relative to non-myotonic contractions exhibited a slower rate of force increase (88.1 ± 63.6 vs. 164.2 ± 141.2 N/s) and a slower electromechanical delay (0.134 ± 0.029 vs. 0.102 ± 0.043 s). The neural activation of muscle was different for myotonic and non-myotonic trials. Most interestingly, the activation of the tibialis anterior was different during the force increase and prior to percussion. Specifically, the EMG power from 35-60 Hz was greater for myotonic trials (343.3 ± 159.9 vs. 66.5 ± 40.3 %). These findings suggest that an altered voluntary drive to the agonist muscle additionally contributes to the channelopathy-induced myotonia.

4-E-26 A reflection on plasticity research in writing dystonia

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Much attention has focused on the hypothesis that there is enhanced plasticity of sensorimotor circuits in patients with dystonia. A common experimental method to assess plasticity in dystonia research is paired associative stimulation (PAS). Excessive, nonfocal effects of PAS were observed in early studies of dystonia; however, these large effects have not been uniformly replicated. We present data from 15 patients with writing dystonia. We suggest that, as in healthy individuals, the effects of PAS are highly variable. A review of previous studies examining PAS in writing dystonia highlights the range of results that have been observed. We conclude that current experimental evidence cannot be fully explained by the notion that PAS responses in writing dystonia are consistently excessive or nonspecific. The variability of PAS responses is such that enhanced plasticity should not be considered a dystonic fingerprint, because the direction of response can



vary, and there is overlap between patient and healthy data. We also discuss evidence questioning the assumption that PAS responses are a clear correlate to levels of synaptic plasticity; we need to define more specifically what PAS responses signify in the dystonic brain. Our conclusions are limited to PAS in writing dystonia; however, much variation exists with other plasticity protocols. Large multicenter studies of both focal and generalized forms of dystonia, probing variability of individual neurophysiological profiles, are encouraged. This will reveal the true role of plasticity in the pathophysiology of dystonia and may expose subject-specific therapeutic interventions that are currently concealed.

4-E-27 Effectiveness of a Community-Based Cycling Intervention for Improving Motor Symptoms of Parkinson's Disease

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Medications are the primary method used to manage Parkinson's disease (PD) symptoms. However, medication effectiveness wanes over time and some PD symptoms are less responsive to medication, requiring adjunctive therapies to mitigate symptoms. Exercise has shown strong potential as an adjunctive therapy for PD. Previous laboratory studies have demonstrated improved PD symptoms following 8 weeks of vigorous cycling, including improved motor symptom severity and motor control (Alberts et al., 2011). Based upon these findings, the Pedaling for Parkinson's (PFP) program was developed as a community-based cycling intervention that follows a similar protocol as the laboratory studies. PFP classes are hour-long sessions, hosted three times a week, by community-oriented exercise facilities. Participants are encouraged to cycle vigorously (80-90 revolutions-per-minute of the pedals; 60%-80% of maximum heart rate) for 40 continuous minutes, in addition to warm-up and cool-down periods. The current study examined the effectiveness of PFP when implemented as a community-based exercise intervention. Twelve individuals with PD completed the motor subscale of the Movement Disorder Society's--Unified Parkinson's Disease Rating Scale (MDS-UPDRS) and the Purdue Pegboard test at baseline and follow-up testing sessions after 4- and 8-weeks of participation in PFP. All participants regularly participated in PFP for at least 8 weeks and were tested off their PD medications. The MDS-UPDRS was rated by a movement disorders specialist blind to participant's time in PFP. Results show a trend for improvements in PD motor severity after 8 weeks of participation in PFP ($p = .06$), as measured by the MDS-UPDRS. The greatest improvements observed were in the gait and postural stability dimensions of the MDS-UPDRS (approximately 8%). While this difference did not reach statistical significance, the observed improvement is considered a moderate clinically important difference (Schulman et al., 2010). Additionally, we found a significant improvement in fine finger dexterity for participant's hand least affected by PD ($p = .03$), but not their most affected hand ($p = .20$). Taken together, these findings provide initial evidence that PFP may serve as an effective, community-based adjunctive intervention for mitigating some motor symptoms of PD.

[4-F-28 A cortical substrate for the retention of saccadic eye movements plasticity](#)

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Sensorimotor adaptation ensures movement accuracy despite continuously changing environment, body and brain. Adaptation of saccadic eye movements is a classical model of sensorimotor adaptation but its neural substrates are still incompletely described. Besides the well-documented implication of the cerebellum and subcortical cerebellar-recipient centers, the involvement of the cerebral cortex has only been recently inferred thanks to behavioral studies in human investigating the effects of saccadic adaptation on visual perception (e.g. Zimmermann & Lappe 2010) and attention (Habchi et al 2015). More direct evidence for the involvement of cerebral cortex in saccadic adaptation has been provided by neuroimaging and neurostimulation approaches (Blurton et al 2012; Gerardin et al 2012, Panouillères et al 2014). More specifically, our previous functional magnetic resonance imaging (fMRI) study highlighted for the first time the potential contribution of the right Temporo-Parietal Junction (rTPJ) in the adaptive shortening of reactive saccades (Gerardin et al, 2012). The aim of the present study was then to provide direct evidence for the causal contribution of the rTPJ in the plasticity of saccadic eye movements using non-invasive brain stimulation. Twelve participants performed 4 sessions of adaptation of leftward reactive saccades, which were separated by one week. MRI-guided single-pulse Transcranial Magnetic Stimulation (spTMS) was applied over the rTPJ at four different timings relative to saccade onset (30, 60, 90 or 120ms) in the four separate sessions. We found that, relative to the other 3 timings, stimulation of rTPJ 60 ms after saccade onset tended to boost, though not significantly, the adaptive decrease of saccade amplitude during the early phase of saccadic adaptation. Interestingly, pooling the stimulation timings revealed a significant retention, from one session to the next, of the amplitude decrease of adapted saccades (repeated-measures ANOVA, $p=0.005$) whereas unadapted (rightward) saccades remained unchanged. The specificity of this adaptation retention over the one week-long delay was tested by re-analysing the data of a previous behavioural study (Habchi et al 2015) and a spTMS study that targeted the intra-parietal sulcus (IPS) region (Panouillères et al 2014), which respectively involved 2 and 4 repeated adaptation sessions per subject. Results of the behavioural study revealed no significant retention from the first to the second adaptation session ($p>0.05$) and the retention measured in the parietal spTMS study, although significant ($p=0.03$), was less than half the size of that observed in the present study (12.4% versus 26.4%, respectively). Altogether, these findings suggest that, while possibly contributing to a minor extent to the acquisition of saccadic adaptation, the right temporo-parietal junction appears to play a major role in the long-term retention of saccadic adaptive changes.

4-F-29 Adaptive Brain Structural Plasticity With Spaceflight

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BACKGROUND: Humans undergo extensive sensorimotor adaptation during spaceflight due to altered vestibular inputs and body unloading. The effects of spaceflight on human brain structure however are still largely unknown. Based on the literature documenting experience-dependent brain plasticity and results from neuroimaging microgravity analog studies, we hypothesized that spaceflight could result in structural brain changes in sensorimotor areas. To investigate this



association we analyzed gray matter volume (GMv) changes from pre-flight to post-flight. Additionally, we explored the relationship of pre- to post-flight changes in GMv to postural control changes to see if spaceflight induced structural brain changes are related to behavioral performance during the re-adaptation process to Earth's gravity. **METHOD:** We used retrospective longitudinal T2-weighted MRI scans of 10 astronauts (mean age 48.0 ± 3.3 years) from the NASA Life Sciences Data Archives. For all subjects pre-flight scans (collected on average 144.1 ± 117.8 days before launch) and post-flight scans (collected on average 6.5 ± 5.28 days after return) were available. Mission duration was either ~ 2 weeks (5 subjects) or ~ 6 months (5 subjects). Longitudinal voxel-based morphometry was applied to test GMv changes throughout the brain. GMv maps were obtained using the segment module of Statistical Parametric Mapping 12. A two-step approach was used to transform the GMv maps into Montreal Neurological Institute (MNI) common space using advanced normalization tools (ANTs). Balance performance that was available in 6 subjects was measured with the Sensory Organization Test-5 (performed with pitch head movements, $\pm 20^\circ$ at 0.33 Hz). Non-parametric randomization tests were used to test if changes in balance control and GMv were related. **RESULTS:** We found extensive increases in GMv, largely restricted to sensorimotor brain structures including bilateral primary and supplementary motor cortices, primary somatosensory cortex, and cerebellum lobules I-V. We observed small regions of significant GMv decreases in the left hippocampus, the right thalamus, and the right temporal pole. Balance control significantly deteriorated from pre- to post-flight. These changes correlated with GMv changes in the right posterior cingulate motor area; subjects with larger GMv increases showed less performance decrease. **CONCLUSIONS:** GMv increases in the posterior cingulate motor area may suggest individual capacity for adaptive neuroplasticity. Sensorimotor novelty and practice in the space flight environment is the most likely explanation as to what led to the sensorimotor structural brain plasticity. GMv decreases in the hippocampus and thalamus could potentially be related to interference in three-dimensional spatial navigation during space flight; hippocampal volumetric declines have also been observed with stress. Studies with longer-term follow up are necessary to determine the persistence of these findings.

4-F-30 Do tit-for-tat exchanges of force escalate?

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In a study by Shergill et al. (Science 2003), pairs who attempted to exchange a force with one another gradually escalated in force; their study suggested that the overestimation of the partner's force may be due to predictive sensory cancellation, by showing that individuals also overestimate forces in a similar manner to pairs. We reinvestigated the tit-for-tat exchanges in force with 16 pairs, and found that more than two-thirds of the partners consistently underestimated the force from the partner. In contrast with the previous study, most pairs estimated the force differently to individuals. What caused the pairs to estimate the force differently to individuals? In psychology, it is established that eye-contact influences interaction between people. To test whether such social bias may have influenced the pairs, we repeated the experiment with 16 different pairs who were separated by a curtain that blocked the line-of-sight to the partner. With the partner outside of the field-of-view, pairs estimated the force similarly to individuals. Our results show that individual force



misestimation explains tit-for-tat exchanges in force in limited conditions, and that social cues like eye-contact may play a larger role during face-to-face interaction between people.

4-F-31 The effect of movement lead-in diversity on the rate of motor learning

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Arm movements have been frequently studied in isolation, although natural movements often follow on from other movements. We previously showed that past movement, such as backswing in ball sports, plays an important contextual role in motor learning and recall. This demonstrated that movements depend on those immediately preceding them. Recently we demonstrated that follow-through could affect the learning rate in immediately preceding movements. More specifically, if one of many future movements directly followed a dynamic leaning task, each separate future direction partitioned the learning in the preceding movement, resulting in slower learning. In contrast, if there were only single future movements, no such partitioning occurred which resulted in faster learning. Since the overall effect of future movement is weaker than that elicited by past movements, lead-in movements might exert even stronger effects on motor learning rate. Here we examine how the corresponding characteristics of lead-in movement affect motor learning in subsequent movements. To do so we use a two-movement paradigm implemented with a robotic manipulandum. First, participants make or experience lead-in movements from a starting location to a central point. Immediately afterwards they make a second active movement during which they are exposed to novel dynamics, implemented using a velocity dependent curl field. We first investigated the effect of changing the variability of active lead-in movements. We found that more consistent lead-in movements gave rise to faster learning than variable lead-in movements. We then examined the effect of using different sensorimotor modalities for the lead-in movement. These involved using passive movement to drag the participant arm for the first movement, or by only displaying a moving cursor whilst the participant's arm was stationary. As a control condition, we also assessed the learning rate in a single movement control task in which no contextual movement was present. We found that the significant difference in learning rate across consistent and inconsistent conditions observed for active lead-in movements was not present in the passive and visual conditions. In addition, the learning rate in these two latter conditions was also similar to that seen with the no-context control task. Overall this suggests that that motor memory activation not only depends on the variability of past lead-in movement used for the lead-in but also on the sensorimotor modality of the lead-in movement. Financial support provided by the Wellcome Trust and the Centre for Robotics and Neural Systems at Plymouth University.

4-F-32 Moving in immersive virtual reality changes visual perspective

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Perception and action are interdependent. How visual information guide movements has been extensively studied, while how movements affects vision is understudied (e.g., Berti & Frassinetti,



2000). Related studies typically focused on the effect of sensorimotor learning on proprioception (e.g., Ostry et al., 2010; Synofzik et al., 2008). Yet few studies address how action affects vision. We postulate that moving in an altered visual environment can modify well-established representations of the world such as visual perspective. Here we invert the rules of perspective in virtual reality by modifying the size-distance relation from distant objects appearing smaller, the normal case, to distant objects appearing larger. Our experiment consisted of a pretest, an adaptation phase and a posttest. In the pretest and posttest, we measured the magnitude of Ponzo illusion, the phenomenon that for two identical objects the one with further apparent depth appears larger, as a quantification of perception of perspective. Subjects performed a two-alternative force choice task to measure the point of subjective equality (PSE) for object size (Fang et al., 2008). The illusion size was defined as the PSE change in the 3D scene from in a 2D baseline scene. During adaptation, subjects wore a head-mounted display (Rift DK2, Oculus) and a data glove (Perception Neuron, Noitom) which measured arm kinematics. Subjects were divided into 3 groups. For the active group, subjects actively engaged with the special virtual scene for 30 mins: they were required to push and release a virtual ball with the right hand. The ball rolled on a desktop and stopped at a target gate. Before each push, subjects adjusted the gate width to predictively minimize the discrepancy between the gate and the ball. For the passive group, visual manipulations remained the same but subjects watched the ball rolling away without any action. For the control group, subjects performed the same task as the active group but with a normal perspective. We computed the reduction of illusion size between pretest and posttest to examine how VR exposure affected perception. Both active and passive groups had significant changes (paired t-test, $p < 0.05$) with significant difference between groups (ANOVA, $p < 0.05$). Post-hoc tests only detected that the active group had larger effect than the control group ($p < 0.05$). This shows that actions in VR can facilitate the change in perception of perspective. Our study suggests that immersion in an altered visual environment can change our well-established perceptual representation and, importantly, motoric interaction can facilitate this change. Immersive VR offers an effective tool to study the interaction between perception and action by quickly reshaping their existing relations. In particular, our study provides a behavioral paradigm to investigate the neural substrate of size perception or interaction between dorsal and ventral visual streams (Schwarzkopf, 2015).

4-F-33 Functional Plasticity in Somatosensory Cortex Supports Motor Learning by Observing

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An influential idea in neuroscience is that the sensory-motor system is activated while observing the actions of others. This idea has recently been extended to motor learning. Action observation promotes sensory-motor plasticity and behavioral changes in both the motor and somatosensory domains. However, it is unclear how the brain maps visual information onto motor circuits for learning. Here we present two experiments testing the idea that the somatosensory system, and more specifically primary somatosensory cortex (S1), plays a direct role in motor learning by observing. In Experiment 1, we tested the hypothesis that the somatosensory system plays a necessary role in motor learning by observing. We applied median nerve stimulation to the arm while subjects observed a tutor undergoing a force field learning task. Median nerve stimulation



served to occupy somatosensory cortical processing with unrelated input during observation. Stimulation disrupted observational motor learning in a limb-specific manner; stimulation delivered to the right arm (same arm used by the tutor in the video) disrupted learning whereas stimulation applied to the left arm did not. This is consistent with the idea that a somatosensory representation of the observed effector must be available during observation for motor learning by observing to occur. In Experiment 2, we tested a more specific hypothesis that primary somatosensory cortex (S1) supports motor learning by observing. Here we assessed changes in S1 cortical processing following motor learning by observing by measuring somatosensory evoked potentials (SEPs). SEP amplitudes increased only for those subjects who observed learning. Moreover, SEPs increased more for subjects who went on to exhibit greater motor learning following observation. Together, these findings support the idea that motor learning by observing relies on functional plasticity in S1. We propose that visual signals about the movements of others are mapped onto motor circuits for learning via the somatosensory system.

4-F-34 Different actions during object manipulation are associated with separate, but interacting, adaptive processes

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When opening a valve or sawing a piece of wood, one repeatedly performs back and forth movements, each of which can involve a different dynamical interaction between the hand and the object. For instance, opening a valve involves repeated cycles of counter clockwise (CCW) and clockwise (CW) rotations of the hand, with the CCW rotation performed with the valve's handle grasped and against the resistance of the mechanism, and the CW rotation performed with the handle released so as to reposition the hand for the next cycle. In such repetitive actions, in which each can be associated with different dynamics, little is known about the interaction of the control mechanisms underlying each action. Here we examine how subjects adapt to dynamics associated with each motion in a repetitive sequence of actions during object manipulation and, in particular, examine if the representations of the dynamics for the two motions are independent. Subjects grasped the handle of a robotic device (wristBOT), which simulated a virtual hammer that they could rotate in the horizontal plane. They rotated the hammer alternately in CW and CCW directions and were required to counteract any dynamics so as to keep the handle as still as possible. Using the robotic interface we could simulate 1) the forces and torques faithfully (full dynamics), 2) just the torques with the handle clamped in place with zero error (error-clamp trials) or 3) only the torques with the handle free to move (null trials). In different phases of the experiment we manipulated the dynamics for the CW and CCW movements so that they could either be the same (i.e. both full dynamics, both error-clamp or both null trials) or could be different (two different dynamics from: full dynamics, error-clamp or null). The data clearly showed that the representation of dynamics for the two motions were not independent. To examine the coupling we fit a series of state-space models (both single-rate and dual-rate), which could either be independent for the CW and CCW motions or had elements that coupled the two processes (e.g., coupling the fast or the slow processes, or both between CW and CCW motions). Model comparison suggested that the processes associated with the CCW and CW were linked through the learning rate, leading to a coupling of



both the fast and slow processes. For example, the fast and slow processes associated with the CCW motion were mainly driven by the errors experienced in CCW direction, but also partially influenced (~10%) by the errors experienced in CW direction, and vice versa. Our results suggest that in cyclical motions during object manipulation, the dynamic representations between two recurrent actions interact, and are coupled through the rate with which error feedback drives adaptation.

4-F-35 Fronto-parietal networks are associated with multi-day savings in visuomotor adaptation

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Humans are able to adapt their behavior to changing environmental or internal demands, enabling us to engage in appropriate sensorimotor performance. Mechanisms underlying such adaptation learning to changing sensory input, such as force field or visual perturbations, have been investigated extensively at both the behavioral and neural level, revealing important insights into how people adaptively modify motor control. Interestingly, several studies have shown that retention of the learned information can outlast the training session, and that adaptation learning can lead to the formation of long-term memories (i.e., those lasting 24h or more). However, not much is known about the neural mechanisms that are involved in multi-day adaptation and retention. The present study therefore aimed to I) identify changes in neural activation that occur over the time course of multiple days of adaptation learning, and II) identify individual neural predictors of sensorimotor memory retention. We collected functional magnetic resonance imaging (fMRI) data from 16 participants (12 males; mean age 40 years) while they performed a manual adaptation task, in which they moved a joystick to hit targets presented on a screen. Initially, they performed the task under normal visual feedback, but then had to adapt to 45 degree clockwise rotated feedback. Participants performed the task during four separate test sessions over a three-month period, allowing us to examine adaptation rates and savings at subsequent sessions (which were completed on average 11 days, 48 days and 86 days after the first session). At the behavioral level, participants' performance improved within each test session and learning rates increased over the sessions. Participants were less perturbed by the rotated feedback in later sessions compared to the initial test session, which reflects savings of adaptation learning. At the neural level, results showed that activation changed over the four test sessions in a variety of frontal, parietal, cingulate, and temporal cortical areas, as well as various subcortical areas. Interestingly, these areas mostly showed activation increases rather than decreases. Furthermore, we found that retention of adaptation learning was associated with the extent of activation in frontal cortical areas including the bilateral middle, medial and superior frontal gyri, as well as parietal and cingulate cortical areas including the bilateral precuneus and anterior cingulate gyrus. These findings suggest that participants may be learning how to better engage cognitive processes across days, potentially reflecting the improvements in action selection that have been shown to occur with savings.

4-F-36 Individual variability in sensorimotor network functional connectivity correlates with the rate of early visuomotor adaptation



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Sensorimotor adaptation is a type of procedural motor learning that enables individuals to preserve accurate movements in the presence of external or internal perturbations. Sensorimotor adaptation can be divided into an early, more cognitively demanding stage, and a later, more automatic stage. In recent years, several investigations have identified significant associations between sensorimotor adaptation and brain structure and function. However, the question of whether individual variability in functional connectivity strength is predictive of sensorimotor adaptation performance has been largely unaddressed. In the present study, we investigate whether such variability in early sensorimotor adaptation is associated with individual differences in resting-state functional connectivity. We used resting state functional magnetic resonance imaging (rs-fMRI) to estimate functional connectivity strength using hypothesis-driven (seed-to-voxel) and hypothesis-free (voxel-to-voxel) approaches. For the seed-to-voxel analysis, we selected several regions of interest from sensorimotor and default mode networks of the brain. We then correlated these connectivity measures with the rate of early learning during a visuomotor adaptation task in 16 healthy participants. For this task, participants lay supine in the MRI scanner and moved an MRI-compatible dual axis joystick with their right hand to hit targets presented on a screen. Each movement was initiated from the central position on the display screen. Participants were instructed to move the cursor to the target as quickly as possible by moving the joystick, and to hold the cursor within the target until it disappeared. Performance was assessed by measuring direction error, defined as the angle between the line from the start to the target position, and the line from the start to the position at peak velocity. Each participant's rate of learning was determined by calculating the slope of direction error across adaptation trials. This slope was used as the primary outcome measure for the rate of early adaptation. Seed-to-voxel results revealed that bilateral putamen and bilateral insular cortex connectivity strength were correlated with the rate of early adaptation, such that faster learners exhibited greater connectivity strength than slower learners. Furthermore, voxel-to-voxel results indicated that left insular cortex connectivity and right postcentral gyrus connectivity were correlated with the rate of early adaptation, such that faster learners exhibited greater connectivity strength within left insular cortex and weaker connectivity strength within right postcentral gyrus. These results demonstrate that the rate of learning during the early stage of visuomotor adaptation is associated with sensorimotor network functional connectivity strength. The findings from this study provide novel insights into the neural processes underlying individual variability in early sensorimotor adaptation.

4-F-37 Movements of avatar in virtual reality can elicit sense of agency

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As an important component of self-awareness, sense of agency (SOA) refers to experiencing oneself as the author of one's action. Studies on rubber hand illusion and its virtual-reality (VR) variants demonstrate that body ownership, another part of self-awareness, can be transferred to external objects or virtual effectors (e.g. Botvinick & Cohen, 1998; Ehrsson, 2004). However, whether sense of agency can be similarly attributed to avatar in VR has never been rigorously examined (Ma et al., 2015). Here we use intentional binding, a well-established implicit measure of SOA, to study whether movements of an avatar can trigger SOA after sensorimotor experience in VR. Participants wore a head-mounted display (HMD, Rift DK2, Oculus) and a data glove (Perception Neuron, Noitom), which measured their upper arm movements. They were immersed in a virtual environment with a first-person perspective and a gender-matched virtual body. The experiment consisted of a pretest, an exposure phase and a posttest. In the pretest and posttest, we measured intentional binding with the Libet clock (Haggard et al., 2002). When a voluntary action is followed by a delayed action outcome, people's estimate of the outcome timing is biased towards the action. In our experiment, participants observed their avatar's right hand press a lever and received a vibrotactile stimulus delivered to their own left hand 250ms later. They were asked to report the time of the stimulus. The bias was computed by comparing this estimate to the estimate from a baseline condition without the avatar's action. During the 25-min exposure phase, participants (n=18; Test group) perform two aiming tasks by moving their upper limb while the avatar arm matched the real arm continuously and simultaneously. Another participant group (n=18; VR-Control group) went through the same procedures except that the avatar was not shown during exposure. We recruited a third group (n=11; Reality-Control group) performed the intentional binding task with their real hand and without HMD. We found that intentional binding was stronger after exposure (-71.1 ± 15.6 and -121.7 ± 15.1 ms before and after, respectively) in Test group. This exposure effect was absent in VR-Control group as no significant difference was detected before and after exposure (-82.73 ± 24.01 and -82.84 ± 21.31 ms, respectively). Interestingly, the size of the intentional binding in Test group was comparable to that of Reality-Control group (-125.2 ± 25.1 ms). Hence, similar to bodily ownership, SOA can also be attributed to virtual identities after a short period of immersive VR experience. Our novel behavioral paradigm offers an opportunity to further elucidate the cognitive and neural mechanisms of self-consciousness. As VR is extensively used in motor control as a surrogate of real environment, our findings intriguingly suggest that virtual body or virtual representation of the body might dynamically affect SOA and its related sensorimotor control processes.

4-F-38 Paired Transspinal and Transcortical Stimulation: A Novel Method for Targeted Cortical and Spinal Neuroplasticity

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The CNS has an extraordinary capacity to change the structure and organization of its neural circuits. One mechanism involves modifications to the strength of neuronal connections through synaptic plasticity. Experimentally, neuronal plasticity at the synapses can be induced by delivering repeated, paired pre- and post-synaptic stimuli. We assessed, for the first time, whether paired transspinal and transcortical stimulation induces persistent changes in cortical, corticospinal, and spinal neuronal excitability when the stimuli are delivered at precise interstimulus intervals for 40 minutes. Paired



transspinal and transcortical stimulation was delivered at interstimulus intervals in which transcranial magnetic stimulation (TMS) was delivered before (transcortical-transspinal PAS) or after (transspinal-transcortical PAS) transspinal stimulation. Before and after paired transspinal and transcortical stimulation, we established 1) amount of intracortical inhibition and intracortical facilitation upon paired TMS with the conditioned TMS delivered at 0.8 (tibialis anterior) TA motor evoked potentials (MEP) resting threshold at interstimulus intervals of 2, 3, 4, 10, 15, and 30 ms, 2) TA MEPs recruitment input-output curves 3) low-frequency homosynaptic soleus H-reflex depression and 4) soleus H-reflex recruitment curves. Transspinal-transcortical PAS decreased intracortical inhibition, potentiated intracortical facilitation, and decreased the stimulus intensity corresponding to MEP-threshold based on the sigmoid function fitted to the TA MEP recruitment curves for each subject. Furthermore, based on the sigmoid function fitted to the soleus M-wave and H-reflex recruitment curves for each subject, transspinal-transcortical PAS decreased the M-wave slope and the stimulus intensities corresponding to M-wave threshold, intermediate and maximal intensities, and decreased the predicted Hmax. Lastly, it decreased the soleus H-reflex homosynaptic depression. Transcortical-transspinal PAS did not affect the amount of intracortical inhibition or intracortical facilitation and TA MEP recruitment input-output curves remained unchanged. Based on the sigmoid function fitted to the soleus M-wave and H-reflex recruitment curves for each subject, transcortical-transspinal PAS decreased the stimulus intensities needed to evoke M-waves at 50 % of maximal M-waves and decreased the predicted Hmax, slope and stimulus intensities corresponding to H-reflex threshold and 50 % of maximal H-reflex. Further, transcortical-transspinal PAS decreased the predicted Hmax, H-reflex slope and stimulus intensity corresponding to H-reflex threshold. There were no significant effects on the soleus H-reflex homosynaptic depression. Our findings reveal that this novel method has distinct effects on cortical, corticospinal, and spinal neuronal circuits, and can be used to induce targeted neuroplasticity. This work was supported by The Craig H. Neilsen Foundation and NYSDOH.

4-F-39 Towards use of TMS as a clinical tool to assess plasticity

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Neuroplasticity is believed to be critical for neurorehabilitation. One way to assess neuroplasticity is to use transcranial magnetic stimulation (TMS) to measure corticospinal excitability (CSE). Traditionally, three different methods have been used to explore changes in CSE, (1) Single motor evoked potentials (MEPs) at fixed stimulus intensity; (2) stimulus-response (SR) curves and (3) TMS CSE maps. Whereas both SR curves and TMS maps provide much more information than a single set of MEPs at fixed intensity, their use is restricted by the time it takes to acquire the data (typically 10-15 min). This restricts the use of SR curves and TMS maps to the laboratory environment. However, we recently demonstrated that data to construct SR curves and TMS maps can be acquired in less than two minutes (Mathias et al., 2014, van de Ruit et al., 2015). This was achieved by reducing the interstimulus interval (ISI), optimising the number of stimuli and pseudorandomising the stimulation intensity (for SR curves) or stimulation position (for TMS maps). A biphasic Magstim Rapid2 stimulator allowed the use of ISIs shorter than the 2-4 s that is routinely used to deliver stimuli. We have demonstrated that reliable SR curves may be acquired with an ISI of 1.5-2 s and 80 stimuli.



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However, the number of stimuli required to produce a good curve is highly variable, ranging from 30-100. To overcome this variability a graphical user interface has been developed that allows online visualisation of the SR curve during data acquisition, enabling the number of stimuli to be optimised for each individual. For the TMS map, ISI is restricted by skill and experience of the researcher as the coil needs to be moved across the motor strip. We have demonstrated that 80 stimuli are sufficient to construct a reliable and repeatable TMS map and the ISI can be as short as 1 s with a skilled user. Similar to the SR curve, the number of stimuli to produce a map varies from 20-90. In both cases, we have demonstrated that reducing the ISI does not cause any accumulating effects on CSE with such a limited number of stimuli. Alongside presenting these novel methods we will demonstrate the methods are successful in studying changes in CSE. As an example, SR curves and TMS maps can be successfully used to study use-dependent plasticity following a single session of learning a visuomotor tracking task. For clinical applicability of the methods it is important patients can tolerate the rapid stimulation. Preliminary evidence will be provided that rapid acquisition of SR curves can also reliably be used to study CSE in stroke patients. These results demonstrate rapid acquisition of TMS measures is possible in motor control experiments but importantly also brings the use of TMS to study plasticity clinically and guide rehabilitation a step closer.