

# 28th Annual Meeting



Society for the  
Neural Control  
of Movement

## Santa Fe, New Mexico

Hilton Santa Fe Buffalo Thunder

**Satellite Meeting  
April 30, 2018**

**Annual Meeting  
May 1–4, 2018**

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# 2018 At-A-Glance Satellite and Annual Meeting Schedule

Hilton Santa Fe Buffalo Thunder



Society for the  
**Neural Control of Movement**

Time	Sunday	Monday	Tuesday	Wednesday	Thursday	Friday
	29-Apr	30-Apr	01-May	02-May	03-May	04-May
8:00	Arrivals, Free Time	Registration / Information Desk Open	Registration / Information Desk Open	Registration / Information Desk Open	Registration / Information Desk Open	Registration / Information Desk Open
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17:00	Satellite Registration (17:00 - 19:00)					
17:15						
17:30						
17:45						
18:00	Satellite Drinks Reception Jernez Terrace (18:00 - 19:00)		NCM Board Meeting (17:30 - 20:30)	Free Time		
18:15						
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18:45						
19:00		Opening Reception Red Sage & Pool Patio (19:30 - 21:30)	Fire Side Chats Red Sage Patio	Fire Side Chats Red Sage Patio	NCM Pub Night The Draft Station in Santa Fe	Free Time
19:15						
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# NCM 2018 Poster Abstracts

## Poster Session 1

### A – Control of Eye & Head Movement

#### **1-A-1 Oculomotor Abnormalities in mTBI**

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Traumatic brain injury (TBI) is increasingly being recognized as a significant cause for problems affecting movement, balance, and spatial orientation (Hoffer et al., 2007; Hoffer et al., 2010), and vergence eye movements (Magone et al., 2014; Suhr et al., 2015). There can be problems with eye movements, eye-head-coordination, and visual-motor transformations underlying goal-directed movements. This can occur after multiple head trauma events, and in some cases this can be the result of a single mild TBI event. Also, there is evidence that symptoms can manifest years after the original trauma and become progressively worse over time. Effects of the natural aging processes probably interact with the pathophysiology resulting from TBI. This ongoing research is part of an effort to evaluate saccadic and pursuit eye movements during binocular viewing in mTBI. The general aim is to characterize the coordinated movement of the two eyes during changes in gaze (e.g., horizontal and diagonal saccades), to compare the eye velocity profiles of the two eyes in the presence of convergence, and to relate the velocity trajectories of the two eyes to vergence dysfunction in mTBI. For this presentation, the horizontal/vertical position and velocity of the left eye versus the right eye is being analyzed. Saccade targets are presented 5 to 25 degrees left/right of center and 5 to 15 degrees above/below center. Sinusoidal pursuit targets have 10 degree amplitudes at 0.15 to 0.60 Hz. For large saccade amplitudes there can be different velocities for the adducting eye versus the abducting eye in mTBI subjects who have convergence insufficiency or convergence excess. Furthermore, there can be a velocity asymmetry for rightward versus leftward saccades and for upward versus downward pursuit. The preliminary results show promise for characterizing binocular eye movements and pursuit asymmetries in mTBI. Further work will evaluate gaze in three dimensions where there are changes in vergence. The results could provide further insight into the underlying pathophysiology affecting the control of gaze in mTBI and suggest possibilities for evaluating vision therapy.

#### **1-A-2 The role of superior parietal-occipital cortex in human reach-to-grasp movement: TMS study**

Mariusz Furmanek<sup>1</sup>, Mathew Yarossi<sup>1</sup>, Luis Schettino<sup>2</sup>, Sergei Adamovich<sup>3</sup>, Eugene Tunik<sup>1</sup>

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Reach-to-grasp movements are thought to be comprised of two components: a transport component that brings the hand to the object, and a grasp component, which involves the shaping of the fingers for object interaction. It is thought that these aspects of control are mediated in parallel by separate parieto-frontal cortical streams. Although much effort has been expended in investigating the neural correlates underlying control of grasp, relatively little is known about the brain areas involved in processing the transport component. The goal of this study was to causally test the role of the superior parietal-occipital cortex (SPOC) in mediating the transport component of reach-to-grasp. Four healthy



right-handed subjects ( $26.5 \pm 6.4$  years old), after providing informed consent, performed reach-to-grasp movements in a virtual environment. Movements were performed in unperturbed conditions toward a 3.6 cm (small) or 7.2 cm (large) virtual object located either 24 cm (near) or 36 cm (far) from the starting hand position. For a minority of the trials (25%), either the object size (small-to-large) or distance (near-to-far) was unexpectedly perturbed (100 ms after movement onset) requiring subjects to make online compensatory responses in the transport and grasp. Transcranial magnetic stimulation (TMS) was used to perturb processing in SPOC (50% of trials) at the time of object perturbation. Movement kinematics of the grasp aperture and wrist transport were analyzed with two separate 2-way rmANOVAs:  $2 \times 2$  (TMS, noTMS  $\times$  distance perturb, size perturb) and  $2 \times 3$  (TMS, no TMS  $\times$  small near, small far, large near). As expected, preliminary results in the no-perturbation trials revealed a significant main effect of condition ( $F(2, 6) = 37.3$ ,  $p = 0.001$ ), but no effect of TMS, and no interaction, suggesting that while grasp and transport were scaled appropriately to different object sizes and distances, TMS to SPOC did not disrupt the execution of movements when updating was not required. Notably, in the object-perturbed condition, there was a significant main effect of TMS ( $F(1, 3) = 49.2$ ,  $p = 0.006$ ). This was attributed to a 9.5% increase in the peak velocity in the distance perturbation, and a small 5% increase in peak velocity for the size perturbation. Our preliminary data suggest that SPOC may be involved in mediating the transport component, and perhaps to a smaller degree the grasp component, of reach-to-grasp actions. Ongoing experiments are testing this in a larger sample size, and pinpointing the timing of SPOC involvement by applying TMS at different delays after the object perturbation.

### **1-A-3 Role of the superior colliculus-pulvinar pathway in blindsight**

Tadashi Isa<sup>1</sup>, Masaharu Kinoshita<sup>2</sup>, Rikako Kato<sup>1</sup>, Kenta Kobayashi<sup>3</sup>, Kaoru Isa<sup>1</sup>, Kazuto Kobayashi<sup>4</sup>, Hirota Onoe<sup>1</sup>

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In patients with visual cortical damage, residual vision can guide goal-directed movements to targets in the blind field without awareness, the phenomenon termed 'blindsight'. The neural mechanism of blindsight is controversial. There is an agreement on the critical role of superior colliculus as the input node, however, as for the thalamic relay of the visual signals to the extrastriate cortex, some literature proposed pulvinar and others claim the lateral geniculate nucleus (LGN). Here, we directly tested the role of SC to ventrolateral pulvinar (vLPul) pathway in unilateral V1-lesioned monkeys, the animal model of human blindsight. First, pharmacological inactivation of vLPul impaired visually guided saccades in the blind field. Next, selective and reversible blockade of transmission through the SC-vLPul pathway by combination two viral vectors, reduced success ratio of saccades. These results claim contribution of SC-vLPul pathway to blindsight. Discrepancy in the arguments would be due the extent of cortical lesion and successive retrograde degeneration of LGN.

### **1-A-4 Head movements towards spatiotemporally separated sound sources**

Guus Bentum<sup>1</sup>, John van Opstal<sup>1</sup>, Marc van Wanrooij<sup>1</sup>

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Humans localize sounds in the horizontal plane by use of interaural timing and level differences. Localization is a sensorimotor process, as humans actively localize sound sources through goal-directed eye-head movements. Sources that are in close temporal proximity are often not identified as separate, typically, favoring the leading sound over the lagging sound, a phenomenon called the 'precedence effect'. These findings contrast with the visoumotor system, which uses spatial maps to initiate orienting

motor commands. Studies show that a lead-lag delay between two sources (one of the key parameters influencing perceptual source separation) above 16ms allows normal-hearing participants to adequately separate sounds. Here, we investigate the combined effect of delay, stimulus duration and spatial separation in free-field localization of double sounds in the horizontal plane. We present localization data from normal-hearing participants who made one or two successive goal-directed head movements towards one or two perceived sound locations. We show that, in contrast to earlier studies, the human audiomotor system needs a delay of at least 80 ms to discriminate two sources in more than 75% of all trials. We observe that participants can make two successive goal-directed head movements for stimuli as short as 3 ms at various spatial separations. Double target localization performance was significantly poorer than single target localization for all conditions. However, we observe an improvement in localization performance as delay time increases. We conclude that localization, as performed by the audiomotor system, is subject to a temporal window that is greater than previously assumed.

### **1-A-5 The Activity of Simple and Complex Spikes in the Vestibular Purkinje Cells is Attenuated During Self-Generated Head Movements**

Omid Zobeiri<sup>1</sup>, Kathleen Cullen<sup>1</sup>

*<sup>1</sup>Johns Hopkins University*

The cerebellum, a structure that is well-conserved across vertebrates, has been suggested to drive sensory-prediction error-based motor learning. Cerebellar Previous findings showed that neurons in the most medial of the deep cerebellar nuclei - the rostral fastigial nucleus (rFN) - are significantly more sensitive to passively-applied compared to self-generated head movements. Further, during motor learning, the sensitivity of rFN neurons is modulated in a manner consistent with the computation of vestibular sensory prediction error. Purkinje cells are the only output of the cerebellar cortex, which send projections to the target neurons in the deep cerebellar nuclei or the vestibular nuclei. Here, to investigate the neuronal basis of these computations, we recorded from Purkinje cells in the cerebellar cortex, which project to the rFN neurons. Single unit extracellular recording was made from Purkinje cells in the cerebellar cortex (Nodulus/Uvula) from rhesus monkeys, during self-generated (active) and externally-generated (passive) head movements. Simple and complex spikes from Purkinje cells were detected via an automated clustering algorithm and sensitivity of each neuron to the head movement was computed using dynamic linear regression method. Analysis of neuronal responses during passive motion first revealed robust simple spike responses to head motion that were either bi or unidirectional. In comparison, simple spike responses during comparable active head motion were markedly attenuated. Moreover, analysis of the complex spike activity during passive and active head movement conditions showed temporal binding between complex spikes and the onset of passive head movement, while fewer complex spikes were present during active head movements and temporal binding was less evident. Taken together, we conclude that both rate and temporal coding of the simple and complex spike responses of Purkinje cells are less robust during active than passive head movements.

## **B – Fundamentals of Motor Control**

### **1-B-6 Dissociation between temporal expectancy and spatial precueing in the neural dynamics of goal-directed movement preparation**

Cesar Canaveral<sup>1</sup>, Frederic Danion<sup>2</sup>, Pierre-Michel Bernier<sup>1</sup>

*<sup>1</sup>Universite de Sherbrooke, <sup>2</sup>CNRS & Aix-Marseille University*

The time necessary to initiate goal-directed reaching movements depends on knowing where and when to move. It is well documented that providing advanced information regarding either the spatial location

of a target stimulus or its timing of occurrence reduces reaction times (RT). Accumulating evidence associates theta- (3-7 Hz) and beta-band (15-25 Hz) oscillatory activity over motor regions to movement planning, yet it is unknown whether the RT gains attributable to spatial precueing and temporal expectancy are associated with similar modulations in these frequency bands. To address this issue, an instructed-delay reaction-time task was designed in which participants ( $n=15$ ) reached as fast as possible toward appearing visual targets following a constant or a variable foreperiod (FP), which was preceded by an informative precue. Electroencephalography (EEG) was recorded throughout the experiment. In the FullCue condition, participants were precued regarding the target location (i.e. straight-ahead) and the FP was constant at 2s. In the SpatialCue condition, participants were precued regarding the target location, but the FP was variable (i.e. 1.25, 2 or 2.75s). In the TemporalCue condition, participants were not precued regarding the target location (i.e. left, straight-ahead or right), but the FP was constant at 2s. Finally, in the NoCue condition, participants were not precued regarding the target location and the FP was variable. RTs as well as theta- and beta-band power over motor regions late in the preparatory period (300ms prior to target appearance) were submitted to repeated-measures ANOVAs with Spatial precueing (one vs. three targets) and Temporal expectancy (constant vs. variable FP) as factors. RT analysis revealed both a main effect of Spatial precueing and a main effect of Temporal expectancy ( $p < 0.001$  for both effects) with no interaction ( $p = 0.14$ ). Specifically, RTs were 32ms faster when spatially precued and 15ms faster with a constant FP. Theta-band power late in the preparatory period revealed only a main effect of Spatial precueing, with power over mid-frontal electrodes being greater when spatially precued. In contrast, beta-band power revealed only a main effect of Temporal expectancy, with power over contralateral motor electrodes being lesser (i.e. more desynchronization) with temporal expectancy. These results demonstrate that although spatial precueing and temporal expectancy both incur RT gains, they are subtended by different preparatory dynamics. The modulation of different frequency bands for spatial precueing and temporal expectancy supports recent evidence suggesting that movement preparation is independent of movement initiation. Theta-band activity may relate to the representation of a movement vector (i.e. preparation), whereas beta-band desynchronization may index the release from inhibition necessary for movement initiation.

### **1-B-7 Neurophysiological correlates of speech motor control**

Adithya Chandregowda<sup>1</sup>, Yael Arbel<sup>2</sup>, Emanuel Donchin<sup>3</sup>

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The project was aimed at elucidating the event related potentials (ERPs) associated with speech production with the overarching goal of contributing to the study of typical and atypical speech motor control. Multichannel electroencephalographic recordings were obtained when participants engaged in a speaking (saying the word "pool") and no-speaking (withholding from saying the word "pool") paradigm. Data from twenty-one right-handed participants (11 females) were subjected to a spatio-temporal principal component analysis (PCA). Two ERP components emerged from the PCA as distinguishing between the speaking and no-speaking conditions: a posterior negative component and a left lateralized positive component. The morphology of the posterior negative component, as well as the correlation of its magnitude with speech response time, suggests that this component is a possible index of speech motor preparation. Further research is required to determine the functional significance of the left-lateralized component.

### **1-B-8 The cost to move affects gaze-limb coordination**

F. Javier Domínguez-Zamora<sup>1</sup>, Daniel Marigold<sup>1</sup>

<sup>1</sup>*Simon Fraser University*

In many of our everyday tasks, motor decisions are affected by the cost to move (hereafter defined as motor cost). For example, when reaching to different objects, we tend to choose the least costly trajectory. Similarly, during walking, we usually select a step length and width that minimizes the energetic cost of foot placement and the overall walking pattern. However, moving optimally is not always an option in cluttered environments. In this situation, vision is particularly important to facilitate the selection of where to move our limbs. Does this imply a link between gaze and motor cost? Here, we determined whether motor cost affects the spatial-temporal pattern of gaze for the purposes of planning and controlling visuomotor behaviours. Subjects (N=5) performed a visually guided walking task that required them to walk across the lab while stepping on the centre of four projected targets in sequence. To create six different levels of motor cost, we manipulated the step vector on a trial-to-trial basis by shifting the second or third stepping target from the established preferred step width. These step widths were equal to 0.13 (the preferred step width and approximate minimal metabolic cost), 0.26, 0.39, 0.52, 0.65, and 0.78 fraction of leg length. We used a motion capture system to track limb and body movement and a high-speed, head-mounted mobile eye tracker to measure gaze. To compare differences in motor performance and gaze behaviour between motor cost conditions we used one-way ANOVAs. Our data show that subjects maintained the same level of foot-placement accuracy, defined as the vector distance between the foot and the middle of the target, across all step motor costs. To determine differences in the visuomotor planning before limb movement initiation, we identified the time interval between a saccade made to a target and toe-off of the foot about to step to the same target. In addition, we defined the online visual guidance of limb trajectory as the time interval between a saccade away from a target and heel contact on that same target. Our data show that subjects made a saccade away from the target they were about to step on sooner when encountering the lowest two motor cost targets compared to the highest two cost targets ( $p = 0.001$ ). However, we found no differences among motor cost conditions in the timing of gaze shifts to the target prior to limb movement initiation. Taken together, our results suggest that subjects adapted to larger lateral foot displacement, or greater motor cost, by increasing the visual online control of the limb to maintain foot-placement accuracy. This suggests that gaze behaviour is sensitive to motor cost, and that people can readily adjust their gaze patterns to ensure movement accuracy in cluttered environments. Funded by: NSERC Canada

### **1-B-9 Plan, Initiate, Execute: The Invigorating Role of the Motor Thalamus**

Matt Gaidica<sup>1</sup>, Daniel Leventhal<sup>1</sup>, Amy Hurst<sup>1</sup>, Chris Cyr<sup>1</sup>

<sup>1</sup>*University of Michigan*

Motor thalamus (Mthal) is a group of subcortical nuclei that receive input from the basal ganglia (BG), cerebellum (CB) and motor cortical structures. How these signals are integrated in Mthal to influence behavior remains unclear. To identify the behavioral correlates of Mthal activity, we recorded single units in rats performing a forced choice task. In this task, a pure tone instructed the rats to quickly initiate movement to the left or right depending on the pitch of the tone. A large fraction of Mthal units were modulated briefly around movement onset and segregated into two functionally distinct groups. "Initiation" unit activity was tightly locked to the tone, did not encode movement direction, and predicted the latency from the tone to movement onset (reaction time, RT). "Execution" unit activity was modulated around movement onset, encoded action selection, and predicted both RT and how



quickly the movement was completed. In contrast to "rate" models of BG-Mthal interactions, behavior-correlated changes in Mthal activity were transient, returning to baseline before movement completion. In conclusion, our study suggests that Mthal plays a critical role in ballistic movement by signaling when to move, how vigorously to move, and in what direction to move. Furthermore, these brief signals occur transiently near movement initiation, as if triggering a pre-set motor plan. Ongoing work is aimed at determining whether these functionally-defined Mthal units correspond to distinct anatomically-defined populations.

### **1-B-10 Neural and behavioral signatures of motor skill in the wild**

Shlomi Haar<sup>1</sup>, Ines Rito-Lima<sup>1</sup>, Pavel Orlov<sup>1</sup>, Aldo Faisal<sup>1</sup>

<sup>1</sup>*Imperial College London*

Most of the research into neural control movement is conducted in the lab under highly controlled conditions, and therefore little is known about the brain activity underpinning motor control in the wild. Even less is known about the neural responses related to performance of motor expertise by highly skillful experts in challenging settings. Here we are looking into the neural responses and body movements in the wild while a professional race car driver is driving in extreme conditions. Our driver, a Formula E champion, drove an Audi R8+ (610hp) on the Top Gear race track, Dunsfold Aerodrome, Surrey (UK), under bad weather conditions (wet/icy road), while the driver assistance systems on the car were turned off. We recorded his 32ch EEG brain activity, his eyes movements, and his hand and foot movements while driving. The car was equipped with a GPS system and a road and cabina camera. Timestamp synchronization was performed across all data streams. The video recordings from inside the car and the head mounted egocentric camera were used to annotate the data and detect events of car drifts and loss of control. This annotation was validated by the inertial data from the sensors on the driver's limbs which enable analysis of the abruptness of both hand and foot movements. Previous studies have recorded EEG activity during driving, in simulators and in the wild, but these studies focused on the drivers' attention and vigilance, not on their motor control. Here, driving is simply the motor skill on which we study neural and behavioral aspects of motor control of a highly skillful individual while practicing his expertise. The extreme driving conditions induced multiple unexpected events (drifts and loss of control) in which the skill of the driver had to come into play, to regain control of the car. On those segments we looked for unique patterns of eye movements, hand movements, and brain activity. We looked at the reproducibility of those patterns and at the timing of their emergence. We also looked at the speed of the response - from the initiation of the neural response to the motor outcome, and compared this difference to those of regular drivers, as reported in the literature. Understanding how the brain and consequently the body of a professional race driver, who is an expert in making fast and accurate motor responses, operate under extreme conditions can provide new insights to human motor control mechanisms and motor expertise. Additionally, it can be used to improve applications of neuroergonomic driving assistance and autonomous cars and their safety procedures.

### **1-B-11 Sensorimotor oscillatory power shapes rhythmic fluctuations in human corticospinal excitability**

Sara Hussain<sup>1</sup>, Leonardo Claudino<sup>1</sup>, Marlene Boenstrup<sup>1</sup>, Gina Norato<sup>1</sup>, Christoph Zrenner<sup>2</sup>, Ulf Ziemann<sup>2</sup>, Ethan Buch<sup>1</sup>, Leonardo Cohen<sup>1</sup>

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Neuronal networks exhibit oscillatory activity that influences brain function across cognitive domains. In

the motor system, oscillatory activity occurs predominantly within the mu (8-12 Hz) and beta (13-30 Hz) bands, but the precise contributions of these rhythms to human motor function is not well understood. Here, we investigated the influence of sensorimotor mu and beta oscillatory phase and power on human motor function, measured non-invasively as corticospinal excitability. Single-pulse TMS was delivered to the scalp hotspot for the right first dorsal interosseous at 120% of resting motor threshold during concurrent EEG recordings in healthy volunteers. To isolate sensorimotor rhythms originating from right motor cortex, data recorded from the C4 sensor (approximately overlying the stimulated right motor cortex) were Hjorth-transformed (central: C4; surround: FC2, FC6, CP2, and CP6). The instantaneous oscillatory phase in the mu and beta bands was estimated at the time of TMS delivery, and pre-stimulus power in each band within 150 ms preceding TMS was also determined. The influence of sensorimotor oscillatory phase, power and their interaction on MEP amplitudes was subsequently evaluated using separate trial-by-trial linear mixed-effects models for each frequency band. For mu activity, there was a significant PHASE x POWER interaction ( $p=0.001$ ), indicating that the magnitude and direction of phase-dependent MEP amplitude modulation varied depending on pre-stimulus mu power. This was evident as a significantly more positive relationship between pre-stimulus mu power and MEP amplitudes for mu trough relative to peak trials (slope for peak trials =  $-0.001$  [95% CI =  $-0.029 - 0.027$ ]; slope for trough trials =  $0.063$  [95% CI =  $0.034 - 0.090$ ]). 16 of 18 subjects showed a positive relationship between pre-stimulus mu power and MEP amplitudes at mu troughs, whereas 9 of 18 showed a positive relationship between pre-stimulus mu power and MEP amplitudes at mu peaks. Overall, MEP amplitudes were largest at mu troughs during periods of high power. For beta activity, there was a significant main effect of POWER ( $p=0.007$ ), revealing a significant positive association between pre-stimulus beta power and MEP amplitudes regardless of beta phase. At the individual subject level, 11 and 12 of the 18 subjects showed positive relationships between pre-stimulus beta power and MEP amplitudes at beta peaks and troughs, respectively. Corticospinal excitability was highest at mu troughs when mu power was also high, and during strong beta rhythms independent of beta phase. These results support the view that sensorimotor rhythms dynamically gate corticospinal excitability, producing windows of opportunity during which motor function is transiently enhanced.

### **1-B-12 Motor cortical changes in preparation for self-paced actions investigated with combined Transcranial Magnetic Stimulation and Electroencephalography**

Jaime Ibanez<sup>1</sup>, John Rothwell<sup>1</sup>, Lorenzo Rocchi<sup>1</sup>, Ricci Hannah<sup>1</sup>

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From seconds before a voluntary action is initiated, preparatory changes can be observed in motor-related cortical areas either by recording the endogenous ongoing brain activity or by probing its responses to external stimuli. In humans, transcranial magnetic stimulation (TMS) of the motor cortex during motor preparation allows the analysis of changes in excitability of circuits projecting to the corticospinal tract. A convenient strategy used in TMS experiments to study cortical changes during the final part of motor preparation is to use reaction time paradigms or variations thereof. Under such conditions, a bimodal evolution of motor cortical excitability can be seen, with an originally unexpected initial phase of cortical inhibition (~200ms before muscles activate) the functional interpretation of which in relation to the subsequent movement has been subject to extensive debate. A recurrent explanation for this inhibitory pattern is that motor cortical circuits are proactively controlled by higher entity structures that allow the preparation of movements, reducing the risk of generating unwanted premature responses. This interpretation is susceptible to be a consequence of the instrumental bias resulting from using highly time-constrained paradigms to probe evolutions in cortical excitability. We

present results from 15 subjects performing self-paced movements with their index finger, while motor cortical excitability is probed with single-pulse TMS during the rest intervals preceding the voluntary actions. The timing of the delivered TMS pulses was selected for each trial (the resting period before a movement) based on the previous intervals that subjects were leaving between movements. This way, a distribution of TMS readings with boosted densities along time points just preceding the movements could be obtained. We used a group level analysis combined with bootstrap statistics of the continuum of TMS motor evoked potentials measured before the self-paced movements. The test returned 2 intervals with significant changes in excitability: (1) an initial (~150ms before the onset of muscle activity) inhibitory part resembling what is observed in cue-guided paradigms; and (2) a steep rise of excitability starting less than 100ms before muscle activity). Subsequently, we run a post-hoc analysis using a 2x2 rmANOVA with time intervals being a baseline period and the point of the trough of excitability before movements and assessing responses in the first dorsal interosseous muscle and a control (task-irrelevant) muscle. This test showed that inhibition was significantly present in both muscles tested with a strength similar to that described in the previous studies using cues. We also observed a speeding in the time to move chosen by subjects when TMS was delivered ~200ms before the expected execution. This could be related to an intersensory facilitation effect. Electroencephalography-based analysis of pre-movement patterns suggested that movements were performed in a natural self-paced manner when TMS was not delivered. These results challenge one of the most popular interpretations of pre-movement excitability changes in cortical activities and suggest further insight into the timing for becoming consciously aware of voluntary actions.

### **1-B-13 Transcranial direct current stimulation (tDCS) of SMA complex impacts the effectiveness of interleaved and repetitive practice schedule**

Taewon Kim<sup>1</sup>, David Wright<sup>1</sup>

<sup>1</sup>*Texas A&M University*

When learning multiple motor sequences concurrently there is evidence that an interleaved as opposed to repetitive presentation of these skills results in superior retention and generalization. In a recent review of this literature, Wright et al. (2016) noted that an interleaved practice schedule was frequently associated with earlier and more consistent recruitment of the supplementary motor area (SMA) compared to its repetitive counterpart. The latter finding is consistent with SMA being implicated in supervising the organization of complex motor sequences. The present work was an initial attempt to perturb the involvement of the SMA during the acquisition of a set of motor sequences in either an interleaved or repetitive practice environment. Specifically, participants were exposed to cathodal transcranial direct current stimulation (tDCS) at SMA of 2 mA during approximately 20-min of interleaved practice or anodal tDCS while practicing within a repetitive format. The basic hypothesis was that cathodal or anodal stimulation would suppress or facilitate the contribution of SMA during practice respectively. If this occurred, it was anticipated that suppressing SMA during interleaved practice should hinder performance during acquisition and retention. Conversely, facilitating SMA, via anodal stimulation, might enhance the effectiveness of repetitive practice resulting in gains in retention performance. Performance of three motor sequences in a repetitive format was administered prior to practice, and 6-hr, 24-hr, 48-hr, and 72-hr after the completion of practice for all participants. Results revealed the typical outcome for training and test performance for interleaved and repetitive practice conditions in sham tDCS conditions. As predicted, cathodal tDCS impaired performance during training for individuals that experienced an interleaved format whereas performance of the motor sequences in the repetitive training condition was enhanced via anodal stimulation. After 6-hrs, a time interval

offering an opportunity to consolidate across a wake-filled interval, participants exposed to interleaved training showed performance enhancement which was absent when this training format was paired with cathodal stimulation. Individuals trained in a repetitive format exhibited forgetting after the 6-hr period irrespective of the stimulation condition. However, participants in the repetitive practice condition that received anodal tDCS during practice exhibited continued performance improvement across the subsequent 3 days of tests at a rate similar to individuals in the interleaved practice conditions which in turn was superior to the rate of improvement of the repetitive condition not afforded stimulation. These data suggest a complex interplay between motor training, exogenous stimulation, and sleep for the ongoing motor sequence learning.

#### **1-B-14 Long-latency reflexes to on-axis and off-axis displacements increase with the target approach consistent with optimal feedback control**

Isaac Kurtzer<sup>1</sup>, Frederic Crevecoeur<sup>2</sup>, Puneet Cheema<sup>1</sup>, Ryan Antonawich<sup>1</sup>, Tetsuro Muraoka<sup>3</sup>

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The long-latency reflex (LLR) is an important window into the organization of feedback control since it is the fastest corrective action through cerebral cortex. Previous studies demonstrated that the LLR is flexibly engaged during reaching movements, but were limited by simplifications inherent to a single-joint paradigm (no interaction torques) or mechanical complexities inherent in the multi-joint paradigm (changing arm dynamics with motion at distal joints). Here we examined reaching movements that primarily involve shoulder motion, the most proximal joint of the arm, while the elbow is free to move. With selective shoulder motion and the elbow actively stabilized against interaction torques, the mass distribution of the arm does not change. Thereby, we could examine the time-varying sensitivity of the LLR to displacements parallel or orthogonal to the unperturbed motion without the additional confound of time-varying arm dynamics. Two experiments were conducted and compared to the behavior of an optimal feedback controller. 12 subjects participated in each experiment (19-28 yro). A robotic device (BKIN Technologies) allowed horizontal motion about the shoulder and elbow and applied torques to the two joints. Surface EMG was obtained (Bortec Biomedical) from shoulder muscles. A projection system presented a hand-aligned cursor, start target, and goal target. Experiment 1 required 45° of shoulder extension. Experiment 2 required 45° of shoulder flexion. Torque pulses (95 ms) were randomly applied at four locations between the targets. They induced pure shoulder motion (1°/50 ms) or the same amount of hand motion in the orthogonal direction. LLRs were calculated as the mean activity 50-100 ms after perturbation onset. A linear model of the two-joint arm was constructed based on anthropometric measurements, first-order muscle dynamics ( $\tau$ : 60ms), a 50 ms sensory delay consistent with LLR, and sensory and motor noise. An optimal feedback control law and state estimator were derived to minimize a quadratic performance criterion penalizing kinematic and effort costs. The start target and end targets were the same as the human experiments. In both experiments, the shoulder flexor and extensor muscles expressed LLRs that monotonically increased as the target was approached. Upscaling of reflex sensitivity occurred to on-axis and off-axis displacements and was dissociated from the background tri-phasic pattern of muscle activity. The optimal feedback controller expressed the same patterns - steadily increasing feedback gain as the target is approached that dramatically differs from the phasic motor commands of the unperturbed movement. The linear optimal control model does not separately specify planned and corrective actions but a sequence of gains which minimize kinematic and motor costs. Our results indicate that LLR may support the gain sequence of an optimal feedback controller.

### **1-B-15 Revisiting the mesencephalic locomotor region: An interface between the basal ganglia and the spinal cord**

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Neurons of the mesencephalic locomotor region (MLR), including the pedunculo pontine nucleus (PPN) and the cuneiform nucleus (CUN) have traditionally been associated with locomotion, gait and control of posture, and constitute one of the main output pathways of the basal ganglia. In addition, electrical stimulation of the MLR induces an increase in muscle tone and initiation of locomotion that can be blocked by cholinergic and glutamatergic antagonists. These effects have been directly linked with MLR projections to the motor nuclei of the lower brainstem arising predominantly from glutamatergic neurons. Here, using anterograde conditional tracing in VGLUT2::Cre mice, we show that PPN and CUN have different projection patterns: glutamatergic neurons of the PPN send dense projections to the basal ganglia, the lower brainstem and the spinal cord, whereas glutamatergic neurons of the CUN preferentially target the upper brainstem. In addition, using conditional monosynaptic retrograde tracing based on a modified rabies virus transducing a fluorescent marker, we observed that glutamatergic neurons of the PPN have a larger number of inputs from the basal ganglia and motor cortex (M1) than the CUN. Optogenetic activation of M1 axons in the slice produced strong activation of glutamatergic neurons in the PPN but not CUN. In vivo head-fixed recordings of optogenetically-tagged PPN glutamatergic neurons revealed distinct functional subtypes, including neurons closely associated with muscle activity, and neurons that preferentially discharge during movement initiation. Our results provide a detailed integrative description of the different elements that compose the MLR and provide novel insights on their role in movement as an output station of the basal ganglia.

### **1-B-16 Causal relationships between EMG, EEG and fNIRS during isometric hand contractions.**

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Functional near-infrared spectroscopy (fNIRS) is a wearable, non-invasive brain imaging technique that can be deployed in unconstrained human motor control experiments. It offers a direct window to assess the neurorehabilitation of an infarcted cortical area with greater spatial resolution than Electroencephalography (EEG), but the signal is subject to variations which covary with movement. To this end, we collected a multimodal dataset (fNIRS + EEG + EMG + kinematics) during a ball-squeezing task. This task allows capturing functional data of muscle contraction with a reduced amount of movement artefacts affecting the remaining sensors. A preliminary analysis of our unique multi-modal data allows us to understand the temporal and spectral characteristics of each signal and their causal relationships. This gives insight into the construction of generative probabilistic state-space models that allow the reconstruction of movement related hemodynamic activity, free from confounding effects. Our advances promise to reduce in confounding effects that undermine the specificity of fNIRS signals boosting its suitability to study the neural mechanisms of goal-directed movement control in the wild, as well as monitoring neurorehabilitation and neurofeedback in the home.

### **1-B-17 Precisely estimating neural population dynamics in motor cortex using deep learning**

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The recent ability to monitor large ensembles of neurons has revealed that motor and premotor cortical neural populations collectively show emergent functional properties ("dynamics") that are not apparent at the level of individual neurons (Churchland et al., Nature 2012, Pandarinath et al., eLife 2015, Michaels et al., PLoS Comp Bio 2016; rev. in Shenoy et al., Ann Rev Neuro 2013). Such findings suggest that the computations performed by motor cortex can be described by the time-varying activity and interactions (i.e., dynamics) of a modest number of underlying latent factors. To-date, dynamics have been uncovered by averaging neuronal activity across trials in order to overcome the variability of neurons' single-trial responses. However, uncovering dynamic structure on a single trial, moment-to-moment basis is essential for illuminating the relationship between neural population activity and behavior, and for advancing therapeutic neurotechnologies such as closed-loop deep brain stimulation and brain-machine interfaces. Here we introduce Latent Factor Analysis via Dynamical Systems (LFADS), a novel deep learning method to uncover latent dynamics from single-trial neural spiking data. LFADS uses a nonlinear dynamical system (a recurrent neural network) to infer the dynamics underlying observed population activity and to extract "de-noised" single-trial firing rates from neural spiking data. This provides, for the first time, a method to accurately derive empirical models of a neural population's nonlinear dynamics based on observed data. We apply LFADS to a variety of monkey and human motor cortical datasets, and demonstrate its ability to: 1) extract precise, moment-to-moment estimates of neural dynamics on single trials; 2) predict observed behavioral variables (e.g., kinematics, reaction times) on millisecond timescales with unprecedented accuracy; 3) infer single-trial estimates of dynamic features previously seen only via condition-averaging (e.g., "rotational" dynamics); 4) predict activity for behavioral conditions (e.g., reach types) that were not used to train the LFADS model; 5) relate data from independent recording sessions, sampling separate neural populations across motor cortex and spanning 5 months of recording, via a single dynamical systems model, and in doing so improve decoding kinematics from individual trials all recording session; 6) infer perturbations to the motor cortical dynamical system in an unsupervised fashion, which we demonstrate by analyzing data from an arm-reaching task involving mid-trial perturbations. By leveraging cutting-edge machine learning techniques, LFADS provides a powerful new tool to uncover motor cortical dynamics and relate them to behavior. Further, as the fundamental assumption of LFADS is that data may be modeled by a dynamical system, its success in modeling the data and predicting behavioral variables lends strong evidence to support the dynamical systems view of motor cortical activity.

### **1-B-18 Temporal dynamics of reach-to-grasp: Evidence for sequential encoding.**

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In reach-to-grasp movements, reaching with the arm and grasping with the hand typically are thought to proceed concurrently. We recently observed, however, that neural control may be more sequential than previously thought, with a focus on location early and grasp shape later in the same movement. In two Rhesus monkeys performing reach-grasp-manipulate movements that dissociated the location to which the hand reached from the object the hand grasped, we simultaneously collected kinematics, EMG activity, and neural recordings from microelectrode arrays implanted in primary motor cortex (M1). We then examined these data using three separate analyses: i) time-varying ANOVA, ii) neural population space analysis, and iii) linear mixture models of neural encoding. Time-varying ANOVA was conducted on all three datatypes. The kinematics showed that joint positions from the shoulder to the digits varied first with the location after which the elbow, wrist, and digit joints all varied with the object being



grasped. Similarly, EMG recordings showed two distinct peaks. Early muscle activity was more related to location whereas the later activity was more related to object. The neural firing rates of most M1 units also were related initially to location and later to object. Interestingly, many of these neurons had firing rates and depths of modulation that were larger for the smaller amplitude movements of grasping than for the initial transport of the arm. Neural population space analysis was performed to explore the dimensionality and dynamics of the neural population. In this analysis, the simultaneous firing rate of all sampled M1 neurons constitutes a state which moves in time, forming a trajectory. We observed that the neural modulation that was specific to the location/object was only 1/3 as large as either the global task modulation or noise. For this location/object modulation, rather than large amplitude modulation in a fixed set of latent dimensions we instead observed progressive shifts of the latent dimensions, suggesting that location and object are encoded in the neural space by active dimensions that change progressively across time. Finally, we examined the relationship between neural encoding and movement kinematics by building mixtures of linear encoders that predicted individual neuron firing rates based on kinematics. Mixture models were compared to i) a single linear model global across all times, and ii) 20 sequential linear models each trained on only a single time point. The mixing of only two linear models predicted firing rates significantly better than a global linear model, with accuracy similar to the time-specific models. We saw no significant improvement with mixtures of more than two linear encoders, suggesting that a mixture of only two linear encoders was sufficient to describe the encoding of the reach-grasp-manipulate kinematics by M1 neurons. Our findings provide converging evidence that the neural control of reaching and grasping is sequential, with distinct features related to location early and then to object later. We hypothesize that such sequential encoding allows for efficient, coordinated motor control that is fast for the initial transport of the arm but also precise for the object manipulation.

### **1-B-19 Co-contraction improves control through neural feedback not muscle stiffness**

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Co-contraction is used when performing uncertain or unstable tasks. It has been assumed that the main impact of co-contraction is to directly increase muscle stiffness of agonist muscles [1]. However, there is evidence that increasing activation does not lead to decreases in limb motion following a mechanical disturbance [2]. How does co-contraction improve control? Subjects (N=11, ages 19-31) interacted with a KINARM Exoskeleton robot. Subjects maintained their fingertip in a target and a perturbation torque (5 Nm, 50 ms pulse) flexed or extended the elbow. The trial was successful if the subject returned their fingertip to the target in <500 ms and stayed in the target for 1000 ms. EMG was recorded for elbow flexors and extensors. Trials were performed with background loads of 1-5 Nm on flexors or extensors; or with no background load and muscles co-contracted to activity levels corresponding to 1, 3, and 5 Nm loads using visual feedback. The loading scenarios resulted in three experimental conditions: loaded muscles stretched or loaded muscles shortened by the perturbation and muscles co-contracted. The task success rate of the group increased 20% to 37% when co-contracting, and on an individual basis, 10 of the 11 subjects improved their performance when co-contracting (paired t-test,  $p < 0.01$ ). Initial limb motion was the same across all experimental conditions and at all levels of muscle activity. This motion was dominated by the inertia of the limb, not muscle stiffness. Kinematic differences between co-contraction and background load conditions, and at different muscle activity levels were observed after 50 ms. Co-contraction provided a faster corrective response to the perturbation, reducing peak elbow displacement up to 35% compared to background loading. Co-contraction also eliminated over-

correction when returning to the target. Additionally, increasing muscle activity produced a faster corrective response. Beyond 50 ms, neural feedback controlled the response of the limb. Under background loading the unloaded muscles did not contribute to control. When the loaded muscles were stretched, their excitatory response scaled with the level of pre-perturbation muscle activity. When the loaded muscles were shortened, their inhibitory response was limited by the level of pre-perturbation muscle activity. Under co-contraction, both the stretched and shortened muscles were used for control. We hypothesize that co-contraction exploits the reciprocal nature of the motor system to improve control by using both agonist and antagonist muscles. By increasing the pre-perturbation activity of both muscle groups, co-contraction provides the potential required for the inhibitory response of the shortened muscles without attenuating the excitatory response of the stretched muscles. This hypothesis can be tested using a computational model and feedback controller. [1] Franklin & Wolpert (2011) *Neuron* [2] Crevecoeur & Scott (2014) *PLOS Comp Bio*

### **1-B-20 Neural substrate for learning novel sensorimotor maps**

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One of the challenges in a new learning environment is to determine the correspondence between movements and sensory effects: a sensorimotor map. Map acquisition can be studied by monitoring participants as they learn an unknown mapping between previously largely unlinked modalities such as movements and sounds. Several studies have characterised this learning process behaviourally but the neural underpinnings remain unclear. In the present work participants learned an audiomotor map in the scanner by making movements to auditory targets using a joystick while their brain activity was measured using functional magnetic resonance imaging (fMRI). Before and after learning resting state brain activity was assessed to track the persistence of information learned during the task. Behaviourally it was observed that participants moved at random initially and then progressively improved their reaching performance, indicating that they were able to learn the mapping. Neural structures involved in the task were defined as those having larger signal during task than during rest and these formed a distributed network comprising cortical primary sensorimotor regions, supplementary motor area, superior parietal lobule, several foci in cerebellum, thalamus and the striatum. Frontal and parahippocampal regions showed lower activity during task than during rest. Changes in functional connectivity between these areas was assessed in subsequent resting state scans in relation to the amount of learning. Taken together, these findings characterise the brain areas that are involved in the earliest stages of learning novel sensorimotor maps and provide a first glimpse into how learned information is maintained when the task is no longer being performed.

### **1-B-21 Modeling neural population dynamics in motor cortex leads to improved kinetic decoding in unstructured motor task**

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Mounting evidence demonstrates that the activity of large populations of neurons in the motor cortex (M1) can be described quite accurately as a "dynamical system", with activity that is dependent, to a significant extent, on its own internal dynamics (Churchland et al., *Nature* 2012, Pandarinath et al., *eLife* 2015, Michaels et al., *PLoS Comp Bio* 2016). Recent theoretical and experimental work suggests that these dynamics may serve to produce muscle-like commands (Kaufman et al., *Nat Neuro* 2014, Sussillo

et al., Nat Neuro 2015, Russo et al., Neuron 2018). We recently demonstrated deep learning tools that can model the dynamics present in M1 of monkeys performing structured motor tasks (highly stereotyped reaches, consistent task timing, a single starting position), and further, that modeling dynamics dramatically improved our ability to decode reaching kinematics (Pandarinath et al. 2017, preprint in BioRxiv). Here we tested whether M1 dynamics could be modeled in motor tasks that lack consistent structure, and further, if modeling these dynamics could improve kinetic decoding accuracy (i.e., muscle activation). We analyzed spiking activity of ~150 neurons recorded in M1 while a monkey performed a random target task, together with electromyographic (EMG) activity from 10 muscles (Cherian et al., J Neurophys 2011). In this task, the monkey moved a planar manipulandum in order to steer an on-screen cursor to rapidly navigate three-target sequences. The task contained random target locations, variable start points, inconsistent timing, and breaks between trials, ensuring a large variety of movements and pacing, with no repeating sequences. We used Latent Factor Analysis of Dynamical Systems (LFADS) to model the dynamics underlying the neural population spiking activity and extract "de-noised" estimates of neural firing rates. In doing so, we modeled the data without regard to task structure - i.e., data from the entire session was modeled in a contiguous fashion, including all start/stop points and breaks between trials. We compared decoding accuracy of the recorded EMG using simple regularized linear regression from the LFADS-inferred representations, vs. regression from representations produced by two standard neural processing methods: Gaussian smoothing and Principal Components Analysis. Despite the lack of task structure, LFADS uncovered dynamics from the M1 population activity, producing representations that were significantly more informative about EMG than either alternative method, yielding improved EMG decoding of 8% to 17% for muscles in shoulder, back and chest, 21% to 50% for muscles in the upper arm, and 11% to 35% in muscles in the forearm. Our results offer more evidence of the critical role of M1 population dynamics in commanding movement, and may provide important new insights into the generation of muscle activity, and tools for the development of more effective brain machine interfaces.

## C – Posture and Gait

### 1-C-21 Adaptation to real-life external environments immersive virtual reality: a pilot study

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**Purpose:** The purpose of this study was to investigate the effect of an immersive virtual environment (VE) on gait using a low-cost head mounted Virtual Reality (VR) device. We hypothesized that there would be differences in the spatiotemporal and kinematic gait parameters demonstrated under different VE's as strategies for effective negotiation in the environment. We also hypothesized that there would be a possible motor adaptation after repeated exposure to the VE's, and that it would be robust enough to not be affected by interference from exposure to the different VE. **Methods:** 15 healthy young subjects successfully completed this study. An 8-camera motion analysis system was used to collect data from 28 reflective markers. Each subject was made to walk on a 7m walkway for 4 trials each of baseline natural walking (NW) and walking under 2 different VE's, i.e. snowy environment and crowded environment wearing a head-mounted VR device displaying the VE videos on a mobile device. After the block trials, subjects experienced a mixed block consisting of random exposure to both VE's and NW (4 trials for each condition). The following gait parameters were analyzed for each trial: Excursion angle (EA), measured as deviation in the CoM relative to the sagittal plane; peak excursion of the CoM in mediolateral (ML) and anteroposterior (AP) directions. In addition, walking speed (WS) and step length (SL) were also analyzed. One-Way Repeated-Measures ANOVA was performed with

bonferroni post-hoc tests. Results: Compared to baseline NW trials, EA and peak ML-CoM excursion were significantly greater on the 1st trial of snow and crowd conditions ( $p < 0.05$ ) with decreased WS and SL ( $p < 0.05$ ). The EA and peak ML-CoM excursion increased significantly from the 1st to 4th snow trials ( $S4 > S1$ ) while they decreased in the crowd conditions ( $C4 < C1$ ). The acquired motor adaptation was retained even after the mix block where there was no difference respectively between S4 and C4 and the last trial of the mixed block for these conditions (S8 and C8). Walking distance was not affected by the snow condition but only crowd with  $NW < C1$  and  $C1 < C4$  and C8 ( $p < 0.05$ ). Both SL and WS decreased in snow and crowd conditions compared to NW, however over trials only snow condition showed significant increase in SL and WS from S1 to S4 which was maintained at S8. Discussion: The results show that healthy young participants demonstrate positive spatiotemporal deviations from their baseline gait when immersed in VE's. In the snow condition they adopt a cautious gait pattern while in the crowd condition they increase their movement patterns to avoid collisions. In both conditions, however they quickly adapt and restore near normal gait patterns. The current cost-effective VR protocol could be employed for assessment and training of impaired locomotor-posture control in clinical environment.

### **1-C-22 Impaired Directional Perception of Whole-Body Perturbations in People with Parkinson's Disease May Contribute to Balance Impairment**

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Parkinson's Disease (PD) is recognized as a motor disorder, with postural instability as a primary cardinal sign and falls due to loss of balance as a disabling sequela. However, the mechanisms underlying impaired balance control and falls in PD are not well understood. Sensory deficits have been observed in PD but it is unknown whether sensory perception is degraded during standing balance, or associated with balance impairments. We hypothesized that reduced sensory acuity in PD is correlated with balance impairments. We tested whether directional acuity to whole body perturbations during standing was worse in people with PD compared to that found previously in healthy young adults (HYA). We then tested whether balance ability as assessed by the Mini-BESTest was associated with poor directional acuity during standing. We used a 2-alternative forced choice (2AFC) paradigm in which participant reported whether two sequential stages in a backward support-surface translating perturbation were perceived to be in the "same" or "different" direction. The first perturbation stage was always in the backward direction, while the second was deviated to the left or right; all other perturbation characteristics were the same (displacement 7.5 cm, velocity 15 cm/s, peak acceleration of 0.1 m/s<sup>2</sup>). We used an adaptive algorithm previously validated in HYA to estimate the direction perceptual threshold with fewer trials than conventional psychometric test, making it feasible to test in balance-impaired individuals. A total of 18 PD patients were enrolled (age= 65.5±6.85, 7F) in a twelve hour off-medication state. Perceptual thresholds for left and right deviations were reclassified as maximum and minimum thresholds, and threshold asymmetry was calculated as the difference between the left and right side thresholds. In 7/18 PD patients, thresholds on one of the two sides could not be reliably determined during the testing period, which may further indicate poor perception acuity. We found that people with PD had larger discrimination thresholds compared to existing HYA values, with statistically-significant difference in minimum threshold (Min:14.5±4.8° vs. 10.0±3.4°,  $p=0.015$ ) and nearly-significant differences in maximum threshold and threshold asymmetry (Max:17.6±6.4° vs. 13.3±4.7°,  $p=0.07$ ; Asym: 5.9±4.6° vs. 3.3±3.1°,  $p=0.16$ ). Lower balance ability was associated with poorer directional acuity. Mini-BESTest scores were negatively correlated with minimum threshold

( $r=0.37$ ,  $p=0.0086$ ), maximum threshold ( $r=0.50$ ,  $p=0.002$ ), and threshold asymmetry ( $r=0.52$ ,  $p=0.026$ ). Therefore, our results show people with PD have impaired perception of whole body motion which could contribute to balance impairments in PD and potentially falls. Moreover, reduced whole-body direction perception could impair the efficacy of compensatory balance strategies that rely on attentional mechanisms that are used by people with balance impairments with and without PD.

### **1-C-23 Identifying Gait Phase Transitions and Perturbed Gait Dynamics Using Switching Linear Dynamical Models**

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**MOTIVATION:** Standard methods of measuring and comparing gait dynamics using motion capture often cannot characterize individual-specific differences in inter-joint coordination or dynamic interactions. Such differences can separate normal from pathological gait, can arise over time from gait rehabilitation, and can often be seen by eye. Rather than relying on traditional methods for comparing time-series of individual joint kinematics, our goal is to use unsupervised, machine-learning approaches to develop compact, predictive models to characterize gait dynamics, and to use them to compare normal and pathological gaits. Such characterizations could lead to better methods for identifying and treating gait impairments. **METHODS:** We developed a novel method to simultaneously model gait phase transitions and gait dynamics within each gait phase, based on switching linear dynamical systems (SLDS). We used data from a previous study where participants walked on a treadmill at a constant speed, either with or without functional electrical stimulation (FES) to the right plantarflexors during late stance phase and the right dorsiflexors during swing phase. We used the sagittal and frontal plane hip and ankle angles and sagittal plane knee angles of both legs to test the ability of SLDS to recognize gait phases and to model joint angle dynamics within each gait phase. For each participant, we trained a model to represent the gait cycle as a set of four linear autonomous systems, each corresponding to a gait phase (left and right swing, double stance with left and right leg forward). We compared the model-predicted gait phases to an independent, standard measure of gait phase obtained by thresholding ground reaction forces from a force plate. We also applied models from baseline walking data to walking with FES to identify changes in interjoint dynamics during gait resulting from stimulation. **RESULTS:** Across four participants, SLDS models accurately labeled the gait phases (94.3±1.4% left swing, 94.4±1.6% double stance left leg forward, 93.2±1.8% right swing, 93.2±1.5% double stance right leg forward). Differences in time between model identified gait phase transitions and gait events identified by force plate were within 60ms (-29±34ms left toe-off, -1±14ms left heel-strike, -54±32ms right toe-off, -3±23ms right heel-strike). When models from baseline walking were applied to walking with FES, model errors increased in the gait phase where the ankle muscle was stimulated (right stance), and errors were largest in ankle angle reconstruction. **CONCLUSIONS:** Our results demonstrate that SLDS can automatically identify individual gait phases without needing ground reaction force data. The model can identify changes in interjoint dynamics during gait without directly comparing individual joint kinematic time-series. SLDS may be useful for identifying individual-specific effects of training and/or disease on gait at the single joint and multi-joint coordination levels.

### **1-C-24 Longitudinal tracking of muscle synergies of infants during the critical months of learning to walk**

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Introduction Human newborns, unlike other mammals, cannot walk at birth. However, they exhibit stepping responses when they are supported erect underarms with their soles touching a flat surface. This behaviour would disappear after ~2 month of age, and not until ~6-10 month of age would the infant display self-initiated gait that requires body-weight support. The infants would gradually start learning to walk from ~12-16 month with and without support. During their development process, the neural circuits that coordinate muscle activations have to be properly organized to maintain balance during walking. Additionally, the biomechanical properties of the infants' body change continuously when they grow. The muscle activation pattern is a lot more complex than simple alternations between "flexors" and "extensors". Since the course of maturation of the lower-limb motor modules (i.e., muscle synergies) during the critical months of "learning to walk" has not been thoroughly characterized, we seek to understand how muscle synergies for walking change by comparing their synergies at different time points with those of healthy adults. Methodology Overground walking of eight healthy infants were longitudinally recorded at three time points: stage I - supported (~6-10 months), stage II - assistive (~8-12 months), and stage III - independent walking (~12-18 months). Surface electromyography (EMG) activities of 14 trunk and lower limb muscles were recorded. The muscle synergies were extracted using the non-negative matrix factorization algorithm by customized Matlab scripts. The adults' overground walking data from other projects served as a reference for comparisons. The similarity between the muscle synergies from different stages of the infants and those from healthy adults were evaluated using both the scalar products between synergy vectors, and the principal angles between the synergy subspaces. Results The muscle synergies of the infants before and after they learned to walk were similar, with the essential muscle coordination patterns present at the first stage when their self-initiated stepping first appeared. Specifically, there were 2 muscle synergies remaining particularly consistent across the three infant walking stages and the adult stage. Some other muscle synergies were only observed in stage III of infant walking, but not in other infant stages nor in adults. Discussion Our results suggest that learning to walk is a process for fine-tuning both the muscle synergies and their temporal activation patterns that exist at stage I (~6-10 months old). The changes of muscle synergies during the critical months of "learning to walk" may be developmental processes that adapt the initial muscle synergies to the changing biomechanical requirements of walking as the infant grows.

### **1-C-25 Muscle synergies during cat locomotion: effects of epidural spinal stimulation on locomotor CPG**

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Epidural stimulation (ES) of the spinal cord is a promising method for rehabilitation of individuals with spinal cord injury (SCI). ES has been shown to evoke rhythmic locomotor activity in rats, cats and humans, including humans with clinically complete SCI (Harkema et al. 2011). However, the ES-evoked rhythmic motor patterns do not provide full weight support and often demonstrate non-physiological co-activation of antagonists and atypical locomotor muscle synergies. Further progress of the promising ES therapies requires a thorough understanding of the mechanisms underlying the generation of distinct muscle synergies during walking activated by ES. The goal of this study was to compare muscle synergies (1) during intact cat locomotion, (2) during decerebrate cat locomotion evoked by ES, and (3) computed by a neuromechanical model of spinal control of locomotion. EMG activity of major hindlimb muscles was recorded during overground walking in intact cats (Markin et al. 2012) and during treadmill walking



evoked by ES in decerebrate cats with intact spinal cord (Musienko et al. 2012). Muscle activity was also computed using the computational neuromechanical model that integrates the musculoskeletal system generating motion-dependent sensory feedback, basic spinal reflex pathways and CPG with a rhythm generator and pattern formation network (Markin et al. 2016). The parameters of the model were tuned to reproduce with high accuracy locomotor mechanics and muscle activity of intact walking in the cat. Muscle synergies from the three sets of muscle activity patterns were extracted by the non-negative matrix factorization method (Cheung et al. 2005). The number of muscle synergies was determined based on their ability to explain at least 90% of the variability of muscle activity patterns. The number of muscle synergies sufficient to accurately reproduce muscle activity patterns of normal level walking and those generated by the computational neuromechanical model was  $n=4$ . The number of synergies accurately reproducing activity patterns of ES-evoked locomotion in the decerebrate cat was reduced to  $n=3$ . The analysis of muscle synergies generated by the model revealed that two synergies were originating from the activity of the flexor and extensor half-centers of the CPG rhythm generator, respectively. These two synergies were present in both intact and ES-evoked locomotion. Synergies number 3 and 4 in the model were generated at the level of the CPG pattern formation network and represented activity of the two-joint hamstrings (HA) and rectus femoris (RF) muscles, respectively. Only HA-related synergy was present in both intact and ES-evoked locomotion, although its temporal profile changed in the latter case. RF-related synergy was absent in ES-evoked locomotion because EMG pattern of RF was similar to that of one-joint knee extensors. These results suggest that during ES-evoked locomotion, the CPG rhythm generator operates normally, whereas operations of the pattern formation network may be disrupted. This disruption may be caused by direct activation of afferent and efferent fibers by ES stimulation. Changes in sensory input are expected to have greater effects on activity of RF and HA than on other hindlimb muscles (Markin et al. 2012).

### **1-C-26 How to define a person walking and running style?**

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Proper walking and running forms are important to improve speed and efficiency while reducing the risk of injury. Several criteria can be used: a decent posture, a good flexibility of the muscle and tendon, adequate leg motions, a good stride and cadence, an adequate coordination between the upper and lower part of the body, an adequate skeletal configuration of the arm and of course an efficient respiratory rhythm, a focus on body sensation and a relaxed attitude. That said, everyone have a different perceptivo-motor style and therefore the question is to what extent these differences are idiosyncratic and/or detrimental and at what point they should be readjusted. In order to investigate these questions, we quantified the body movements of 18 subjects during walking and running on a treadmill and we specifically focused our study on their intra and inter-individual differences. Walking was performed at three different velocities: comfortable walking, an imposed walking velocity of 4 km/h and maximum vitesse of walking; running was performed at maximum velocity. The Cartesian Optoelectronic Dynamic Anthropometer (CODA) motion analysis system was used to capture the vertical, horizontal and rotational movements by tracking 24 markers' position in real-time at rest and during these three conditions. The markers were positioned on the head, shoulders, sternon, low back, right and left tibias, right and left ankles and feet. We calculated the skeletal configurations of the subjects at rest and when the body's mass reached its highest point, which coincided with the period of unipodal support. Our data showed that the skeletal configuration was distinct at rest, during walking and running but differed amongst subject. it was not correlated with velocity, sex, age, height or weight

while some correlation was observed with the expertise of running in each subjects. We also studied on the dynamics of each marker and their intra and inter-individual variability during walking and running. Our result showed that dynamics was very variable both at the intra and inter-individual level for the frontal, sagittal and horizontal plane and tend to decrease from the lower extremities to the head. These differences could be used to characterize the perceptive-motor style of each investigated subject.

### **1-C-27 Cerebral glucose metabolic abnormalities in Parkinson's Disease with freezing of gait during complex walking**

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**Background:** In Parkinson's Disease (PD) with freezing of gait (FOG) there is a dysregulation of supraspinal locomotor control that is particularly problematic during complex walking (e.g., turning). Adaptations in complex locomotor control that may be present in PD with FOG has not yet been investigated during real locomotion. Therefore, the aim of this research was to determine whole-brain metabolism in PD with FOG using [18F]-fluoro-deoxy-glucose positron emission tomography ([18F]-FDG PET) during an upright steering (i.e., complex locomotion) and straight walking (i.e., simple locomotor reference task) paradigm. **Methods:** We included 17 patients with idiopathic PD in the off-medication state (i.e., overnight withdrawal of all anti-Parkinson medication) that were further classified as experiencing FOG (FOG+, n=8, aged  $67.6 \pm 6.3$ ) or not experience FOG (FOG-, n=9, aged  $64.6 \pm 4.9$ ). All PD subjects were Hoehn & Yahr stage 2 or 3, free from cognitive impairment, and matched for disease severity (UPDRS-III). All subjects underwent [18F]-FDG PET imaging on two occasions. Cerebral glucose metabolism was measured during two gait tasks, steering and straight walking, performed during the radiotracer uptake period just prior to scanning. Spatiotemporal measures of gait were measured using an inertial-based system (APDM). Whole-brain voxel wise analysis was used to determine task associated change in rCGM between groups using a flexible factorial design, with clusters considered significant at  $p < 0.005$  (uncorrected). **Results:** During steering, PD subjects increased activity of the left superior parietal lobule (BA 7), inferior parietal lobule (BA 40), and decreased activity in the thalamus. FOG+ additionally increased activity in the mesencephalic locomotor region, supplementary motor area (BA 6), right superior medial gyrus (BA 8), left dorsolateral prefrontal cortex (BA 9), and occipital gyri (BA 19). Interestingly, activity in the mesencephalic locomotor region with severity of freezing (NFOGQ score) ( $r = 0.825$ ,  $p < 0.012$ ). Group comparison demonstrated that compared to FOG-, FOG+ had increased metabolic activity of the supplementary motor area (BA 6), and frontal gyri (medial, superior, BA 8, 9), reduced activation of the inferior and superior parietal lobule (BA 40, 7), and less deactivation of the thalamus. Gait outcomes demonstrated that FOG+ had reduced stride length (FOG+:  $M = 72.06$  SE = 2.42, FOG-:  $M = 81.51$  SE = 2.28,  $p = 0.013$ ) and stride velocity (FOG+:  $M = 1.18$  SE = 0.05, FOG-:  $M = 1.38$  SE = 0.05,  $p = 0.018$ ) during straight walking, whereas there was no difference between groups in stride length (FOG+:  $60.50$  SE = 2.66, FOG-:  $M = 54.31$  SE = 2.51,  $p = 0.111$ ) and stride velocity (FOG+:  $M = 0.89$  SE = 0.06, FOG-:  $M = 0.84$  SE = 0.06,  $p = 0.524$ ) during steering of gait. **Conclusion:** FOG+ patients have reduced activity of parietal regions and increased activity of the supplementary motor area compared to PD without FOG during upright complex walking. In addition, FOG+ demonstrated activity in the mesencephalic locomotor region that correlated with severity of freezing, a region that has been previously linked to FOG. These results may demonstrate an alternate control mechanism used for complex locomotion in FOG that could be linked to gait impairments.

### **1-C-28 Task difficulty-related modulation of peroneus longus neural excitability during standing in young adults**

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In standing, optimal neural excitability is necessary for generating muscle forces to counteract gravitational force. When task difficulty is increased by limiting the safe zone for center of mass movements, neural excitability is modulated to maintain balance. Within a posture, transcranial magnetic stimulation (TMS) evoked neural excitability varies considerably between individuals, reflecting neural characteristics which could influence the response to difficulty manipulation. The primary purpose of this study was to examine how neural excitability changes when the mediolateral base of support is systematically decreased, i.e., wide, narrow, tandem, and one leg stance. The secondary purpose was to determine whether control condition (i.e., wide stance) excitability is associated with the difference between conditions, i.e., the magnitude of neural response. TMS was used to measure motor evoked potential (MEP), short interval intracortical inhibition (SICI), long interval intracortical inhibition (LICI) and intracortical facilitation (ICF) in healthy young adults (n=23). Reliability was measured in each condition, and only TMS outcomes with ICC>0.5 were further analyzed. With increasing task difficulty, MEP ( $p<0.01$ ) and LICI ( $p=0.03$ ) increased; SICI ( $p<0.01$ ) and ICF ( $p<0.01$ ) decreased. Eight of the 23 participants exhibited atypical facilitation in LICI and when divided into sub-groups, an interaction effect ( $p<0.001$ ) was revealed. LICI increased with increasing task difficulty, only in the facilitation sub-group. LICI in wide stance correlated ( $p<0.01$ ) with the difference between wide and - narrow ( $\rho=-0.74$ ), tandem ( $\rho=-0.66$ ) and one leg ( $\rho=-0.79$ ). Wide stance ICF correlated with difference between wide and narrow stance ( $\rho=-0.44$ ,  $p<0.01$ ). Such associations were absent for MEP and SICI. High MEP and low SICI can help sustain increased muscle contraction in difficult conditions, but high LICI and low ICF appear to be counterproductive. Since the TMS pulse acts as a perturbation, some of the observed neural excitability changes could represent preparatory activity to prevent a fall, and hand studies suggest that preparatory inhibition is necessary to improve response speed and accuracy. Alternatively, LICI and ICF may reflect cognitive influences, sensorimotor integration or other aspects of postural control. Also, individuals with high ICF and LICI in wide stance demonstrated large changes in response to difficulty modulation and vice-versa. We conclude that when postural task difficulty increases, both inhibition and facilitation are modulated, the magnitude of change being influenced by individual characteristics. However, the direction of change suggests that not all the measured neurophysiological processes contribute to increasing muscle contraction. Further studies will determine how decreasing ICF and increasing LICI influence net M1 output and consequently muscle contraction; and the underlying cause for individual differences.

### **1-C-29 Sensory integration for control of frontal plane body orientation during stance and gait in younger and older adults**

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Control of body orientation during stance and metronome paced stepping-in-place (SiP) gait was measured in 20 younger (25-43 years) and 20 older (65-82 years) adults. Balance was perturbed by continuously applied pseudorandom rotational stimuli (six 36.6-s cycles) at 3 amplitudes (1°, 3°, 6° peak-to-peak) that evoked frontal plane sway in 3 stimulus conditions: surface-tilt with eyes open and closed, and visual scene tilt. Lateral displacements of the body at hip and shoulder levels were measured and

used to estimate center-of-mass (CoM) tilt angle with respect to an axis at ankle height centered between the feet. For each test, the frequency-dependent relationship between evoked CoM sway angle and the stimulus tilt angle was represented by a frequency response function (FRF) that characterized response sensitivity (gain) and timing (phase). Parameters of a relatively simple feedback control model of balance control were estimated from fits to average FRFs. Parameters included 1) sensory weights that represent the relative contribution of different sensory systems to balance control with a proprioceptive weight ( $W_{prop}$ ) estimated from surface-tilt tests, and a visual weight ( $W_{vis}$ ) estimated from visual-tilt tests, 2) neural controller parameters that translate integrated sensory information to corrective torque, 3) torque feedback parameters, and 4) time delay. On both stance and SiP tests, for each of the 3 test conditions, and for both younger and older subjects,  $W_{prop}$  and  $W_{vis}$  decreased with increasing stimulus amplitude. On both stance and SiP tests, for each of the 3 test conditions, and for each stimulus amplitude,  $W_{prop}$  and  $W_{vis}$  were larger for older than for younger subjects indicating age-related differences in sensory utilization for balance. For both younger and older subjects on surface-tilt tests,  $W_{prop}$  on SiP tests was about 40% smaller than on stance tests indicating a reduced ability to use proprioception for balance control during gait. For both younger and older subjects on visual-tilt tests,  $W_{vis}$  was remarkably larger (~13 times) on SiP than on stance tests indicating a greatly enhanced reliance on vision for balance during gait. Additionally, older subjects were less able to reduce  $W_{vis}$  with increasing stimulus amplitude on SiP than younger subjects. At the 1° stimulus amplitude,  $W_{vis}$  in older subjects was only 5% larger than in younger subjects, but at the 6° amplitude,  $W_{vis}$  was 2 times larger in older than in younger subjects. Finally, the dynamic characteristics of orientation control represented by the overall shape of the FRFs differed greatly between stance and SiP with SiP FRFs showing a prominent gain peak and rapid progression of phase lag near the SiP frequency consistent with resonant behavior. This resonant behavior may enable the balance control system to easily generate the lateral body oscillatory motions needed for gait while still maintaining control over body orientation. Support: VA RR&D IO1RX001951

### **1-C-30 Dissecting changes in perception following locomotor adaptation**

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Motor adaptation is a form of learning that can improve a movement pattern, but paradoxically can also recalibrate the perception of movement to be inaccurate. This has been demonstrated in walking and reaching: people learn a movement calibration to account for a predictable change in the environment, while simultaneously reducing their perception of the change. Here we describe the dynamic range of perceptual recalibration, and how this relates to the magnitude of motor adaptation. We studied locomotor adaptation via a split-belt paradigm, where people learn to walk with their legs moving at different speeds (e.g. right faster than left). As participants adapt to the split-belt treadmill, they correct their limping gait pattern by learning to take symmetric steps. They also recalibrate leg speed perception so that they perceive their legs to be moving at more similar speeds than they actually are. When the speed perturbation is removed, subjects inaccurately perceive the opposite perturbation (e.g. left faster than right). In the first experiment, we studied people walking before, during and after a 3:1 split-belt perturbation (belt speeds at 1.5 and 0.5 m/s). We investigated the time-course of learning via 3 groups that walked with split-belts for 3, 15, and 30 minutes. Motor and perceptual changes evolved from 3 to 15 minutes, but then plateaued and did not change from 15 to 30 minutes. Interestingly, the motor and perceptual recalibrations plateaued at different magnitudes: the motor recalibration fully corrected the limp, but the perceptual recalibration only accounted for a portion of the speed difference (~0.4 out of

1.0 m/s difference, or 40%). By the end of adaptation, subjects could walk symmetrically, but still felt perturbed by the split belt environment. Next we attempted to modify the amount of perceptual recalibration by changing the size of the perturbation or how it was introduced. We tested subjects learning a smaller speed difference (0.8 and 0.4 m/s) to see if perceptual recalibration could account for the 0.4 m/s perturbation (i.e. the amount of recalibration in experiment 1), or account for 40% of it ( $\sim 0.16$  m/s). Results showed the latter, suggesting that the perceptual recalibration is a fixed proportion of the perturbation. Finally, we asked if introducing the same speed difference (i.e. 0.4 m/s) gradually would lead to a larger proportion of perceptual recalibration. The gradual condition had no effect on the amount of perceptual recalibration when compared to the abrupt condition. Together, these results show that the amount of perceptual recalibration during walking adaptation is proportional to the perturbation size ( $\sim 40\%$ ), develops in 15 minutes, and is not easily modified. Importantly, perceptual learning does not parallel the process of motor adaptation--subjects never fully change their perception despite fully correcting their motor pattern. Supported by NIH NS090610.

### **1-C-31 A method for identifying impending postural instability and the responsible mechanisms**

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**BACKGROUND** Finding effective methods capable of assessing balance prior to a fall and identifying the responsible mechanisms will improve the quality of life of people, reducing their fall risk, and maintain independence. In an attempt to better understand postural instability, Chagdes et al. (2016a; 2016b) investigated a simple inverted pendulum mathematical model of upright balance and identified two unique mechanisms of instability. (1) When neuromuscular feedback gain is low, a leaning instability emerges. (2) When the combination of neuromuscular feedback gain and delay is excessive, an oscillatory instability occurs. In this work, Chagdes et al. (2016a; 2016b) identified postural instability in individuals with advanced neuromuscular impairments (i.e., multiple sclerosis, Parkinson's disease, and concussion). One of the limitations of their method is that while postural instability was identifiable, progression towards instability was not. This abstract presents a method that evaluates the specific neuromuscular mechanism (e.g., delay, feedback gain, or muscle strength) leading to instability by manipulating feedback through virtual reality. **METHODS** We adopt the mathematical model of Chagdes et al. (2016a; 2016b) to incorporate manipulated visual feedback through virtual reality which can magnify, attenuate, and delay postural movements perceived by vision. A delay in the visual information in conjunction with a person's intrinsic neuromuscular delay increases the effective delay in feedback control. Similarly, an increase (or decrease) in the scaling of visual information in conjunction with their natural neuromuscular gain increases (or decreases) their effective gain in feedback control. Combinations of these manipulations, in theory, can induce either type of instability (i.e., leaning or oscillatory) in individuals with no apparent signs of motor deficit. We test this idea in the adapted mathematical model with virtual reality feedback by investigating the stability of the upright position and inherent bifurcation as visual feedback is magnified, attenuated, and delayed.

**RESULTS/CONCLUSIONS** The bifurcation analyses revealed that the amount of manipulations to visual feedback for which stable balance can be maintained depends on the state of postural control. When the model has lower passive ankle stiffness the visual feedback must be attenuated by a large amount to elicit the leaning instability. On the other hand, when the model has a lower neuromuscular feedback gain, the visual feedback must be magnified by a large amount to elicit the oscillatory instability. It was found that ankle stiffness did not have an effect on the amount magnification of visual feedback required to induce the oscillatory instability. When the model has an increased neuromuscular delay

visual feedback requires a small amount of delay to produce the oscillatory instability. Preliminary experimental data show that instability can be induced in a population of healthy young adults. Future studies will begin to test the method in populations with known balance deficits to examine its feasibility as a new identifier in balance deficits. REFERENCES Chagdes JR et al., (2016a) J Sport Heal Sci Chagdes JR et al., (2016b) J. Biomechanics.

### **1-C-32 Consequences matter when performing a behavior with multiple goals**

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Individuals are often required to complete two tasks simultaneously, such as walking while talking. Although the dual-task cost of performing a cognitive task during upright standing has been extensively researched, less is known regarding how individuals prioritize the performance of multiple goal-directed tasks that are governed by similar neurological pathways. Goal-directed task control is mediated by frontal-striatal pathways, including the associative loop of the dorsolateral striatum circuit. Habitual tasks are governed by the motor loop, located in the dorsomedial striatum pathway. (Hernández, Redgrave, & Obeso, 2015; Redgrave et al., 2010). The purpose of the study was to examine how young adults prioritize the performance of two goal-directed tasks while standing: communicating about a topic while performing a precision manual task. Reach distance (near or far), opening size of the fitting board (large or small), and speech task (with speech or without speech) were modulated to vary the difficulty of the tasks. Fifteen young adult female participants completed the standing manual task; a control condition of standing and speech (no precision fitting) was also completed. Accuracy was defined as precisely holding a block without hitting the sides of an opening and communicating about a specified topic. Kinematic measures were collected using a 3D motion capture system, and included maximum trunk velocity, average wrist velocity, acceleration/deceleration time, straightness of the wrist, and wrist velocity standard deviation. Duration and frequency of pauses, speech rate, sound pressure level, and syntactic complexity were used to assess communication. Results indicated that participants generally prioritized communication over accuracy in the manual task. While few significant changes were noted in speech measures, maximum trunk velocity, wrist velocity, and standard deviation of the wrist increased in some speech conditions. Additionally, accuracy was lower for manual task conditions with speech and small opening size. We propose that young adults viewed the consequences of failure in the communication goal as more negative than that of failure to achieve the manual goal. In future studies on prioritization, research should consider manipulating the consequences of task failure explicitly in goal-directed dual tasks and extend these ideas to research on older adults and patient populations.

### **1-C-33 Cortical dynamics of compensatory balance control**

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It is now accepted that the cerebral cortex participates in human balance control, but there is limited knowledge about cortical mechanisms that support balance recovery. The aim of this study is to establish the cortical oscillatory dynamics of compensatory balance control, contrasting stepping and feet-in-place strategies for balance recovery. We recorded high-density EEG from 10 healthy participants (24±3.5 years) while they responded to backward movements of the support surface using stepping or feet-in-place strategies (50 trials each), as indicated by a visual cue. We decomposed the



EEG signals with independent component analysis and computed event-related spectral perturbations (ERSP) at group level, after clustering independent components (ICs) that were similar across participants. We obtained mean time-frequency ERSP maps per strategy and compared them with permutation statistics ( $n=1000$ ,  $\alpha=0.05$ ,  $\alpha$  corrected). In addition, we computed time course and confidence intervals for specific cortical rhythms ( $\alpha=0.05$ ). Distinct compensatory behavior resulted in largely similar modulations of cortical rhythms in sensorimotor, premotor, and prefrontal areas, indicating an overall engagement of a cortical network for movement control. Full-body movement during balance recovery elicited power decrease of mu and beta rhythms in supplementary motor area (SMA), posterior parietal cortex (PPC), and bilateral sensorimotor cortices (M1/S1), for both balance recovery strategies. Stepping behavior was distinguished by stronger beta power decrease in M1/S1 contralateral to the stance leg during single support. The lateralized beta activity could be related to direct cortical control of muscle contraction for stabilization of the stance body side, which may occur via neural synchronization (e.g., coherence) with or without concurrent power modulations. In agreement with previous studies, balance perturbations elicited broadband (3-17 Hz) power increase in SMA and theta power increase in anterior cingulate cortex (ACC), prefrontal cortex (PFC), PPC, and bilateral M1/S1. These responses likely indicate the detection of a challenge to standing balance and the activity of a cortical network for monitoring balance recovery. Furthermore, our results suggest that theta band activity in PFC is highly relevant for monitoring balance recovery, because stronger and longer-lasting power increase occurred under conditions of higher postural demand (feet-in-place strategies). Additional analyses in four participants who incorrectly stepped in 10-14 trials requiring feet-in-place strategies, suggested increased beta power in SMA preceding incorrect step initiation; and increased theta and beta power in PFC regardless of performance. Our results outline the cortical dynamics that contribute to compensatory balance control. Future studies will focus on quantifying causal corticomuscular connectivity and determining the role of midfrontal theta activity in balance control.

### **1-C-34 Examining spatiotemporal and kinematic parameters for backward stepping: Are volitional and reactive step responses different?**

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**Introduction:** Evidence indicates that improving compensatory stepping responses to stance perturbations can significantly reduce fall risks, yet success rates of such implicit training can be improved via explicit training. Contrary, researchers have also explored rapid volitional step (VS) training and examined translation to reactive stepping (RS). Yet, it remains unclear if the motor strategies implemented and kinematics are similar during volitional and reactive responses. The purpose of this study was thus to compare spatiotemporal parameters and movement kinematics between VS and RS in backward direction. **Methods:** Fifteen healthy young adults performed VS rapidly to an auditory cue in the backward direction. After which were exposed to a forward slip-like perturbation via the Active step treadmill (Simbex) to elicit a backward reactive step. An 8-camera 3D motion capture system analysis was used to collect full body kinematic data and a customized MATLAB program was used to compute the following variables: postural stability (body's center-of-mass position (COMP) and velocity (COMV) relative to base of support), trunk angle (TA), trunk angular velocity (TAV) and joint angles (hip, knee, and ankle). These variables were obtained at the instants of liftoff(LO) and touchdown(TD) of the step and analyzed using a 2x2 ANOVA. In addition step length, and step initiation and execution times were also computed and compared using paired t-tests. **Results:** Step length and step initiation and execution

times were significantly lower during RS than VS ( $p < 0.001$ ). From LO to TD during a RS when compared with a VS, stability significantly increased explained an anterior shift in the forward COMP and decreased backward COMV. However, the VS stability remained higher at both LO and TD than RS. The TA at liftoff was significantly more extended for the RS than VS and decreased more at TD. While there was no difference in TAV between reactive and volitional step at LO, the volitional group showed an increase forward velocity at TD while reactive group showed a decrease. At LO there was no significant difference in hip and knee angles, while the ankle showed greater plantarflexion during VS. From LO to TD for both voluntary and reactive step, the hip showed decreased flexion, while the knee demonstrated greater flexion only for RS and angle showed decreased plantarflexion only for VS. Conclusion: These results therefore provide a comparative biomechanical analysis between a VS and RS in backward direction. Based on the differences observed between the two types of stepping it is suggested RS training should focus on improving plantarflexion at step liftoff and decrease knee flexion at step touchdown, both of which could result in improved step lengths. However, such improvement often induced by reactive perturbation training might not be cost-effective and widely available to clinicians. Thus, VS training for fall-risk prevention can thus focus on decreasing reaction time of stepping. Future training studies need to validate the above postulations and examine the findings could extend to healthy older adults or people with sensorimotor impairments.

### **1-F-35 Obstacle-induced trip perturbation training: proactive and reactive adaptation to reduce falls in community-dwelling older adults**

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Trip-related falls constitute a large portion of environmental falls in community-dwelling older adults. Previous evidence from healthy young adults indicates that repeated exposure to real-life trip perturbations in a safe environment during walking can result in adaptive strategies to reduce fall-risk. The purpose of this study was to investigate if and to what extent healthy older adults could adapt to such trip-perturbations to reduce their forward fall-risk. Twenty community-dwelling older adults ( $66.8 \pm 4.3$  years) were exposed to twenty-four unannounced trips induced by a sudden release of an obstacle, 8-cm in height, during their over ground gait. Twenty-four trips were given in three blocks. Subjects received two blocks of eight trips (T1-T8) and (T9-T16) separated by three natural walking trials. The last block comprised a mix of eight trips and natural walking (T17-T24). A trip was given to all the subjects again 30 minutes after the training as an immediate retention test (Ret\_T). Data of center-of-mass (COM) stability and body kinematics were analyzed at the instants of pre-trip (30ms before obstacle contact) and post-trip (recovery-foot-touchdown), that were respectively indicative of proactive and reactive adaptive performances. On their first novel trip, 75% of participants lost their balance and 43.8% fell. Subsequently, fall rate rapidly dropped down to 12.5% on T2 and 6.25% by T8 with 0% fall on the last, 24th trip (T24). Similarly the forward balance loss reduced to 35 % by T8 and 25% by T24. The decrease in the incidence of fall correlated with reduced post-trip forward instability where subjects went from being unstable on T1 in comparison with natural walking trials (Nat) before perturbation (stability:  $T1 < \text{Nat}$ ,  $p < 0.001$ ) and regained their stability by T8 ( $T8 > T1$ ). After the washout walking trials, stability decreased ( $T9 < T8$ ). However, it increased rapidly again during the 2nd training block ( $T16 > T9$ ) and then was maintained throughout the mixed block ( $T16 = T24$ ,  $p > 0.05$ ). Such improvements in the control of stability could have resulted from a decrease in forward velocity of the COM achieved quickly in the first block ( $T8 < T1$ ) and a posterior shift of the COM at recovery foot touchdown ( $T8 < T1$ ). Participants also significantly reduced their trunk forward rotation over the training

trials ( $T1 > T24$ ,  $p < 0.05$ ). These reactive changes were accompanied by proactive changes with an elevated toe clearance ( $T1 < T24$ ) such that 50% of the older adults crossed over the obstacle without hitting it on their last training trial. Such adaptive adjustments both proactively and reactively diminished the need for taking longer compensatory steps (recovery step length:  $T1 > T24$ ,  $p < 0.05$ ). The training effects were retained in the immediate re-test such that there was no difference on the post-trip stability and COM states (i.e., position and velocity), step length and toe clearance between T24 and Ret\_T. The current protocol successfully and safely reproduced falls among older adults, who could acquire appropriate adaptations to repeated obstacle-induced trips similar to previously shown in young adults and thus reduced their likelihood of falls. Future studies need to establish efficacy of such perturbation training for real-life fall risk reduction.

## D - Integrative Control of Movement

### 1-D-36 Emotionally reacting to being "off-course": the role of cognitive and limbic circuits during movements in humans

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Nonmotor brain regions in humans are rarely studied during motor control due to their secondary, nontrivial, or even nonexistent role. Furthermore, capturing neural data from these regions may be cumbersome during movement, especially if motor regions are being probed simultaneously. However, it is important to understand what nonmotor regions encode for during movements to not only treat nonmotor neural diseases that impact movement (such as depression) but also to design brain-computer interfaces (BCIs) that rely solely on recordings from some of these areas. Such BCIs may provide the opportunity for patients with damaged motor cortex to regain motor control. We exploited a rare opportunity to record local field potential (LFP) activity from 680 contacts covering over 70 nonmotor structures in 9 human subjects as they executed a goal-directed reaching task using a robotic manipulandum. These subjects are medically refractory epileptic patients implanted with multiple depth electrodes for clinical purposes using the stereoelectroencephalography (SEEG) technique. SEEG provides both high spatial and temporal resolution data. The question we set out to answer is whether or not nonmotor regions encode any path related information. To explore our relatively large data set, we developed a method that both quickly scans overall electrode contacts, trials, and subjects and accurately extracts meaningful neural correlates of behavior. First, a behavioral signal was derived for each trial that captures modulating properties of path trajectory. That is, this signal increases or decreases when the subject's path deviates or is "off-course" from the target. Neural data was then transformed into spectrograms (time x frequency matrices) that were summarized as one-dimensional signals using singular value decomposition. These neural signals captured time periods where the spectrogram significantly modulated during trials at any frequency. Finally, the behavioral and neural signals during movement execution were cross-correlated for every trial and contact. The top contacts with a significant number of trials with high correlations between brain and behavior signals were extracted. Preliminary results show that limbic and visual cortical areas were most highly correlated with path modulation. This suggests that when subjects move "off-course", they see the deviation and then may emotionally react to it. Our findings provide the first evidence of the important role that nonmotor regions have during motor control, suggesting that these regions should no longer be overlooked during sensorimotor control.

### **1-D-37 Time-dependent impact of urgency on corticospinal excitability during action selection**

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Action selection involves a tight balance between the competing demands of decision speed and accuracy. Recent work suggests that this balance is adjusted by an urgency signal that operates as a modulator of neural gain, boosting activity in motor areas when speed is of essence and reducing it when the focus is on accuracy. Importantly, the level of urgency changes during action selection, typically increasing as time passes. Here, we investigated the impact of varying the pattern of this time-dependent increase in urgency on corticospinal excitability in humans by applying transcranial magnetic stimulation (TMS) over the primary motor cortex. Subjects performed a modified version of the tokens task (Thura and Cisek, 2014, Neuron). In each trial, 15 tokens jumped one-by-one every 200 ms from a central circle to one of two lateral target circles; participants had to guess which of those targets would ultimately receive the majority of the tokens, and to report their decision before the final token jump on a key-board with either the left or right index finger. Importantly, in two separate blocks, we manipulated the within-trial increase in urgency, by providing different penalties for incorrect responses as a function of time. In one block type, the cost of making an error was lower for fast decisions than for slow ones, producing a context where urgency was initially high and increased only marginally during the course of action selection (Urge-Early block). In contrast, in the other block type, the penalty was higher for fast decisions than for slow ones. Hence, here urgency was initially low but then increased drastically later on (Urge-Late block). TMS was exploited to elicit motor evoked potentials (MEPs) at different timings during the decision process (i.e., either early or late in the trial) in a right hand muscle when it was either selected for the forthcoming response (right index response), or non-selected (left index response). MEP amplitudes provided us with a muscle-specific assay of corticospinal excitability at the time of the stimulation. Our results indicate that varying the temporal pattern of urgency alters corticospinal excitability during action selection. As such, when elicited early on, MEPs were more facilitated in the Urge-Early than in the Urge-Late block, regardless of whether the target muscle ended up being selected or non-selected. Conversely, when elicited later on, MEPs showed more suppression in the UrgeLate compared to the UrgeEarly block, specifically when the target muscle was not selected. Hence, whereas urgency globally amplified the facilitation of corticospinal excitability at early stages of action selection, it selectively boosted inhibitory changes occurring at a later time in the non-selected effector.

### **1-D-38 Consolidation of human somatosensory memory during motor learning**

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Sensorimotor learning is a bidirectional process associated with concurrent neuroplastic changes in the motor and somatosensory system. While motor memory consolidation and retention have been extensively studied during skill acquisition, little is known about the formation and consolidation of somatosensory memory associated with motor learning. METHOD: Using a robotic exoskeleton, we tracked markers of somatosensory and motor learning while healthy participants trained to make goal-directed wrist reaching movements over five days and evaluated retention for up to 10 days after practice. Markers of somatosensory learning were changes in wrist position sense bias (systematic error) and precision (random error). RESULTS: First, somatosensory (proprioceptive) memory consolidation shows signs of cost savings with repeated sensorimotor training - the same feature is known for motor

memory formation. Moreover, somatosensory learning generalized to untrained workspace. Second, somatosensory learning over days can be characterized as an early improvement in sensory precision and a later improvement in sensory bias. Third, the time course of learning gains in position sense acuity coincided with improvements in spatial movement accuracy. Finally, the gains of somatosensory learning were retained for several days. Improvements in position sense bias were still visible up to 3 days after the end of practice for the trained workspace positions, but decayed faster in the untrained workspace. Improvements in position sense precision were retained for up to 10 days and were workspace independent. **CONCLUSION:** The effects of 4 days of sensorimotor learning on somatosensory memory can still be seen 10 days after the end of practice. The findings are consistent with the view that an internal model of somatosensory joint space is formed during motor learning.

#### **1-D-39 Wild monkeys structure motor variability to maintain a stable bipedal stance while using stone hammers**

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Humans learning to use a hammer are thought to be more challenged to master movements of the arm(s) and hand(s) than of the lower body. Wild capuchin monkeys proficient at cracking nuts with stone hammers moved a hammer through highly consistent trajectories while standing bipedally. Using an uncontrolled manifold (UCM) analysis, we show that variability in the movement of the foot and shank contributed directly to variability in the hammers trajectory, whereas variability in the movement of the lower arm and hand did not, indicating that coordinating movements of the lower body is more challenging than controlling movements of the upper body for monkeys using stone hammers. The findings suggest that, for occasional bipeds, maintaining bipedal balance could limit the range of actions with tools.

#### **1-D-40 Effects of hand prosthesis operational parameters on user performance and cognitive agency**

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Improving hand grasp function impaired by neuromuscular pathology is a critical clinical objective to rehabilitate performance in activities of daily living. Standard rehabilitation protocols following neuromuscular pathology, such as stroke, rely on the repetitive practice of grasp to better re-formulate neuromotor connections. Virtual reality (VR) environments have been utilized to heighten cognitive engagement with designs to accelerate rehabilitation progress. Typically, VR environments are largely predicated on visualized interactions between the user and virtual objects. In this study, we are investigating how agency, the perception of being the "true author" of one's movements, may be mediated according to visual operation cues and whether it directly impacts functional performance. We hypothesize that improved grasp performance will be achieved with a greater sense of agency. To our knowledge, altering a person's cognitive perception of rehabilitation training to improve functional performance has not been thoroughly examined. The VR environment provides a programmable interface for systematically altering agency through visual feedback of operation of the virtual hand. The notion of agency is especially apt for virtual neurorehabilitation given the virtual hand acts as a surrogate for the intact hand. Our methodology aims to systematically vary a subject's perception of agency over a virtual hand and to observe the correlation with performance of grasp tasks. Demonstrating how individuals perform with greater agency will potentially provide a powerful basis for creating neurorehabilitation protocols that are more intuitive and efficient. If the functional connection

between agency and performance is established, agency can be a highly viable criterion to optimize rehabilitation protocols that rely on repetitive task execution. Currently, we have completed collecting data with over 15 able-bodied individuals performing reach-to-grasp tasks whereby the virtual hand motion is based on marker-based tracking of the subject's real hand. The base motion is altered in the virtual environment through variations in speed, addition of noise, or gradually relying more on automated motion trajectories. Our long-term objective is to develop a VR platform that facilitates the role of cognitive agency in hand grasp performance for various rehabilitation assistive methodologies. Agency-driven rehabilitation solutions may be pursued for exoskeletons, functional electrical stimulation, and sensory-feedback prostheses to address spinal cord injury, stroke, or upper-limb amputation. Expected outcomes include more optimal parameters for controllers, greater motor gains with fewer practice repetitions, and better incorporation of the user in assistive device operation.

### **1-D-41 Tactile and non-tactile inputs are linearly integrated for the estimation of fingertip distance**

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Dexterous manipulation relies on the ability to coordinate digit forces as a function of position. When subjects can choose where to grasp an object, they modulate digit force distribution to compensate for trial-to-trial variability in digit placement prior to object manipulation, e.g., object lift-off. These findings indicate that the central nervous system (CNS) can rapidly integrate motor commands for force control with feedback of digit position to attain the task goal, e.g., generate a torque to prevent object tilt. Importantly, lack of visual feedback of digit position on the object affected only minimally this sensorimotor integration. A recent study has further shown that passive positioning of the fingertips leads to a comparable level of accuracy of digit force-to-position modulation. This demonstrated that motor commands for finger positioning, which are thought to play an important role for sensorimotor integration, are not necessary. However, despite this evidence for the CNS' robust ability to reliably transform feedback of digit contacts into accurate force distributions, we have also shown that estimation of digit position can be biased by the distribution of fingertip forces. We asked subjects to sense fingertip distance while exerting digit tangential forces in opposite directions and match it with the same fingertips. Surprisingly, digit force direction biased subjects' response, leading to consistent over-estimation of fingertip distance. We interpreted this previous finding as evidence for a contribution of the expected sensory consequences of force-related motor commands (i.e., efference copy) to the estimation of vertical digit distance during manipulation. However, this result also raised important questions regarding the CNS' limited ability to integrate feedback from separate sensory modalities and efference copy for fingertip distance estimation. In the present study, we address these questions by quantifying the relative contribution of tactile afferents and non-tactile inputs (proprioception and efference copy). We asked subjects to match fingertip distance relying on either tactile (Experiment 2) or non-tactile inputs (Experiment 3) of force from the thumb and index finger, and then we compared their performance with the condition where both types of inputs are combined. We found that the bias in the estimation of the fingertip distance persisted when tactile and non-tactile force-related signals were decoupled. Importantly, the sum of the matching errors observed in Experiment 2 and 3 resembled the matching performance exhibited when both tactile and non-tactile inputs were available. Furthermore, tactile signals provided the highest contribution to the bias. These findings indicate that estimation of fingertip distance depends on linear integration of tactile afferents and non-tactile inputs, with tactile inputs being characterized by a higher weight.



### **1-D-42 Neuronal activity during action observation and execution in macaque somatosensory cortex**

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A mirror neuron is defined as a neuron that fires both when an animal manipulates an object in a specific way and when it sees another animal (or the experimenter) perform a similar action. Such neurons were found in the ventral premotor cortex, inferior parietal lobule, as well as primary motor cortex. So far, no literature indicates the equivalent neurons in the somatosensory cortex except indirect evidence from a few human neuroimaging experiments. We trained a monkey to perform and observe a delayed reach-to-grasp task with different grip types: 1) pulling a ring-shaped object with the index finger (RING) and 2) grasping a bar-shaped object with precision grip between the thumb and index finger (PINCH). In the monkey's turn, the monkey was instructed to perform these grasping by themselves. In the human turn, the monkey was instructed to observe the same actions performed by an experimenter sitting in front of the monkey, without making an overt own movement (checked by EMGs). We presented the RING and PINCH items in a random order to prevent monkey from predicting the next item. The order between the human's and the monkey's turn was also randomized. Each trial started with the right hand of both human and monkey on a home plate, one of the items would be placed in front of either the monkey or human and after a go signal (both light and tone) they had to reach towards the item and pull on it until getting another signal followed by the reward. For recording neuronal activity, we implanted a recording chamber over the contralateral primary somatosensory cortex (SI). Nerve cuffs were implanted around the muscle (deep radial: DR) and cutaneous (superficial radial: SR) afferent to identify the peripheral input to the neurons. We found that a significant portion of the neurons in area 3a and 2, but not in area 3b, showed increased activity during both action execution and action observation. During action execution, a peak of activity in 3a neurons occurred during reaching toward the object, before a touch of the object. In contrast, neurons in areas 1 and 2 responded mostly after contact with the object and pull, less during reaching. Area 3b neurons exhibited both characteristic with smaller magnitude. During action observation, some of these characteristics specific to each area were preserved on the top of weak, consistent suppression. We suggest that neurons in the primary somatosensory areas exhibit "mirror-neuron like" activity.

## **E – Disorders of Motor Control**

### **1-E-43 Temporal and spatiotemporal organization of muscle patterns is affected by cerebellar damage**

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The role of the cerebellum in motor control and motor learning has been investigated extensively but its contribution to the spatiotemporal organization of muscle activation patterns underlying goal-directed movements is still largely unknown. The decomposition of muscle patterns as combinations of different types of muscle synergies may reveal their spatial, temporal, and spatiotemporal structures and may thereby allow to identify their specific changes due to neurological lesions. In this study, we recorded surface EMG activity from 13 shoulder and arm muscles in a group of individuals with various forms of hereditary and sporadic cerebellar ataxias (CA) and in age-matched healthy control (HC) individuals while performing reaching movements in multiple directions. We assessed whether cerebellar damage affects the organization of muscle patterns by extracting different types of muscle synergies from the muscle patterns of each HC individual and using these synergies to reconstruct the muscle patterns of all

other HC and CA individuals. Synergies could characterize the organization of muscle patterns across muscles irrespective of time (spatial or time-invariant synergies), in time irrespective of the muscles (temporal synergies), and both across muscles and in time (spatiotemporal or time-varying synergies). Considering inter-individual variability, if spatial, temporal, and spatial-temporal structures are affected by cerebellar damage we expect a lower average reconstruction quality of the CA muscle patterns than the average reconstruction quality of the HC patterns with the corresponding type of synergies. We found that CA muscle patterns could only be accurately captured by spatial muscle synergies, as the reconstruction R2 values were not significantly different between CA and HC populations. In contrast, there were significant differences in the reconstruction R2 values for both spatiotemporal and temporal synergies, with an interaction between the two types of synergies indicating a larger difference for spatiotemporal synergies. We also found that the quality of reconstruction by spatiotemporal synergies correlated with the gravity of impairment, as assessed by the International Cooperative Ataxia Rating Scale (ICARS). These results indicate that temporal and spatiotemporal organization of the muscle patterns but not their spatial organization is affected by cerebellar damage. They suggest that, in a modular control architecture, the spatial structure of motor modules is determined by the cortico-spinal connectivity while cortico-cerebellar loops shape their spatiotemporal structure.

#### **1-E-44 Proprioceptive training can enhance proprioceptive-motor function in people with Parkinson's disease**

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Proprioceptive impairment is a characteristic feature in people with Parkinson's disease (PWP). Anti-parkinsonian medications can enhance proprioceptive function. However, medicated PWP show significant proprioceptive deficits when compared with healthy adults. Somatosensory-based training that challenges proprioceptive system are shown to improve proprioceptive acuity and translates to improved motor function in healthy adults. It is unknown whether proprioceptive function can be enhanced in PWP by means of such somatosensory-based training. We administered a visuo-proprioceptive training on PWP using a wrist robotic device coupled with a real-time virtual visual environment to identify whether proprioceptive function can be enhanced by specialized training and to determine if such proprioceptive improvements lead to improved motor performance. 13 participants (Mean age = 61.8 yrs; mean disease duration = 2.5 yrs) diagnosed with primary Parkinsonism were tested in their ON medication state. Training involved tilting a virtual table to position a virtual ball on a target by making precise small amplitude wrist flexion/extension movements. All participants completed 60 training trials taking on average about 30 minutes for completion. With increasing proficiency, task difficulty was increased by adjusting the responsiveness of virtual ball. Wrist position sense acuity and spatial precision of an untrained goal-directed wrist movement were assessed without vision before and after training. Wrist position sense discrimination thresholds were obtained by controlled robotic passive motion providing paired stimulus wrist positions for the participants to discriminate. Mean movement precision error was determined using the absolute difference between passively presented target of 15° wrist flexion and subsequent active movement to the target by the participant. All participants showed improvements in wrist proprioceptive thresholds (mean: pre/post = 1.6° / 1.1°). On average, all patients showed 34% improvement in wrist proprioceptive thresholds after training. Wrist movement precision improved in 10/13 participants (mean: pre/post = 2.4° / 1.8°) by about 31% on average in those participants who showed improvements. Wrist proprioceptive function improved in

PWP after a brief specialized visuo-proprioceptive training. Movement precision in the untrained motor task improved in most participants, indicating that such somatosensory-based training directly benefits motor function. These findings are promising and suggest that somatosensory-based training may enhance sensorimotor function in PD.

#### **1-E-45 Integrating data from speech and limb sensorimotor learning tasks in children and adults who stutter**

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Stuttering is a neurodevelopmental speech disorder in which speech fluency is disrupted by repetitions and prolongations of articulatory and/or laryngeal movements. Although approximately 50% of affected children experience spontaneous recovery, stuttering persists in approximately 1% of the world-wide population. Currently, treatments for stuttering beyond the pre-school years continue to be atheoretical and prone to relapse. Developing effective clinical management approaches will require a theoretical framework of stuttering that accounts for various primary and associated speech characteristics, and that is consistent with empirically-verified models of sensorimotor control and neural functioning. Numerous studies have demonstrated that, even when producing fluent speech, stuttering individuals move more slowly than nonstuttering individuals. It is also known that many stuttering adults experience immediate improvements in fluency when auditory feedback is artificially manipulated. Other lines of research further support the hypothesis of sensorimotor integration deficits: we have shown that adults who stutter lack the pre-speech auditory modulation that is observed in fluent control subjects but that this difference disappears when speaking with altered auditory feedback. Moreover, as compared with control subjects, speech production in stuttering subjects tends to show over-activation in sensorimotor areas primarily in the right hemisphere and under-activation of left auditory areas. Structurally, stuttering is associated with atypical grey and white matter volumes and disrupted white matter organization across numerous brain regions. In the context of motor learning, several studies have demonstrated that stuttering participants show sequence learning deficits for both finger-tapping and verbal tasks. Controversy has arisen, however, about the question whether stuttering is also associated with sensorimotor learning problems. It has been claimed that sensorimotor adaptation deficits are observed only in adults who stutter and, thus, may be related to consequences - rather than onset - of the disorder. Here, we integrate data from a series of experiments investigating not only speech auditory-motor learning but also limb visuo-motor learning in both children and adults who stutter versus matched nonstuttering individuals. Speech auditory-motor learning was quantified by systematically perturbing real-time auditory feedback during speech production and measuring changes in participants' acoustic speech output. Limb visuo-motor learning was quantified by systematically perturbing real-time visual feedback during center-out-and-back reaching movements and measuring changes in initial movement direction. Analyses to date suggest that both stuttering children and stuttering adults show slower or reduced sensorimotor adaptation as part of a generalized limitation that affects both speech and limb motor learning. [Funding: NIH R01DC007603, R01DC014510]

#### **1-E-46 Effects of evoked cutaneous afferents on voluntary reaching movement in patients with Parkinson's Disease**

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**Abstract Background:** Resting tremor in Parkinson's disease (PD) is an involuntary rhythmic motion [1], which interacts intimately with the control of voluntary movements in PD patients [2]. The main effect of tremor is to prolong the reaction time of movements. Recently, we proposed and tested a novel non-invasive technique to inhibit resting tremor in PD subjects [3], based on the hypothesis that the cortical descending tremor signals were disrupted at the spinal propriospinal neurons by evoked cutaneous afferents that exert strong inhibitory inputs. In this study, we further examine the question whether evoked cutaneous afferents by transcutaneous electrical nerve stimulation would also affect the descending motor commands of voluntary movements in PD subjects, and if so, to what extent and by what neural pathways? **Methods:** In a pilot study, 2 patients with tremor dominated PD were recruited to participate in this study. A cutaneous afferent stimulation was applied to the dorsal skin of the hand for tremor inhibition [3]. This stimulation was switched on or off randomly during the trials, in which patients were instructed to perform fast front reaching (FR) movements. The patients began to move their arm with an arm brace apparatus on a platform with reduced friction after a "go" acoustical cue. During task performance, the upper arm was not visible to the subject, except for the start and target points. A MotionMonitor II system was used to register kinematics and six muscles surface EMGs of the moving arm. A computational method was used to extract the trajectory of voluntary movements from tremor-corrupted trajectory [2]. The reaction time (RT) and movement time (MT) of reaching movements were calculated using the extracted voluntary movements. Statistical comparison of end-point accuracy and kinematic performance was made between movements with and without stimulation. **Results:** Preliminary results in the 2 patients indicated that evoked cutaneous afferents that inhibited tremor did affect voluntary movements in PD subjects in a consistent way. In each subject, their RT was significantly shorter with stimulation than that without stimulation; and their MT was significantly longer with stimulation than that without stimulation. The movement variability was enlarged with stimulation than that without stimulation. **Conclusions:** Results appear to suggest that the cutaneous stimulation that inhibits resting tremor also improves the RT of movement, but affects the execution of movement with increased MT. It is interesting that cutaneous stimulation seems to augment end-point variability of reaching movements. Further experiments and analysis are needed to understand the neurophysiological mechanisms underlying these effects of evoked cutaneous afferents on voluntary movement control in PD subjects. **References:** [1] Gelb, D. J., et al., 1999. Diagnostic criteria for Parkinson disease. *Arch. Neurol.* 56, 33-39. [2] Hu, Z. X., et al., 2018. Tremor Interaction with Voluntary Movement Control in Patients with Parkinson's Disease (in revision). [3] Hao, M. Z., et al., 2017. Inhibition of Parkinsonian tremor with cutaneous afferent evoked by transcutaneous electrical nerve stimulation. *Journal of neuroengineering and rehabilitation*, 14(1),75.

#### **1-E-47 Impaired motor abilities during prediction in children with autism spectrum disorder**

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Anecdotal reports and selected research results suggest that individuals with Autism spectrum disorder (ASD) exhibit difficulties in motor coordination, especially when interacting with dynamic objects, like catching a ball. A recent theoretical framework from our group proposes that the seemingly distinct manifestations of ASD in multiple domains may have a common core: an impaired ability to make predictions. We tested this hypothesis in the motor domain. Specifically, we examined whether individuals with ASD show impaired motor coordination when interacting with moving objects, especially in fast feedforward-controlled actions that rely on internal prediction. A number of studies

have already examined predictive abilities of children with ASD, although with inconsistent results due to heterogeneity of ASD samples and task designs. Therefore, we designed a test battery of multiple motor skills with systematic variations of task parameters and control tasks to take into account potential low-level confounds. 11 ASD children (high-functioning, age 7-12 years) and 25 neuro-typical, age-, gender-, and IQ-matched children (NT) performed 5 interception tasks in a virtual environment. The set-up afforded controlled manipulation of the time window for prediction, while simplifying the coordination challenges for hand movement. Subjects either pressed a button to predict the time or location of a launched ball (low coordination challenge), or they moved a paddle to catch or bounce a ball to hit a target (high coordination challenge). The gaze profiles during the button-pressing tasks were recorded using an eye-tracker. Additionally, subjects performed naturalistic ball catching, where 3D kinematics of joint movements and muscle activity of arm, leg, and trunk muscles were recorded to quantify anticipatory postural responses. A set of control tasks assessed more elementary motor abilities, such as postural control, reaction time, and smoothness of hand movements in very similar conditions. Results showed that, in virtual catching, ASD's accuracy decreased disproportionately relative to NTs when the ball trajectory was partially occluded. Also, when bouncing a ball to a target, ASDs exhibited lower accuracy. Motor impairments in ASD became more pronounced during tasks with high coordination challenge. Additionally, ASDs stagnated their gaze when the moving object was occluded; in contrast, NTs continued their gaze in time with the predicted ball trajectory. In naturalistic catching, EMG and the ball-hand distance profiles indicated that ASDs moved abruptly to catch the ball, whereas NTs showed more advanced planning of contact. Importantly, ASDs did not differ from NTs in control tasks such as reaction time, postural control and reaching to a static target. These results reveal that, despite considerable inter-individual differences, ASD children show impaired motor performance when prediction is an essential component. These findings are consistent with our hypothesis that the ability to predict may be a common denominator across ASD individuals despite their phenotypic variations. Given its broader theoretical embedding, this study has implications for autism beyond motor skills.

#### **1-E-48 Functional connectivity between motor brain areas and basal ganglia in Parkinson's Disease patients with and without freezing of gait.**

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Background and aim: Freezing of gait (FOG) is a debilitating motor symptom in advanced Parkinson's Disease (PD), characterized by brief motor blockages of the lower limbs while initiating gait, turning, or passing through a narrow space. The neural mechanisms underlying freezing are poorly understood. It is known that in PD, locomotion impairments come from dysfunctional cortico-striatal-thalamic-cortical loops and thus, projections to the striatum are impaired, making it important to adopt a network perspective when investigating PD-induced changes in brain functions. Changes in resting-state functional connectivity between important locomotor regions may help explain neural correlates of this motor impairment. Currently, only few studies have looked at resting-state functional connectivity in patients with PD with FOG, but it seems that functional connectivity between the right subthalamic nucleus and the supplementary motor area is reduced compared to PD patients without FOG. Therefore, the purpose of this study was to investigate the functional connectivity between different motor brain areas and the basal ganglia in PD patients with and without FOG using resting state fMRI functional connectivity. Methods: Fourteen participants with PD, eight with FOG ( $68 \pm 5$  years old) and six without FOG ( $66 \pm 3$  years old), as determined by the New-FOG questionnaire, participated in this study. All

participants were in Hoehn and Yahr Stage 2 or 3 and did not present cognitive impairment (MOCA > 26). All participants underwent a resting-state fMRI with a 3T scanner (5-minute BOLD sequence echoplanar images). Data analysis was performed using a resting-state pipeline relying on FSL and Matlab software. A seed-based analysis was used to identify voxels in motor areas (i.e. primary motor cortex, premotor area and supplementary motor area) temporally correlated with seed regions in the basal ganglia (i.e. caudate nuclei, striatum, globus pallidus, putamen and subthalamic nuclei) and in the thalamus, bilaterally. Between-group differences were determined using a fixed effect model. Results: PD with FOG had less functional connectivity of the bilateral supplementary motor areas and the bilateral premotor cortices with the thalami and important output nuclei of the basal ganglia (i.e. globus pallidi and subthalamic nuclei). In addition, patients with FOG had increased thalamic functional connectivity with multiple basal ganglia nuclei (i.e., striatum, ventral striatum, putamen and subthalamic nuclei). Conclusions: FOG in PD seems to decrease functional connectivity of thalamus and subthalamic nuclei with cortical motor-related regions and increase connectivity of the thalami with subcortical nuclei. These results may represent a reduced capacity for cortical inhibition of motor programs required for initiating and/or preforming uninterrupted locomotion, aspects impaired in FOG. This compensatory subcortical mechanism present in patients with FOG might reflect a maladaptive mechanism of the motor network.

### **1-E-49 Comparing upper extremity post-stroke proprioceptive impairment using 3 different methods**

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Proprioception is commonly impaired after stroke. These deficits can impact quality of movement and therefore recovery after stroke. Previously, our group has utilized proprioceptive matching tasks to interrogate the nature of proprioceptive impairment after stroke. These tasks use the stroke-affected arm as the reference arm, while the unaffected arm matches sensed behavior of the reference arm. These tasks are useful, in that they can test multiple aspects of proprioception while eliminating the confound of motor impairment. Less common is utilization of single-arm tasks that use the stroke-affected arm as the proprioceptive reference to determine a proprioceptive threshold. Here we make comparisons between tasks that assess proprioception across arms and a 2-alternative forced-choice test of proprioception that assesses proprioceptive discrimination of the stroke-affected arm. Nine controls and six stroke subjects performed robotic tasks measuring within and between arm proprioception: 1) Single Arm Proprioception (SAP) - Two-alternative-forced-choice task to determine proprioceptive sensitivity thresholds. The robot moved one arm and the subject used the opposite arm to indicate whether the robot had moved the arm left or right, with correct answers leading to smaller movements by the robot. 2) Position Matching (PM) - Without vision, the robot moved the subjects' arm to one of 9 locations and subjects mirror-matched the end position of the robotically moved arm, 3) Kinesthetic Matching (KIN) - Without vision, the robot moved the subjects' arm in one of 6 directions and subjects mirror-matched the robotic movement. For stroke subjects in all tasks, the robot moved the stroke-affected arm. For SAP, a median proprioceptive threshold was calculated from the magnitude of movements delivered by the robot. For PM, a task score was calculated from subject variability, shift, and area measures. For KIN, a task score was calculated from spatial and temporal parameters. Subjects also performed a visually guided reaching task (VGR) to compare motor and proprioceptive performance. Overall, we found that individuals with stroke had higher proprioceptive thresholds compared to controls in the SAP task (control=0.6± 0.2cm, stroke=5.2±5.6 cm, p=0.003). Further, we found that the SAP task was significantly correlated with both the PM (r=0.77, p<0.001) and KIN (r=0.70,

$p < 0.001$ ) tasks, where stroke subjects that had impairment in KIN and PM also had the highest SAP thresholds. Whereas, VGR performance was not significantly correlated with SAP ( $r = 0.48$ ,  $p = 0.09$ ). Preliminary results show that some individuals with stroke have proprioceptive impairments of the stroke-affected arm as detected by a single-arm test of proprioception (SAP). Further, the SAP task significantly correlates with between arm proprioceptive tests that use the stroke-affected arm as a proprioceptive reference (PM, KIN). Lastly, we see that impaired motor function of the affected arm did not correlate with within arm proprioceptive thresholds, suggesting that motor impairment of the affected arm is not a good predictor of impairments in proprioception and provides further evidence for the dissociation of proprioceptive and motor impairment in a clinical model.

### **1-E-50 Attacking abnormal arm muscle synergies after stroke using myoelectric computer interface training**

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Abnormal co-activation patterns of arm muscles, also called abnormal muscle synergies, cause substantial impairment of arm function after stroke. We designed a myoelectric computer interface (MCI) training paradigm to help stroke survivors reduce this abnormal co-activation. The MCI maps the activity of a pair of abnormally-coupled muscles to orthogonal components of cursor movement in a video game, and the user learns to decouple the muscles by moving the cursor to targets along the orthogonal mapping directions. We evaluated in-laboratory MCI training (18 sessions over 6 weeks) in 32 chronic stroke survivors. Subjects were split into three groups, two with different durations of isometric training (60 vs. 90 minutes per session), and one with 90 minutes of movement-based training conditions. Outcome measures included arm function, impairment, amount of co-activation, and elbow kinematics. We also examined the effects on muscle synergy patterns (i.e., motor modules)--during training and during a free reaching task to multiple targets--using non-negative matrix factorization during and after training in 6 subjects of each of the 90-min groups. Each group showed a trend of reduced arm impairment after 6 weeks of training--Fugl-Meyer Assessment of Upper Extremity, improvement of  $3.4 \pm 2.8$  (mean  $\pm$  SE) for 60-min group,  $3.8 \pm 3.6$  for 90-min isometric group, and  $3.5 \pm 3.4$  for the 90-min movement group). MCI training also improve subjects' arm function as measured by the timed Wolf Motor Function Test ( $-4.0$  s,  $-7.8$  s, and  $-6.9$  s for the 60 isometric, 90 isometric, and 90 movement groups, respectively, although only the 90 isometric group change was statistically significant) and Motor Activity Log (3.9, 5.5, and 1.2 point gains for the 3 groups). Overall, there was a trend to improved function with longer training; no statistical difference was seen between movement-based and isometric training. Elbow extension (tested during the reaching task) also improved by  $9.4 \pm 5.6^\circ$ ,  $8.2 \pm 7.1^\circ$ , and  $17.8 \pm 12.6^\circ$  for the three groups, and by  $10.7 \pm 4.3^\circ$  over all subjects ( $p = 0.03$ , Wilcoxon signed-rank test). Most gains persisted, but at a reduced level, at one month after training stopped. Subjects also displayed reduced co-activation during the training. This was seen in the identification of abnormal synergy patterns as well - the trained pair of muscles showed decreased co-activation during training. There was a greater number of synergies (3) required to explain 95% of the total EMG variance during training than during the reaching task at baseline (2). During the reaching task at week 6, the 90-min isometric group required 2 synergies to achieve 95% VAF, while the movement group required 3 synergies. Overall, this suggests that subjects learned to break up parts of synergies during the MCI training and that generalization of motor learning to the free reaching task may be better with movement-based training than with isometric training.

### **1-E-51 Portable, interactive motion-capture device for upper-limb movement rehabilitation: A feasibility study**

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This study developed and tested the feasibility of a custom-manufactured interactive portable motion-capture device (MAGIC table). This device can serve as 1) an assessment tool for upper-limb motor functions providing highly accurate evaluation metrics to satisfy criteria for laboratory research, as 2) an assessment tool for clinical diagnostics, and as 3) a movement rehabilitation device with multiple rehab-gaming options for children with upper extremity impairments, such as in individuals with Cerebral Palsy (CP). A 3D printed cup is magnetized with tunable intensity, adjusting its contact with the tabletop surface. A video camera with a portable computer tracks real-time kinematics of the hand-held cup on the 2D table surface, using a computer-vision algorithm. For motivational feedback, the 2D cup coordinates are used to provide real-time, audio-visual feedback about performance quality. Depending on the severity of the impairments, a metal ball that rolls in the shallow container can be added to enhance the challenge; New board games are easily created by drawing or placing targets on the whiteboard. Hence, users can creatively design their own games. Data are recorded on cloud networks that allows immediate transfer to researcher or therapist for post-hoc data analysis, enabling tele-rehabilitation. In addition to the board games drawn on the white board, virtual games are designed to assist practicing goal-directed movements suitable for upper-limb rehabilitation while engaging and entertaining children. As a feasibility test, kinematic data from the MAGIC table were acquired during prescribed discrete and rhythmic planar hand movements from three children with dystonia due to CP. The recordings demonstrated that the device could produce accurate evaluation metrics such as time-to-target or deviation from template tracking and also successfully demonstrated speed-accuracy trade-off with varying indices of difficulty. The strength of the device in the clinical environment was further demonstrated by the kinematic data acquired from a child with dystonia in the Intensive Care Unit (ICU) who had implanted a deep brain stimulator (DBS), where conventional motion capture system is not admitted. The device leverages new technology to address three key needs: First, it aims at increasing the volume of at-home physical therapy. Since the device has no hard constraints and the tasks and the motor challenges can be configured by the child, they will be motivated for longer time, requisite to improve their motor control. Second, the motor tasks of our device are inspired by daily motor challenges, such as self-feeding, and creative activity, such as drawing, which will develop self-confidence to participate in day-to-day activities. Third, the data acquisition software and hardware will provide both the precision of recording that is suitable for research purposes and also facilitates cloud monitoring of the progress of the therapy at home. The MAGIC table bridges the gap between therapeutic home use and laboratory research: patient data can be analyzed for scientific purposes and research insights can be immediately transferred to a therapeutic setting.

### **1-G-52 Rhythmic manipulation of complex objects with nonlinear and linearized dynamics**

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Manipulation of objects and tool use are vital components of the human behavioral repertoire. Surprisingly, how humans control objects or tools is still little understood. Interacting with objects is particularly challenging when the object has internal degrees of freedom that add complex dynamics. A mundane example is leading a cup of coffee to one's mouth to drink: the transporting hand applies a force not only to the cup, but also indirectly to the liquid, which in turn acts back onto the hand and



requires sensitive adjustments to avoid spilling the coffee. This study examined the transport of an object with internal dynamics mimicking the basic dynamics of a cup of coffee. A previous study showed that this nonlinear system can display chaotic, essentially unpredictable behavior, but subjects developed strategies that increased the predictability of the interactive behavior. This study compares how humans control the nonlinear and the linearized system, the latter where chaos is absent. The task of carrying a cup of coffee was simplified to a 2D cart-and-pendulum model, where a ball represented the liquid rolling in a semicircular cup manipulated by the subject. The system was linearized and rendered in a virtual environment; subjects interacted with the cup and ball via a robotic manipulandum. In 28 trials, subjects ( $n=16$ ) moved the cup and ball rhythmically between two spatial targets move for 35s in synchrony with a metronome-paced at 7 different frequencies between 0.6 and 1.2Hz; in 16 interspersed trials subjects moved at their own preferred frequency. Importantly, this dynamic system coupled to the hand has two resonances (0.67Hz; 1.08Hz), separated by one anti-resonance or dynamic zero (0.75Hz). We hypothesized that subjects: 1) avoid the anti-resonance frequency and move at one of the two resonance frequencies in both linear and nonlinear systems, 2) attempt to linearize the nonlinear system using small ball angles to make object behavior predictable, and 3) solidify their preferred frequency of motion at resonance, after exposure to the wide range of frequencies. Results showed that subjects strongly avoided the anti-resonance only in linear conditions, but they adopted one of two frequencies, which were close to the resonance of the coupled hand-object system. This preference was robust and not influenced by metronome-induced moving at other frequencies. Subjects did not attempt to linearize the nonlinear system using small ball angles. Subjects preferred smaller oscillation amplitudes at higher frequencies with an anti-phase relation between cup and ball motion. These results present first insights into how human achieve dexterous control of complex objects in continuous rhythmic movements that can pose complex interaction dynamics. These findings are of theoretical importance to understand human strategies in manipulating dynamically complex objects.

### **1-E-53 Impairment of human ocular tracking with low-dose alcohol**

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Previous studies have documented adverse effects of alcohol on oculomotor performance. For example, moderate-dose alcohol (yielding a Blood Alcohol Concentration or BAC of 0.04-0.1%) has been shown to decrease steady-state pursuit gain (Fransson et al., 2010, *Clin Neurophysiol*, 121(12): 2134; Moser et al., 1998, *J Neurol*, 245(8): 542; Roche & King, 2010, *Psychopharmacology*, 212(1): 33), to increase saccade latency (Moser et al., 1998, *J Neurol*, 245(8): 542; Roche & King, 2010, *Psychopharmacology*, 212(1): 33), to decrease peak saccadic velocity (Fransson et al., 2010, *Clin Neurophysiol*, 121(12): 2134; Roche & King, 2010, *Psychopharmacology*, 212(1): 33), and to increase the frequency of catch-up saccades (Moser et al., 1998, *J Neurol*, 245(8): 542). Here, we administered two doses of ethanol on different days, yielding moderate (0.06%) and low (0.02%) levels of initial BAC, to examine the effects on human ocular tracking over BACs ranging from 0.00 to 0.07%. Twelve subjects (8 females) participated in a 5-day study. Three days of at-home measurements of daily activity and sleep were monitored, followed by two laboratory days where, ~5 hours after awakening, we administered one of the two possible single doses of alcohol. Using a previously published paradigm (Liston & Stone, 2014, *J Vis*, 14(14): 12), we measured oculomotor performance multiple times throughout the day with three pre-dosing baseline runs and bi-hourly post-dosing test runs until the subject recorded a BAC of 0.00% for two hours. BAC was measured before each run using an Alco-Sensor IV breathalyzer (Intoximeters, Inc., St. Louis, MO).

For each of the oculometric measures, for each subject, we computed the within-subject % deviation for each test run from their baseline averaged across their three pre-dosing runs. We then averaged the data across subjects in 0.01% BAC bins. Finally, we used linear regression to compute the slope and x-intercept (threshold) of the mean binned % deviation as a function of BAC. We found that pursuit initiation was impaired at very low BAC levels, with significant ( $p < 0.002$ ) linear trends in latency (+1.3%/0.01%BAC) and initial acceleration (-4.6%/0.01%BAC) with extrapolated absolute thresholds at or below 0.01% BAC. We also found that steady-state tracking was impaired showing significant ( $p < 0.002$ ) linear trends in gain (-3.8%/0.01%BAC) and catch-up saccade amplitude (+9.1%/0.01%BAC), again with extrapolated absolute thresholds around 0.01% BAC. We also found a significant ( $p < 0.02$ ) increase in pursuit direction noise (+9.8%/0.01%BAC) with an extrapolated absolute threshold below 0.01% BAC. Many aspects of ocular tracking are impaired in a dose-dependent manner beginning at a BAC level around 0.01%, with significant effects at levels lower than previously reported and up to 8-times lower than the legal limit for driving in most states.

## F – Adaptation & Plasticity in Motor Control

### **1-F-54 Head movement during functional gait assessment predicts clinical measures in vestibular patients**

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A wide range of functions, from basic reflexes to high-level behaviors, depend on the vestibular system. By sensing head motion and then generating the appropriate reflexes, the vestibular system is vital for maintaining balance and stabilizing gaze. Using clinical measures, it has been shown that following unilateral vestibular loss, patients experience dizziness, headache, and impaired balance, postural, and gaze control. However, to date, much less is known about the effects of vestibular loss on voluntary behavior. Here, we assessed whether locomotive behavior can predict clinical measures in a group of patients with a diagnosis of vestibular schwannoma (VS) who had undergone a primary surgical resection of their tumor via suboccipital craniotomy and retrosigmoid approach with sectioning of the vestibular nerve. Head movements were recorded during Functional Gait Assessment (FGA) using a six-dimensional motion sensor (3-axis linear acceleration and 3-axis gyroscope) in (1) healthy volunteers and (2) patients before and six weeks after surgery. We computed measures of gait speed, asymmetry, and variability during FGA and then compared these with the clinical measures; dizziness handicap inventory (DHI), activities-specific balance confidence (ABC), Beck anxiety inventory (BA), FGA score, postural sway, and vestibulo-ocular reflex gain. Our results showed negligible correlations between gait parameters and clinical measures in the healthy volunteers. In contrast, we found significant correlations with multiple clinical measures in patients. First, before surgery, patients with higher head movement variability during walking also had larger postural sway. Correlations between gait parameters and clinical measures were even more common six weeks after surgery. Notably, gait variability correlated with multiple the clinical measures. Moreover, patients with lower anxiety and dizziness and higher confidence and FGA scores showed higher variability, and patients who walked faster had more dizziness and less FGA scores. Taken together, our results suggest that computed measures of gait speed, asymmetry, and variability from the FGA can be a predictor of the clinical measures and can be used for monitoring patients with unilateral vestibular loss.

### **1-F-55 Fatigue induces long lasting changes in motor skill learning**

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Fatigue due to physical exertion is a ubiquitous phenomenon in everyday life and especially common in a range of neurological diseases. While the effect of fatigue on limiting the execution of skills has been studied extensively, its influence on learning skills is unclear. The latter is of particular interest as it is common practice to train athletes, musicians or perform rehabilitation exercises up to and beyond a point of fatigue. In a series of experiments, we found that fatigue impairs not only execution but also learning of motor skill. The negative effect on learning is independent and beyond the detriments on execution, evidenced by impaired task acquisition on subsequent practice days even in the absence of fatigue. Further, we found that this effect is, in part, mediated centrally and can be alleviated by altering motor cortex function. Thus, the approach of training near the fatigue level should be carefully reconsidered.

### **1-F-56 Repeated bout rate enhancement is elicited by passive finger tapping**

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The freely chosen frequency of voluntary finger tapping is considered to be controlled by spinal central pattern generators (CPGs) in an interrelationship with supraspinal descending input and sensory feedback [1,2]. Besides, it has been shown that the freely chosen finger tapping frequency increases in the second of two consecutive tapping bouts separated by a rest period. The phenomenon has been termed repeated bout rate enhancement [3]. The overall aim of the present study was to further investigate the repeated bout rate enhancement phenomenon. In more details, it was elucidated whether sensory feedback, caused by passive finger tapping, would be sufficient to elicit repeated bout rate enhancement. Healthy individuals ( $n = 21$ ; 16 men and 5 women,  $1.83 \pm 0.08$  m,  $82.6 \pm 13.1$  kg, and  $25.3 \pm 3.1$  years) participated. Each participant reported to the laboratory twice, referred to as Session A and B. The sessions were separated by a three-week washout period. In Session A, two 3-min index finger tapping bouts were performed at freely chosen tapping frequencies. In Session B, a 3-min passive index finger tapping bout was followed by a 3-min tapping bout at freely chosen frequency. It applied to both Session A and B, that the bouts were separated by 10 min rest. The passive tapping was performed by using a custom-built machine that could move the passive finger. The tapping frequency during the passive tapping bout corresponded to the average tapping frequency that the participant had applied during the first tapping bout in Session A. The tapping frequency in the first bout in Session A was considered a baseline tapping frequency. The tapping frequencies in the second bouts in session A and B were  $12.9 \pm 14.8\%$  ( $p < 0.001$ ) and  $9.9 \pm 6.0\%$  ( $p = 0.001$ ) higher than the baseline tapping frequency, respectively. These differences were not significantly different ( $p = 0.438$ ). The results from Session A support previous findings by replicating the phenomenon of repeated bout rate enhancement [3,4]. The elicitation of repeated bout rate enhancement in Session B constituted a novel finding. It has been suggested that an increased CPG-mediated movement frequency output might be caused by increased supraspinal descending drive [5]. However, it is also possible that an increased movement frequency can occur without increased supraspinal descending drive as a result of excitation of the rhythm generating part of the CPG. The latter could be caused by neuromodulators released as a consequence of e.g. afferent feedback [6,7]. The present results from Session B might support the latter. References: [1] Hansen & Ohnstad 2008 Exp Brain Res 186: 365-73. [2] Shima et al. 2011 Conf Proc IEEE Eng Med Biol Soc: 4443-48. [3] Hansen et al. 2015 J Mot Behav 47: 490-96. [4] Mora-Jensen et al. 2017 Motor Control

21: 457-67. [5] Prochazka & Yakovenko 2007 Integr Comp Biol 47: 474-81. [6] Cropper et al. 2017 J Neurophysiol 118: 1861-70. [7] Frigon 2017 J Neurophysiol 117: 2224-41

### **1-F-57 Savings in muscle activation patterns during a virtual surgery task**

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Individuals post-stroke often exhibit "abnormal synergies", pathological patterns of upper limb muscle co-activation that lead to a compromised ability to perform daily life activities. Reducing abnormal muscle co-activation via a myoelectric computer interface has been shown to be feasible for a small set of muscles using arbitrary muscle-to-cursor mappings (Wright et al. 2013). Our long-term goal is to investigate whether abnormal synergies can be reduced by gradually normalizing the activity of multiple muscles via "virtual surgeries". A virtual surgery is a type of myocontrol task in which participants control the position of a cursor on a screen using EMG signals collected from multiple upper limb muscles while isometrically producing forces at the wrist (Berger et al. 2013). Here, we investigated how non-disabled participants learn a virtual surgery task that mimics the abnormal synergies observed post-stroke. Because such surgeries generate low controllability for some directions, and are consequently hard to learn (Berger et al. 2013), we compared learning virtual surgeries abruptly to gradually. In addition, we investigated whether learning such a task exhibits savings, which consist of an enhanced adaptation to a previously learned and subsequently washed-out task. Our experimental design comprised a baseline phase of EMG-force myocontrol, a virtual surgery phase, a washout phase, and a re-exposure to the same virtual surgery. During the baseline phase of the myocontrol task, the mapping from EMG signals to cursor position corresponds to the direction and magnitude of the forces generated at the wrist on the horizontal plane. Afterwards the virtual surgery is introduced: the mapping is modified, and participants must learn to complete the task under the new mapping. We quantified task performance as the error in cursor initial direction. Preliminary results show that subjects learned how to decrease initial angular error to baseline levels, and exhibited similar levels of washout in the two conditions. In addition, for both the abrupt and gradual groups, the error in initial direction became markedly smaller at the onset of the second virtual surgery phase, indicating the presence of savings in the adaptation to the virtual surgery, and the formation of a novel muscle activation pattern memory. Our results suggest that virtual surgery training could be effectively applied in a post-stroke rehabilitation protocol comprised of multiple short bouts of training.

### **1-F-58 Stepping in time: exploring locomotor adaptation and learning in persons with ET**

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Essential tremor (ET), the most common movement disorder, is associated with dysfunction in the the cerebellothalamocortical circuit. Gait impairment in persons with ET is becoming increasingly recognized, yet little is known about how dysfunction within this circuit affects locomotor adaptation. The ability to adapt one's walking pattern is critical for everyday ambulation, such as when approaching an obstacle or walking over uneven terrain. Herein, locomotor adaptation was compared between persons with ET and healthy older adults (HOA) as they were exposed to split-belt treadmill (SBT) walking. Participants walked with the belts moving in a 2:1 ratio for ten minutes and then washed out the pattern. They were then exposed a second time to the SBT to readapt for three minutes, followed by five minutes walking with the belt speeds in a 1:1 ratio to deadapt. Spatiotemporal asymmetries during baseline treadmill walking, adaptation, readaptation and deadaptation were compared, as well as the

rate of adaptation. Because step length during SBT walking can be manipulated by altering the location and timing of foot placement as well as the velocity of the foot relative to the hips, spatial, temporal, and velocity contributions of SLA were analysed. At baseline, persons with ET exhibited a statistically significant SLA while HOA walked symmetric at baseline. Both HOA and persons with ET demonstrated typical pattern of SLA adaptation from the beginning to the end of the adaptation period. HOA adapted their SLA closer to zero than did persons with ET in mid and late adaptation, and were less perturbed during readaptation than were persons with ET. Interestingly, while HOA adapted back to their baseline SLA, persons with ET did not adapt back to their baseline asymmetry. The groups similarly adapted the spatial and velocity contributions to SLA. However, HOA adapted temporal contributions to SLA, while persons with ET were unable. Our results suggest that persons with ET retain locomotor adaptation capabilities and adapt at the same rate as HOA. Unlike HOA, persons with ET did not adapt their gait back to baseline asymmetry but rather adapted their SLA close to symmetry. Compared to HOA, persons with ET seem unable to adapt the temporal contribution to SLA, suggesting an alteration in temporal control. Although the effects of ET on gait has been recently realized, the effects on locomotor adaptation are unclear. This study is one of the first to focus on understanding locomotor adaptation in persons with ET. These findings strongly support temporal locomotor adaptation impairment in persons with ET, which may contribute to gait difficulties in ET.

### **1-F-59 Perceived depth modulates visuomotor adaptation**

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Visuomotor adaptation in reaching is thought to reflect the update of a forward model, caused by an error between the desired and actual sensory feedback of the movement. This theoretical framework requires a critical assumption: In order to successfully learn a new movement, vision must provide motor planning with unbiased estimates of the spatial features of a scene, otherwise learning could be grossly inappropriate. But this line of reasoning produces two further assumptions: 1) Learning is based on an unbiased 3D representation of the external world and 2) only errors that are visually relevant to the task should affect motor learning. Surprisingly, these assumptions have only little support in the literature. Research on depth perception shows ample evidence that 3D information is often not recovered veridically in a variety of perceptual tasks. Moreover, errors in the computation of spatial properties such as distance and size do not simply affect perception: A growing number of studies has shown that reaching and grasping movements are affected by the same biases. Thus, it remains a puzzle how we successfully interact with the physical world given that the motor system does not escape perceptual biases. In this study, we addressed this problem by manipulating 3D information during a reaching-in-depth task, and we investigated whether motor learning changed as a consequence of these changes. In a virtual environment, subjects viewed a 6 degrees wide circular target at a simulated distance of 2 meters. In a blocked design, two different groups saw the target either alone (No-depth condition) or in the center of a virtual 3D scene (Depth condition). Both groups were instructed to reach forward to throw a virtual cursor at the center of the target. Visuomotor adaptation was induced via a task-irrelevant-error clamp: Regardless of the actual hand's direction, the cursor always appeared off the target by a fixed horizontal offset. As a result, trial after trial subjects unknowingly reached more and more in opposite direction to the visual error induced by the clamp. More importantly, this motor learning was stronger in the No-depth condition compared to the Depth condition, although neither directly interfered with the goals of motor task, in principle. Remarkably, these results mirrored those of a perceptual task, which showed that the perceived size and location of the target were different under

the same two visual conditions. As a result, the target appeared to occupy a wider portion of the visual field in the No-Depth condition compared to the Depth condition. These findings demonstrate that the visuomotor adaptation is the product of a more complex error analysis than previously thought, such that visuomotor adaptation is susceptible to 1) perceptual distortions of space and 2) errors that are perceptually, but not objectively, relevant for movement execution.

### **1-F-60 RoboBird: A passive exo-tendon for guinea fowl**

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Limb orthoses, including exo-skeletons, are externally worn braces or devices used to improve locomotor deficits, aid rehabilitation or augment human locomotor performance. While robotic and passive exo-skeletons have been shown to improve locomotor performance, the limitations of human experimentation have left unanswered how exo-skeleton design influences neuromechanics<sup>2</sup>, and, in turn, locomotor performance. To fill this gap, we present here the first ever wearable robotic device for a locomoting animal model (*Numida melaegris*). An untethered exo-tendon for a bipedal animal that closely mirrors human mechanics enables the study of the influence of wearable robotics on structure-function relationships up and down the temporal and spatial ladder - from short-term adaptations in musculoskeletal dynamics and sensorimotor signaling within a step to broader behavioral and physical changes that come with long-term use. The fundamental challenge of this work was to design an exo-tendon with the structural integrity to provide adjustable but consistent parallel elasticity while simultaneously minimizing discomfort and mass. Our design parallels current human passive, elastic ankle exoskeletons (hereafter: 'exo-tendon') in function. We found that a soft-exosuit design distributes forces, minimizes discomfort and could provide attachment points for the interchangeable, variable length springs. The spring path spans the ankle and MTP joints, mirroring the path of several digital flexors and supplementing elastic energy storage during stance phase. Flexion of the phalanges act as a natural clutch, disengaging the device during swing phase. Joint torques were quantified on an anesthetized animal with a custom force instrumented jig. Limb torques at MTP and ankle joints without the exo were subtracted from those with to quantify contribution of the exo-tendon across the span of limb configurations. This allowed determination of the moments at each joint from limb configuration during kinematic data collection with a tether free system. Birds wearing the exo-tendon were able to walk and run on a treadmill with minimal gait disturbance while 5 to 10% assistive torques at each joint. Variations in metabolic energy consumption with changing spring properties suggests that birds adapt body and limb-level neuromechanics in response to exo-tendon assistance. This preliminary work is proof-of-concept of the feasibility of an animal model for wearable robotics and opens new paths of research to answer questions before inaccessible: What sensorimotor feedback systems modulate neuromechanical adaptations to robotic augmentation? What type of long-term augmentation results in neuromechanical and musculoskeletal changes that maximize running efficiency, jumping ability or potential for recovery from neuromuscular injury? How do assistive interventions during growth alter the adult locomotor system?

### **1-F-62 Implicit adaptation is driven by the update of an inverse model, not a forward model**

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The motor system's ability to recalibrate motor commands in response to sensory prediction errors is widely thought to occur through error-based updating of an internal forward model which predicts the

consequences of motor commands. This forward model can later be used to guide action selection. It has alternatively been suggested, however, that recalibration might occur by using errors to directly update an underlying controller (inverse model), without the need for a forward model. Here, we show how these two proposed mechanisms of implicit adaptation can be dissociated. A major advantage of forward-model-based learning is that, whenever the observed sensory feedback disagrees with model predictions, the resulting sensory prediction error can be used directly to update the forward model (Jordan and Rumelhart, 1992). In inverse model adaptation, however, the motor system additionally needs to know how errors in sensory coordinates relate to errors in motor coordinates. Normally, leftward errors can be reduced by shifting motor output rightwards. This approach works well for small miscalibrations, including moderate ( $<90^\circ$ ) visuomotor rotations. For tasks like a mirror reversal, however, this approach fails: a rightwards correction following a leftwards error actually increases the error in the next trial. In this case, the same update rules that work for a shift or a rotation make the motor output drift further and further away from the target from one trial to the next. By contrast, the update rules for a forward model should be equally effective for a rotation or for a mirror reversal. Mirror reversal can thus serve as a litmus test to distinguish whether learning is driven by updating a forward model or an inverse model; only in the latter case would we expect to see initially small errors amplify into larger and larger errors across trials. We tested how the motor system implicitly responds to an inversion of visual feedback in order to determine whether implicit recalibration is driven by a forward or an inverse model. Participants (N=12) reached through 4 different targets arranged along the cardinal directions. After a baseline, unperturbed period, we introduced a mirror reversal of the cursor across the y axis. Participants were briefed on the perturbation and, in order to isolate implicit adaptation, were instructed to keep aiming their hand, rather than the cursor, through the target - i.e. avoid engaging in any explicit re-aiming strategies, in spite of cursor errors. We found that, despite these instructions, participants consistently drifted away from the targets positioned along the mirroring axis (12 and 6 o'clock targets): small initial errors were amplified through implicit adaptation, consistent with our predictions for inverse-model-based adaptation. Our results thus suggest that, contrary to commonly accepted views, implicit recalibration does not rely on updating a forward model but instead occurs through directly updating an inverse model.

### **1-F-63 Functional vestibular cortical changes with spaceflight**

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Microgravity influences both central vestibular processing and vestibularly-mediated behaviors such as balance and mobility; however, the relationship between central vestibular processing and behavior is not well understood. Previously, we identified differences in the neural correlates of vestibular processing and in balance and functional mobility after 70 days of exposure to a microgravity analog (head-down-tilt bed rest, HDBR). Here, we examine whether six months of exposure to a microgravity environment on the International Space Station influences the neural correlates of vestibular processing in 8 astronauts. Using functional magnetic resonance imaging (fMRI), we measured brain activity in response to pneumatic cheekbone taps, a validated method of vestibular stimulation. Participants completed fMRI scans as well as balance and functional mobility testing two times preflight and up to four times post-flight. This has allowed us to examine the time course of recovery of brain and behavioral metrics after re-adaptation to Earth's gravitational environment. Preliminary results

indicated several regions (e.g., left thalamus and bilateral superior temporal gyri/insula) in which flight subjects showed greater changes in activation in response to vestibular stimulation pre- to immediately post-flight compared to changes in ground-based controls over a 90-day period (n = 15). Astronauts also showed increased brain activation in several frontal and sensorimotor regions (e.g., pre and postcentral gyrus) immediately post-flight followed by a slow but complete recovery to their baseline state by three months post-flight. Similarly, astronauts showed increased deactivation in the vermis of the cerebellum immediately post-flight followed by slow recovery to baseline levels by three months. Further, among the astronauts, increased activation pre to post-flight in several regions (e.g., thalamus) was associated with poorer functional mobility post-flight, and decreased brain activation in several regions (e.g., superior frontal gyrus) was associated with poorer vestibularly-mediated balance post-flight. These findings suggest that astronauts experience reduced neural efficiency (i.e., more neural resources needed to process vestibular inputs) and/or sensory reweighting from pre to post-flight. Further analyses will include comparisons of the astronaut cohort and individuals (n = 11) who underwent 30 days of HDBR in an elevated carbon dioxide environment, which is intended to mimic conditions on the International Space Station. We expect to identify some overlap in vestibular brain and behavioral changes among both groups, but also some differences due to the specific effect of microgravity on the vestibular system. Taken together, these findings have implications for better understanding the neural mechanisms of spaceflight-induced changes in functional behaviors (e.g., balance and mobility) that are mediated by the vestibular system.

#### **1-F-64 Reorganizing muscle coordination using mental imagery and augmented visual feedback**

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Understanding how to reorganize muscle coordination to produce skilled movements is a key aspect of motor learning. In this regard, two common strategies - mental imagery and augmented visual feedback - have been widely used as tools to teach skilled movements. However, how these strategies directly affect underlying muscle coordination is not well known. Here, we examined the impact of mental imagery and visual feedback on muscle coordination when learning a new task. We designed an isometric myocontrol reaching task where the muscle activity of 8 muscles in the arm were mapped to the position of a cursor on the computer screen. Participants were college-aged adults, and were asked to activate their muscles to move the cursor as fast as possible into targets presented in pseudorandom order in one of eight directions. Specific muscle pairs were mapped to either the up, down, left, or right directions, and synergistic activation of muscle pair(s) would allow for successful movement into a target. This type of control of the cursor was intentionally designed to be difficult so that we could evaluate the effect of providing mental imagery and augmented visual feedback. In the mental imagery condition, participants were asked to imagine their arms as a joystick that needed to be moved forcefully to move the cursor. In the augmented visual feedback condition, participants were shown the activity of each of their 8 muscles as they moved the cursor on the screen. Participants performed the task for 30 trials, and the entire session lasted for approximately an hour. The hypothesis we are testing is whether the mental imagery practice condition would be superior to augmented visual feedback in improving task performance by reorganizing muscle coordination. Preliminary results showed that the mental imagery practice condition exhibited a trend towards increased use of synergistic muscles for specific directions i.e. activation of the correct muscle pairs. The results of this experiment will provide the basis for reorganizing muscle coordination in participants with coordination deficits, such as chronic stroke survivors.



### **1-F-65 Use-dependent biases due to movement repetition are small and unaffected by rewards**

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Current theories of sensorimotor learning suggest that when a movement is repeated, it becomes less variable and future movements are biased in the direction of the repeated movement. This process is referred to as use-dependent learning (UDL). Recent work using an isometric pinch task has suggested an interaction between UDL and reinforcement processes, with rewards for task success enhancing UDL (Mawase et al., 2017). However, little is known about how these findings generalize to dynamic movements involving many more degrees of freedom. Also, given that the role of reinforcement was ambiguous in earlier UDL studies, the goal of the current study was to systematically explore the interaction between UDL and reinforcement during reaching. In an initial pilot study, we used a reaching task similar to that employed in a seminal study on UDL by Verstynen and Sabes. Participants (n=10) made repeated reaches to one location with infrequent reaches to probes located  $\pm 30$ ,  $\pm 60$ , and  $\pm 90$  from the repeated location. Whereas participants in the Verstynen study were given performance-related reward information on all trials, we only provided online visual feedback of the cursor representing hand position during reaches to the repeated location, with no feedback on probes. Despite the removal of overt rewards, the hand heading angles revealed biases towards the repeated target that were comparable in size to those reported in the Verstynen study ( $\sim 15^\circ$  maximum). However, a finer grained analysis revealed that a significant number of reaches to probe targets were curved, and that many of these curved reaches began as movements towards the repeated location. This suggests that participants may have erroneously planned to reach to the repeated location and then corrected the movement online. Thus, a component of what appears to be UDL may actually result from an action prediction bias (i.e., tendency to anticipate the most frequent action; Marinovic et al. 2017), with removal of curved reaches from our analyses revealing only a  $4^\circ$  bias. We directly examined the effect of reward feedback in a second experiment in which online visual feedback was never provided. Instead, one group of participants (n=12/group) received rewards for accurate reaches to the repeated location. To signal success, the target doubled in size and changed color, and a pleasant sound was played. No feedback was given on misses or reaches to probe locations. For the control group, all reaches were made without feedback. To eliminate the action prediction biases observed in the pilot study, we added a 500 ms delay between target onset and an auditory "go" cue. The delay was effective, eliminating all curved reaches. In terms of reaching biases, both groups demonstrated only small biases of  $\sim 3^\circ$  towards the repeated location. Taken together, these studies provide preliminary evidence indicating a very modest impact of UDL on reaching, with no enhancement of the effect from reward.

### **1-F-66 Integration of non-automatic and automatic motor control policies during novel bimanual motor task**

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When humans perform novel motor tasks that require highly skilled visuomotor coordination such as mirror-reverse reaching (Gritsenko and Kalaska, 2010; Telgen et al., 2014), the corrective response to sudden visual perturbations (e.g., cursor jumps) separates into automatic ( $\sim 90$  ms) and non-automatic ( $\sim 200$  ms) epochs. In such situations, the former response increases the visual error, whereas the latter appropriately reduces the error. Such dichotomization is based on two distinct control policies, both of which define how to perform a motor action (Scott, 2016). After some practice, subjects become able to

suppress the automatic response, but speeding-up the timing of the later appropriate corrective response has yet to be shown. The current study uses a bimanual motor task to investigate whether extensive practice can convert the non-automatic control policy into a faster automatic policy. Twenty healthy subjects practiced a novel bimanual reaching task with an exoskeleton robot (KINARM Exoskeleton, BKIN Technologies, Canada) for 3 consecutive days. The lateral mid-point of the index fingertips of both hands and the lateral distance between the fingertips were transformed into cursor motion in the x- and y- positions, respectively. Subjects performed 3-minute training blocks 10 times each day, in which a target randomly appeared at one of 9 locations (3 × 3 matrix, with an interval of 75 mm) on the monitor. The target position shifted when the cursor was held in a target for a specified duration; therefore, the subjects were instructed to hit the target as many as possible during 3 minutes. Before (Day 1) and after (Day 1-3) the training blocks, we evaluated the latency of corrective visuomotor responses by applying sudden vertical cursor jumps during 200 mm of center-out reaching to the left or right target (testing block). The number of targets hit in a training block significantly increased during 3 days, and reached the amount equivalent to the control training block which was performed with the right hand and a cursor displayed directly above the fingertip. The latency of appropriate corrective response to cursor jumps was delayed at the beginning of Day 1 compared to corrective responses when using only the right-hand (right-hand,  $142.8 \pm 17.9$  ms; bimanual,  $257.6 \pm 51.3$  ms) but significantly decreased after 3 days (bimanual,  $189.0 \pm 31.6$  ms), though it was still longer than the control block. These results indicate that the use of visual information for goal-directed motor actions was recalibrated and sped up with practice. Much greater practice may be required before such non-automatic control policies can be fully converted into fully automatic motor skills.

### **1-F-67 Unimanual contribution to bimanual coordination in musicians: differential impact of the left and right hands**

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We previously demonstrated superior bimanual coordination in musicians performing a complex finger sequence task compared to non-musicians. Specifically, while musicians appeared to spend a longer time in planning the entire sequence, they were faster, more accurate, and less variable in task performance. Additionally, only musicians demonstrated increased left (L) to right (R) interhemispheric inhibition (IHI) which was related to the observed better bimanual coordination. This unequal contribution of the two hemispheres to transcallosal inhibition in musicians compelled us to determine the role of each individual hand in bimanual performance. Thus we investigated the association between unimanual motor performance and bimanual coordination in musicians and non-musicians. Thirty-six musicians and 36 non-musicians were recruited. There were no group differences in hand dominance. Three 4-element finger sequences were used to determine unimanual (L and R hand) performance. Participants were instructed to press the keys as fast and accurately as possible while maintaining an even key pressing interval. Total time to complete the sequence, reaction time (time between sequence appearance and first key press), movement time (time between first and final key press), accuracy, and variability of key pressing interval (standard deviation, SD) were recorded. Three 8-element bimanual sequences comprised the bimanual task and generated the same measures as above. Similar to bimanual performance, reaction time was significantly longer while movement time was significantly shorter in musicians for both the L and R hands compared to non-musicians. The L hand in musicians also demonstrated reduced total time as well as SD of key pressing interval compared to non-musicians. In both groups, total time, reaction time and movement time measured in the bimanual task

were significantly related to the same measures in both L and R hands (all  $r$  values  $> 0.7$ ). In non-musicians, SD measured in the bimanual task was significantly related to unilateral hand performance ( $r = 0.41, 0.50$  for L and R hands, respectively). In musicians, SD of the bimanual task was significantly associated with SD of the R hand ( $r = 0.45$ ) only. However, accuracy of the bimanual task in musicians was related to accuracy of the L hand ( $r = 0.34$ ) only; while neither hand performance was related to bimanual accuracy for non-musicians. As in bimanual performance, musicians took longer than non-musicians to plan the sequences, but were faster while accurately executing the action with either the L or R hand. Timing outcomes were highly correlated between bimanual and unimanual performance regardless of hand and group. Only in musicians, did the performance of a single hand (L hand: accuracy, R hand: variability) relate to bimanual coordination. This differential motor performance may be reflective of the unequal inhibition between the two hemispheres (i.e. increased L to R IHI) seen in the musicians only.

### **1-F-68 Generalization of internal models of limb dynamics**

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Humans can learn a variety of novel movement patterns in many different contexts. Here we are investigating whether, how and to what extent the nervous system learns and generalizes intersegmental limb dynamics in humans and monkeys. We do so by locking the shoulder joint during pure elbow movements. Locking the shoulder joint cancels the interaction forces that arise at the shoulder during forearm rotation and thus removes the need to activate shoulder muscles. If the nervous system learns a novel internal model of limb dynamics, we expect participants to learn to reduce shoulder muscle activity over trials. We also predict that this learning generalizes to novel situations. Forty-five humans and two macaque monkeys generated voluntary pure elbow movements using a robotic exoskeleton (KINARM, BKIN Tech). This device permits shoulder and elbow rotation in the horizontal plane. First, participants did the task with the shoulder free to move (baseline phase). We then physically locked the shoulder joint and participants repeated the same pure elbow movements (adaptation phase). Last, we unlocked the shoulder joint and participants again had to counter the intersegmental dynamics to generate pure elbow movements (post-adaptation phase). We introduced probe trials at the end of the adaptation phase to test whether and to what extent this learning generalizes to a) different elbow orientations, b) different shoulder orientations, c) different reaching distances. In the baseline phase, we found robust activation of shoulder flexor muscles for pure elbow flexion trials - as required to counter the intersegmental dynamics. In the adaptation phase, we found a substantial reduction in shoulder muscle activity - as appropriate for the novel intersegmental dynamics. We also found a reduction in shoulder muscle activity when probed in a different shoulder orientation but not elbow orientation or reach distances. Thus, the nervous system locally learns novel intersegmental dynamics rather than a general model of the altered limb dynamics. We are now beginning to dissect the neural circuit that underlies this learning via large scale neural recordings in monkey primary motor cortex.

### **1-F-69 Proprioceptive changes associated with complex motor skill learning**

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Motor learning involves changes in behavior through practice. This process is known to be associated with plasticity in motor brain regions, including motor cortex and cerebellum. It is well established that

sensory information is important for motor control, yet its role in learning has only recently been investigated. Motor adaptation, a paradigm in which performance errors improve trial-by-trial in response to an external perturbation, has been linked to plasticity in somatosensory cortex and shifted proprioception, or limb position sense, in the direction of the perturbation. The association between proprioception and learning has been found for different adaptation paradigms, as well as simple planar reaching. However, the link between proprioception and more complex skill learning is unknown. Unlike adaptation that perturbs performance during well-learned movements, skill learning involves the acquisition of new movement patterns in the absence of a perturbation with performance limited by the speed-accuracy tradeoff. Here we investigate the link between proprioceptive function and motor skill learning in the right upper limb. 16 right-handed healthy young adults made visually-guided 2D reaching movements through an irregular-shaped track (20 cm x 20 cm horizontal workspace) as quickly and accurately as possible using a KINARM Endpoint robotic manipulandum (BKIN). Subjects practiced movements over two consecutive days at a restricted movement time range. Skill was quantified by measuring motor performance (percentage of movement inside track) across 5 movement time ranges before practice on day 1 (baseline), and 24 hours after practice on day 3 (retention). Proprioception of the right hand was measured before and after motor practice on each day, and at retention, in the left-right axis (N= 16) and forward-back axis (N = 11 of 16). The assessment positions were determined using an adaptive staircase algorithm that allowed us to quantify proprioceptive bias (i.e. accuracy) and sensitivity (i.e. acuity). After two days of practice, there was a significant shift in the speed-accuracy function, indicating improvement in motor skill, at retention relative to baseline performance ( $F(1,15) = 15.03$ ,  $p < 0.001$ ). There were differential effects in proprioceptive bias and sensitivity. Proprioceptive bias appears to improve after training on day 1 and day 2, but the effect does not persist at retention. In contrast, improvements in sensitivity seem to occur on a slower time scale, with the largest changes observed at retention. These findings may have implications for the role of proprioceptive improvements in motor control and complex skill learning.

### **1-F-70 Differential involvement of the posterior-parietal cortex in consolidation for procedural and declarative learning**

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Previous research suggests that human memory is modular with different neural substrates mediating multiple memory processes. Evidence from transcranial magnetic stimulation (TMS) studies investigating declarative memory show that a network involving the prefrontal cortex mediates much of the consolidation process, whereas motor cortex has been shown to mediate the consolidation of procedural memory. When learning two different kinds of tasks in quick succession, the memory of the second task interferes with the memory of the first task, causing the consolidation of the first event to be impaired. Cohen and Robertson (2011) tested this interference effect by having participants learn a procedural task and then declarative task (or vice versa) in immediate succession, and then provided TMS to the dorsolateral prefrontal cortex (DLPFC) and the motor cortex (M1) immediately after learning. They discovered that declarative interference was prevented when downregulating DLPFC and procedural interference was prevented when suppressing M1 activation. Using continuous theta-burst stimulation, we downregulated the left posterior-parietal cortex (IPPC) immediately after participants learned two different kinds of skills (Declarative: word-list task and Procedural: implicit sequence-learning task) to investigate the extent to which IPPC is involved in the consolidation of memory. We hypothesized that because the PPC is involved in sensorimotor transformations, that we could prevent

the interference of procedural memory similar to how the motor cortex prevents this same interference from occurring, and did not expect to see any effects for declarative consolidation due to limited research for this particular paradigm. Results demonstrate that downregulation of IPPC prevents interference for procedural memory, similar to the prevention of procedural interference when activity in M1 is downregulated, whereas participants who received sham stimulation saw a significant increase in reaction times for the learned motor sequence, indicating that interference was not prevented for that condition. Difference in reaction times between participants who were provided with sham stimulation and those with stimulation to IPPC and M1 was only present in the subset of participants who implicitly learned the motor sequence, and participants who explicitly learned the motor sequence experienced similar amounts of interference occurring across stimulation conditions. Interference was not extinguished for declarative memory, indicating that other networks are involved in the interference of explicitly learned information. The present results suggest that the the IPPC may play a causal role in the consolidation of procedural memory but not declarative memory. More research is necessary to uncover the different networks involved in memory interference.

### **1-F-71 Implicit adaptation is modulated by task relevance of multiple cursors**

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Implicit sensorimotor adaptation is driven by discrepancies between 'predicted' and 'actual' feedback, or sensory prediction errors (SPEs). Data suggest this process is automatic and obligatory, even when detrimental to task success (Srimal et al., 2008; Mazzoni & Krakauer, 2006). One explanation for this apparent insensitivity to task success is that sensory predictions are generated relative to the efferent motor command, irrespective of the context. To explore whether implicit adaptation is truly insensitive to task conditions, we manipulated the relevance of the sensory feedback. Using a center-out reaching task, multiple feedback cursors with different rotations were presented simultaneously (Kasuga et al, 2013). By using redundant feedback signals, the movements and feedback could be held constant while instructions were used to manipulate the task relevance of the feedback cursors. In experiment 1, three cursors were simultaneously presented as participants reached towards a target located at one of three locations. In the baseline phase, the cursor rotations were -45°, 0° and 45° with respect to hand position and participants were instructed to hit the target with the middle, 0° cursor. Three conditions in the training phase were compared. For each condition we varied the mean rotation of all three cursors, and the "task-relevant" cursor, defined by the one they were instructed to hit the target with. The other two cursors were irrelevant distractors. If adaptation was insensitive to task relevance, adaptation should be driven equally by all three cursors. If on the other hand, adaptation was sensitive to task relevance, adaptation should be driven only by the rotation of the task-relevant cursor. In all groups, participants learned to successfully hit the target using the correct cursor, effectively ignoring the irrelevant cursors. After the training block, we probed implicit adaptation and generalization by instructing participants in all groups to move their hand directly to the target in the absence of visual feedback. The results demonstrated that for each group, aftereffects were dependent on the rotation of the task-relevant cursor, rather than the overall rotation of all of three cursors. In experiment 2, we provided a further within subject test by counterbalancing the target configuration as well as the cursor configurations. On each trial, two targets were presented, at -45° and 45° relative to the midline. Two feedback cursors were presented with constant rotations of -45° and 45°. Participants were instructed to hit the -45° target with the -45° cursor. Thus, each participant had a task-relevant and a task-irrelevant target-cursor pair throughout the training block. Consistent with the hypothesis of the task-relevant cursor being

more heavily weighted, we observed significantly larger aftereffects at the task-relevant compared to the irrelevant target location.

### **1-F-72 Evidence of mixed reference frame representations for both implicit and explicit learning in a visuomotor adaptation task**

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To successfully interact with the physical world, the brain must learn novel visuomotor transformations between the body and the environment. A central issue in sensorimotor control is how these newly learned visuomotor transformations are represented. To elucidate this representation, studies typically perform postural manipulations to determine the extent to which the learned transformation is linked with the state of the body (i.e., intrinsic reference frame) or the environment (i.e., extrinsic reference frame). Despite extensive experimental work, there remains no consensus: studies have reported intrinsic, extrinsic, and mixed reference frames. Overlooked in this approach is that learning is often multifaceted, consisting of both implicit and explicit forms of learning. These distinct forms of learning could hypothetically occur in separate reference frames, and therefore the proposed mixed representation may well reflect the combination of separate implicit and explicit components with different reference frames. To investigate this possibility, we employed recently developed techniques to isolate the effects of implicit motor adaptation and explicit re-aiming in a visuomotor rotation task. We then tested generalization across different limb postures to dissociate intrinsic and extrinsic reference frames of representation, and determine if they mapped cleanly onto implicit and explicit forms of learning. Implicit generalization appeared to display an even mixture of intrinsic and extrinsic representations (51% extrinsic and 49% intrinsic), as the peak of generalization shifted to an intermediate location between postural changes. Explicit generalization also appeared to display both intrinsic and extrinsic representations, but with a different mixture ratio (70% extrinsic and 30% intrinsic). Interestingly, the extent of explicit generalization was reduced with changes in limb posture whereas the extent of implicit generalization was maintained. With the generalization functions of implicit and explicit learning characterized in isolation, we then sought to determine if we could predict the generalization function when implicit and explicit learning combine in a standard visuomotor rotation task. Here, we employed a simple model whereby the overall generalization function is the result of a linear combination of explicit and implicit learning, whose individual functions are the result of a gain field of intrinsic and extrinsic representations. Remarkably, we show that this model, without any free parameters, is able to account for nearly 85% of the variance associated with the generalization pattern in a typical visuomotor task. Alternative models in which the weighting of the implicit and explicit components were allowed to vary or single process models that arise from a combination of intrinsic and extrinsic representations did not produce a significantly better fit. Taken together, these results show that both implicit and explicit forms of learning contribute to visuomotor learning and subsequent generalization. Each form of learning features distinct contributions from both intrinsic and extrinsic reference frames, and the combination of these distinct features shapes the generalization pattern observed at novel limb postures.

### **1-F-73 Combining reward and M1 transcranial direct current stimulation enhances the retention of newly learnt sensorimotor mappings**

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It is well known that levels of motor retention, i.e., the process by which acquisition of skilled motor performance can be translated into long-lasting behavioral changes are influenced by the type of feedback given when learning a new sensorimotor mapping. For instance, providing positive feedback (i.e. reward) while individuals learn to account for systematic perturbations does not enhance learning, but increases retention of the new motor memory. Interestingly, applying transcranial direct current stimulation (tDCS) over the primary motor cortex (M1), an area suggested to play a vital role in retention, during learning also results in a marked increase of retention of the newly learnt transformation. While previous physiological studies have demonstrated that reward and tDCS are capable of modulating GABAergic mediated short intracortical inhibition (SICI) within M1, it remains unknown, however, whether combining reward and tDCS results in an additive benefit of motor retention and whether these interventions interact with overlapping neural mechanisms. In this study, we investigated whether the combination of rewarding feedback and M1 tDCS while participants learned to account for 30-degree visuomotor transformation resulted in enhanced motor retention. To do this, our study followed a 2x2 factorial design with participants were assigned to receive either reward-stimulation (n=14), reward-sham stimulation (n=14), null feedback-stimulation (n=14), null feedback-sham stimulation (n=14) during visuomotor adaptation. We characterized memory retention by measuring the gradual drift back to baseline performance when visual feedback of performance was removed ("retention" phase; a total of 288 retention trials). Furthermore, to determine if reward and tDCS share common physiological mechanisms underpinning learning, we used transcranial magnetic stimulation to assess motor cortical excitability and inhibition (i.e. SICI) before and after all participants learned the visuomotor rotation. We found that both the reward-stim and reward-sham groups had increased motor retention at the beginning of the retention phase (i.e. first 80 trials). However, only the reward-stim group had prolonged retention at the end of the phase (i.e. final 80 trials). Surprisingly, we also found that only the reward-stim had a significant increase in SICI after exposure to the perturbation (i.e. prior to retention assessment), whereas no significant increases were found in M1 excitability. These findings demonstrate that the combination of reward and M1 tDCS results are additive in providing stronger retention of motor adaptation. Furthermore, these results indicate that the reliability and validity of using tDCS within a clinical context may depend on the type of feedback individuals receive when learning a new motor pattern.

#### **1-F-74 Lack of generalization between explicit and implicit visuomotor learning**

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Adapting to a novel visuomotor condition during targeted reaching movements has been traditionally thought to mainly involve implicit, as opposed to explicit, processes. This view was challenged by recent findings, which suggest that visuomotor adaptation involves both explicit and implicit learning processes. The objective of this study was to determine the extent of generalization between an "explicit" learning condition, in which subjects were asked to reach toward imaginary targets under a veridical visuomotor condition by using a cognitive strategy, and an "implicit" condition, in which subjects were asked to reach toward visual targets under a typical novel visuomotor rotation (i.e., 30 degrees CCW) condition. It was hypothesized that if the two conditions had a reasonably large overlap in terms of their processes (i.e., the latter condition also involves explicit processes), initial visuomotor learning under one condition would facilitate subsequent visuomotor learning under the other condition to a great extent. Healthy, right-handed young adults were separated into 2 groups: Implicit-to-Explicit, or Explicit-to-Implicit. Subjects in the former group experienced familiarization, implicit learning, and

explicit learning sessions; and those in the latter group experienced familiarization, explicit learning, and implicit learning sessions. The extent of generalization was also investigated in three additional subject groups who first experienced the explicit condition, then one of the three following conditions: an implicit condition with a specific instruction (i.e., to use the cognitive strategy developed during the explicit condition), an implicit condition with an opposing direction of visuomotor rotation, and a reaching condition with no visual feedback. Results indicate that initial explicit learning did not facilitate subsequent implicit learning; and initial implicit learning did not facilitate subsequent explicit learning either. Results also indicate that when provided with an instruction (i.e., to use the cognitive strategy developed during the explicit condition), subjects adapted to the visuomotor rotation faster. However, the rate of learning in this condition was still significantly slower than that in the explicit condition, indicating that generalization between the explicit and the implicit conditions is limited even when a specific instruction is provided. Finally, results demonstrated that initial explicit learning did not facilitate subsequent implicit learning when the opposing direction of visuomotor rotation (i.e., 30 degrees CW) was provided. Collectively, these results suggest that the extent of overlap between the cognitive and/or neural processes underlying implicit and explicit learning conditions is minimal, which in turn suggests that explicit processes may not play a significant role in typical visuomotor adaptation.

## G – Theoretical & Computational Motor Control

### **1-G-75 The neural substrates of error and success in adaptation to visuomotor rotation**

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A prominent view in the computational motor control community is that adaptation to sensorimotor perturbations occurs through an error-based mechanism where sensory prediction errors lead to updates of forward and inverse internal models. Nevertheless, adaptation was recently shown to be also affected by reward signals that could directly drive changes in the motor plan. The involvement of multiple computational mechanisms in sensorimotor adaptation suggests that multiple brain networks may be active during the processing of feedback in an adaptation task. Here, we localize the areas that show sensitivity to the presence and size of errors and to success feedback. Lying in a 3T MRI scanner (Philips), 17 participants made fast out-and-back movements with their wrist. They were instructed to position their movement reversal point at a target. After movement completion, visual feedback was given at the reversal point and a change in the color of the target informed about failure or success. Following a baseline session with no perturbations, the visual feedback rotated with respect to movement direction according to a random walk algorithm. In 20% of the trials, participants did not receive feedback. To extract activation patterns on a trial-by-trial basis, we used a slow event-related fMRI design with ITI of 6-10 seconds. Behavioral results show that due to the random walk perturbations, participants were experiencing errors throughout the entire experiment. However, these errors gradually reduced and became smaller than the applied rotation, indicating a trial-by-trial adaptation. Despite the lack of differences in kinematics between feedback and no feedback trials, a vast network of brain areas showed higher BOLD activity for the former. These areas include the PPC, primary and premotor cortices, lateral occipital areas, and areas in the anterior lobe of the cerebellum. A portion of these areas (primarily in the parietal cortex) showed increased activation for error feedback. A parametric analysis in search of areas that are sensitive to the size of errors revealed areas only in the anterior lobe of the cerebellum. Contrasts between the successful trials and the no-feedback trials revealed increased activation in the basal ganglia and decreased activation in the primary motor cortex. Our results delineate the neural substrates of error based and reward based learning processes



that operate simultaneously during adaptation to sensorimotor perturbations. The study is supported by the NIPI (138-15-16), the ISF (607/16) and the ABC Robotics Initiative.

### **1-G-76 Do neuromechanically-based effort variables represent the metabolic cost of reaching?**

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We make hundreds of reaching movements every day that exhibit an amazing consistency. This consistency has led to the proposal that there is a certain cost to making an arm reaching movement that humans attempt to minimize and that this cost is conserved across individuals. Energy cost likely plays a role in partly determining this cost and ultimately determining movement kinematics with arm reaching. However, objective energy costs such as metabolic cost can be difficult to measure. Thus a proxy for metabolic cost is often used. Here we examine how five model-based neuromechanical variables, often used to represent energy costs, relate to the measured metabolic cost of reaching. We developed a biomechanically accurate model of the arm that estimates multiple biomechanical variables and related them to experimentally measured metabolic cost of reaching. Experiment: Metabolic rate was collected from eight subjects that made 10 cm reaches. Subjects made reaches to and back from four different targets at 45, 135, 225, and 315 degrees from the right horizontal around a central point. Four masses, 0, 5, 10, and 20 lbs, were added to the hand. Reaches were made at six different velocities. Model: The biomechanical model of the arm consists of two joints (shoulder and elbow), two arm segments (upperarm and forearm), and eight muscles. The model simulated planar reaching movements from a minimum jerk trajectory using the experimentally constrained movement durations. Using inverse dynamics, we calculated joint torques from the trajectory to eight simulated targets with four different added masses at the hand. To calculate the muscle force, we distribute the force across muscles according to different minimization functions. Once muscle force has been determined, we calculated muscle active state and determined neural drive to the muscle. Lastly, a model for energetic expenditure was used for an estimate of metabolic rate at each time point. We then integrated the time-series data for joint torque, muscle force, muscle active state, neural drive, and estimated metabolic rate for each mass and speed condition and fit these sums to collected metabolic data using either a linear or quadratic function. The best fit linear to measured metabolic cost was the energy expenditure model with an R2 value of 0.71. A common function for estimating cost of arm reaching, the rate of torque squared, performed significantly worse (R2=0.49). The three remaining variables tested, force, active state, and neural drive, provided similarly low explanatory power (R2 values 0.47, 0.48, and 0.59 respectively). Nonetheless, these variables are able to predict the general shape of the collected metabolic cost. However, they are poor at describing differences between conditions and fail at faster speeds. Our analysis highlights the importance of exercising caution when representing metabolic cost via model-derived biomechanical variables.

### **1-G-77 Elucidating the role of sensorimotor cortex for motor adaptation using hierarchical optimal feedback control theory**

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The brain consists of multiple control loops that orchestrate adaptive, robust motor control. For instance, spinal, cerebellar and cortical circuits are all involved in motor adaptation. How do these distributed systems robustly coordinate control? To approach this questions, we study a simple two-

level hierarchical system comprised of two optimal feedback control loops that control the movement of an arm model. The low-level system has access to the the state of the arm in joint coordinates, while the higher level controller operates in task space. Both systems' output torque control signals are generated by using the iterative linear quadratic regulator method (Li & Todorov, 2004; ICINCO). The target position is provided to the high-level controller, where it is incorporated in the cost function and used improve the task space trajectory over multiple trials. The desired task space trajectory is then used to calculate target joint angles for the low-level controller to use in its own cost function. <p />Such a system can reproduce recent behavioral findings from motor adaptation studies in mice (Mathis et al. 2017; Neuron). Briefly, both mice and the two-stage controller system can adapt to pulsed-force fields across trials, and exhibit fast online-corrections when presented with an unexpected perturbation. Crucially, inactivating the high-level controller during force-field perturbations results in a failure to adapt, while still allowing successful task completion (i.e. motor execution, which requires the low-level controller), as was found behaviorally. Moreover, with temporally-specific inactivation of the high-level controller model mid-way through a block of perturbation trials, further adaptation was blocked, as was empirically found in mice by closed-loop optogenetic-based inactivation of somatosensory cortex.

### **1-G-78 Spatial encoding of reaches in preparatory motor cortical activity**

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One of the open questions in motor neuroscience asks how movements are specified before they are executed. Several studies have examined neural activity that precedes movement in order to understand what aspects of a movement are planned prior to execution. During preparation for hand reaches, individual neurons in premotor cortex (PMd) are known to reflect the direction and distance of upcoming movements, as well as speed (Churchland et al. 2006), target location in visual space (Shen et al. 1997), and target location relative to the eye and hand (Batista et al. 2007). While such evidence provides clues, it is still up for debate exactly how the nervous system plans movements. A crucial step in this process will be to identify the independent parameters present in motor cortical activity. In this study, we asked two main questions (1) what are the spatial factors that describe the upcoming movement in PMd?, and (2) how precisely are they planned before movement onset? Answering these question could help elucidate the role of PMd during motor preparation. Most studies of preparatory activity have examined how the activity of single neurons correlate with external parameters. Since information is encoded with high redundancy between neurons, population-level analyses can reveal the latent and primary factors of the entire population of neurons in a certain area. It can also be used to quantify the amount of information encapsulated by the factors available in the recorded area. Here, we used population-level analyses to reveal the neural structure of rhesus macaque PMd during an instructed delay reaching task. We found that the primary independent spatial factors do not appear to be direction and distance, but rather appear to be the location in Cartesian space. While the structure of the neural states for upcoming reaches is Cartesian, the distribution of single trials forms an ellipse whose principal axis is oriented in the direction of the reach in neural space. As in behavioral studies of preparation (Messier & Kalaska, 1997), the variance in neural state is smaller for direction than distance. However, while there is less information about distance than direction in preparatory activity, for the purposes of decoding, they can be estimated with equal precision (std = 1.6 cm). This can partially be explained by the fact that speed is also reflected in preparatory activity. Our findings shed light on the neural structure and the spatial factors encoded in PMd during movement preparation, and how precisely those factors are planned. Revealing the Cartesian structure of preparatory activity gives

further insight into the process by which voluntary movements are planned and supports the view that PMd is involved in "high-level" planning of reaches. As one translational application of these results, mapping the population level factors and their decoding precision can be used for designing optimal target locations for brain-machine interfaces.

### **1-G-79 Cerebellar activity reflects the attenuation of self-touch**

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It has previously been shown that the perception of self-touch, i.e., touching one hand with the other, is attenuated compared to externally produced touch of the same intensity (Blakemore et al., 1999; Shergill et al., 2003; Bays et al., 2005). Earlier neuroimaging studies have related this attenuation to a modulation in the cerebellar activity ipsilateral to the moving hand (Blakemore et al., 1998; Shergill et al., 2013). However, these studies have neither behaviourally quantified the sensory attenuation in order to isolate those neural responses that are related to the phenomenon, nor they have included proper control conditions to account for the simple effect of moving and receiving touch at the same time. Moreover, they have not reached a consensus on the role of the cerebellum in sensory attenuation, since one study reported decreased activity (Blakemore et al., 1998) and the other reported increased activity (Shergill et al., 2013) of the cerebellum ipsilateral to the moving hand, when comparing self-generated touch to externally generated touch. To address these issues we conducted an fMRI study with thirty volunteers. We employed a 2x2x2 factorial block design with the movement of the right index finger (yes/no), the touch on the left index finger (yes/no) and the distance between the hands (0 cm/25 cm) as within-subjects factors. In a behavioural session performed immediately after the scanning, we quantified the participants' attenuation with the classic force-matching task (Shergill et al., 2003): participants reproduced external touches applied to their relaxed left index finger by pressing their right index finger against a sensor placed either on top of their left index finger (0 cm), or at distance (25 cm) from it, or by using a slider (control condition). Our main finding is a significant activation of the left cerebellar hemisphere (Lobule VI) that is ipsilateral to the receiving hand, for the three-way interaction reflecting the specific effect of sensory attenuation, i.e., the difference between the externally generated touch and the self-touch when the hands are close compared to when there are distant. At the behavioural level, we confirmed that participants attenuated more during self-touch (0 cm) compared to when their hands were distant or they used the slider. We conclude that the cerebellum is playing a key role in somatosensory attenuation and discuss this within the context of internal forward models and sensorimotor predictions (Wolpert and Flanagan, 2001; Kawato et al., 2003; Wolpert and Kawato, 1998).

### **1-G-80 Decomposition of endpoint jerk during arm movements of stroke survivors and unimpaired controls**

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Neurological deficits may affect the smoothness of arm movements. The smoothness of the upper limb endpoint trajectory depends on joint angular velocities, accelerations and jerks and on arm pose and on its rate of change (quantified by the Jacobian and its derivatives with respect to time). We decomposed the time integral of the squared endpoint jerk into terms related to the aforesaid constituents and studied whether the smoothness of endpoint movement is dominated by the smoothness of individual

joint rotations or by the change of arm pose. A former analysis of 3-joint planar arm movements of able-bodied participants found that total endpoint jerk is dominated by individual joint angular jerks [1]. This analysis is extended for stroke survivors and for unimpaired controls performing planar 2-joint movements. 6 right handed, unilateral, hemiparetic stroke survivors (36-69 yrs.) and 6 right handed controls (38-73 yrs.) participated in our study. They were seated in a chair fixed in front of a horizontal planar robot. The wrist was fixed to the robot's handle. Each subject performed 164 repetitions of a point-to-point reaching task: they moved the hand from a central starting position to one of two radial targets projected in the horizontal plane. The robot monitored hand position at 1000 Hz [2]. When executing a motor task, the structure of endpoint jerk as a function of jerks at the joint level may vary among subjects and trials depending on the rate of change in arm pose. The endpoint jerk is the sum of 3 terms. One term (a) is the product of the Jacobian and joint angular jerk. This gives the contributions of angular jerk at the shoulder and elbow joints to endpoint jerk, distinct from the contributions of joint angular velocities, accelerations and change of arm pose. The two other terms, (b) and (c) depend on change of arm pose, but not on joint angular jerk. For all participants, the endpoint jerk was dominated by term (a). The integral of the square of this term explains over 90% of the integral of the squared endpoint jerk, for all participants. Surprisingly, for severely-impaired stroke survivors, the time integral of the square of term (a) was larger than 100% of the integral of the squared endpoint jerk itself. This can occur because the square of the sum of the 3 terms has four components:  $a^2$ ,  $b^2$ ,  $c^2$ , and  $2(ab+ac+bc)$ . Note, the integral of the fourth one can be negative. We found that it is negative for severely-impaired stroke participants. This negative term may reflect deficits in neural control and impaired ability of stroke survivors to compensate for multi-joint interaction torques. [1] Laczko J, Jaric S, Tihanyi J, Zatsiorsky VM, Latash ML (2000), J. of Applied Biomech. V.16.pp.14-26. [2] Laczko J, Scheidt RA, Simo LS, Piovesan D. (2017), IEEE Trans Neural Syst and Rehab Eng. V.25/7pp.:798-810 This work was supported by grants R01 HD053727 and GINOP 2.3.2-15-2016-00022.

### **1-G-81 Towards goal-driven deep neural network models to elucidate human arm proprioception**

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Proprioceptive signals are a critical component of our ability to perform complex movements, identify our posture and adapt to environmental changes. Our movements are generated by a large number of muscles and are sensed via a myriad of different receptor types. Even the most important ones, muscle spindles, carry highly multiplexed information. For instance, arm movements are sensed via distributed and individually ambiguous activity patterns of muscle spindles, which depend on relative joint configurations rather than the absolute hand position. This high dimensional input (~50 muscles for a human arm) of distributed information poses a challenging decoding problem for the nervous system. Given the diversity in muscle activity, what are the necessary computations that the proprioceptive system needs to perform to sense our movements? Here we studied a proprioceptive variant of the handwritten character recognition task to gain insight into potential computations that the proprioceptive system needs to perform. We focussed on handwritten character classification of muscle length configuration patterns that were required to draw that character. We started from a dataset comprising of pen-tip trajectory data recorded while subjects were writing individual single-stroke characters of the Latin alphabet (Williams et al. ICANN 2006), and employed a musculoskeletal model of the human upper limb to generate muscle length configurations corresponding to drawing the pen-tip trajectories in multiple horizontal and vertical planes. Using this model we created a large, scalable

dataset of muscle length configurations corresponding to handwritten characters of varying sizes, locations and orientations ( $n > 105$  samples). To determine the difficulty of this problem, we trained support vector machines (SVM) to solve a binary one-vs-all classification task on the dataset, which achieves an accuracy of  $0.89 \pm 0.08$  (mean  $\pm$  s.e.m). Contrary to naive expectation, reading out the character at the level of muscles is much easier whereas SVMs trained on the same task using pen-tip coordinates performed relatively poorly:  $0.75 \pm 0.14$ . This suggests that the musculoskeletal system itself serves as a non-linear projection to a higher dimensional space, which simplifies character recognition. Next we focussed on goal-driven deep neural network architectures to achieve higher accuracy. Training deep neural networks requires a large, diverse datasets and challenging tasks. We found that the scalable dataset for character recognition we generated is large enough to constrain deep convolutional architectures. We are currently exploring the performance of different deep-learning architectures in solving the handwritten character classification task to investigate which representations are learned and what computations are most efficient. We found that convolutional neural networks factoring out temporal and inter-muscle ('spatial') information achieve almost perfect accuracy for the multi-class problem. These preliminary results suggest that neural networks can learn pose-invariant character recognition from muscle configurations.

### **1-G-82 Stability and predictability in the control of dynamically 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, bidirectional forces come into play; the hand applies forces on the cup and coffee inside, and the sloshing coffee also exerts forces on the hand. To avoid spilling the coffee, a subtle control strategy is required to preempt and compensate those complex interaction forces. To date, motor neuroscience has primarily focused on simple movements like reaching to a target, or grasping static or transporting rigid objects. However, findings from simple actions are difficult to extrapolate to tasks with complex dynamics. For such complex nonlinear interactions, the slow neural transmission and neuromotor noise make feedback control insufficient while prediction based on internal models of complex dynamic objects seems computationally implausible. Previous work on continuous interactions showed that humans exploited dynamic stability in simple interactions or 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 perturbations. Since these complex tasks are transient in nature and occur far from an equilibrium point, traditional Lyapunov stability analysis is inapplicable. Instead, contraction analysis was used to assess stability. We expected that with practice subjects learned to exploit contraction regions to stabilize their trajectories, 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) For both assistive and resistive perturbations, subjects learn to harness contraction regions to stabilize the interaction. 2) Contraction regions are utilized differently, depending on the perturbation type. To compute the contraction regions, a contraction metric was obtained by

numerically solving a partial differential equation relating the system dynamics to this metric. Results show that subjects stabilized their trajectories and attenuated the perturbations by moving through contraction regions of the free, unforced system. This stabilized the performance and made the dynamics more predictable. Moreover, subjects chose the contraction regions with relatively slow guaranteed convergence rates, which is a trade-off between stability and flexibility. These results demonstrate that humans are sensitive to stability properties of the task and simplify the dynamics to make safe interaction with dynamically complex objects possible.

### **1-G-83 Cost functions as a language for internal communication in the sensorimotor system**

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What does the brain control? The brain as a whole can only control muscle activity, but nevertheless this question is fundamental because of the (often implicit) assumption that the sensorimotor system is organized into high-level and low-level controllers. Thus the actual question is, what commands do the high levels send to the low levels? Here we propose cost functions as a language for internal communication between levels. Traditional optimal control models postulate a parsimonious cost which the organism has good reasons to optimize, and proceed to show that the behavior is close to the optimal solution. This works well in simple laboratory tasks. Consider however a parsimonious cost for a real-world task such as getting into your car. On the surface this resembles reaching or eye movements: the cost would penalize energy expenditures along the way and reward being inside the car at some final time. But the behavior can be long and complex: find the keys, open the garage door, walk around whatever is in the way, unlock and open the car door, maneuver your body into the car. How can optimal (or even sub-optimal but plausible) solutions be found in cases where the cost specifies so little about the movement details, and there is no simple heuristic (e.g. "move towards the target") that works? This question faces organisms having to perform such computations in their brain, scientists having to understand what happens in someone else's brain, and engineers having to control robots with or without understanding the brain. The hierarchical optimization we consider here is a divide-and-conquer strategy, aiming to make the above computation more tractable. The role of the high level is to replace the original parsimonious cost with a more elaborate intermediate cost which has the following defining properties: (1) it is easier to optimize than the original cost; (2) the resulting solution is close to the optimal solution for the original cost. The high level then sends this intermediate cost to the low level, which optimizes it in the usual sense of optimal control. What makes a good intermediate cost? The answer depends on what the low level is good at optimizing. From the viewpoint of the high level, the sensorimotor periphery together with the low-level controller can be considered an augmented dynamical system, whose control inputs happen to be cost functions instead of muscle activations. The high level then has to solve an unusual optimal control problem which is nevertheless well defined. We present computational results illustrating these ideas in tasks involving full-body movements and dexterous hand manipulation. In these multi-contact behaviors, managing the discontinuous contact dynamics is a major control challenge which is naturally handled by the low level. This enables the high level to optimize on long time scales despite the daunting movement complexity present on short time scales.

### **1-G-84 A predictive framework to indicate task invariance of distal upper limb muscle synergies**

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Dexterous hand control requires coordination of multiple joints and muscles, putatively achieved through synergistic activation of small groups of muscles. Invariance of muscle synergies across related but different functional tasks is critical to the hypothesized framework of synergistic control. The present study was designed to test whether a relatively small set of hand/forearm muscle synergies is shared across task and posture during behavior. To do so synergies were derived during finger spelling, grasp mimicking in two postures, and an unconstrained exploration task. Cross-classification was used to probe task invariance via prediction of the EMG patterns of new hand postures. Ten healthy right hand dominant subjects (3F, 24.3±7.6 years) participated following informed consent. All subjects completed 3 tasks (Finger Spelling [FS], Grasp Mimicking [GM], Free Movement [FM]). EMG was recorded from 16 muscles of the distal right upper limb. Task order was randomized and counterbalanced; rest was provided as needed. Subjects were seated with their right forearm supported in a trough and instructed to restrict movement to the wrist, hand, and fingers. In the FS task, subjects mimicked hand postures of the American Sign Language alphabet presented on a computer screen (33 characters, 3x/character, 99 trials). In the GM task subjects mimicked 14 grasp postures in either prone (GM-P) or semi-prone (GM-SP) position presented on a computer screen (14 grasps, 3x/grasp, prone and semi-prone position, 84 trials). For both tasks subjects had 2 sec to form the posture, 6 sec to maintain it, and 2 seconds to return the hand to rest. In the FM task subjects were instructed to freely move their hand and wrist as to not spend time in a specific posture (3x/2 min). EMG was filtered (10-300 Hz) and divided into 300ms epochs (during static hold for FS and GM tasks). The root mean square from each epoch was subjected to non-negative matrix factorization to identify a set of synchronous muscle synergies and activations from each task. To assess prediction accuracy of synergies within and across tasks a support vector machine with a radial basis function kernel was used for classification. To obtain data for classification across tasks, the extracted synergies for one task were used to obtain the activation matrix for a different task using non-negative least squares estimation. Hyper-parameters were optimized by ten-fold cross validation. The number of synergies was selected by finding the peak prediction accuracy from the classification. This procedure was repeated for random synergies and random activations drawn from a Gaussian distribution with the same mean and variance. Across all 5 tasks, 7.42±0.68 synergies yielded the peak predictive power (77.76±2.60%) for the 4 constrained tasks (FS, GM, GM-SP, GM-P). At 7 synergies classification accuracy of prediction of each constrained task from each task-derived synergy basis was significantly greater ( $p>0.05$ ) than chance, estimated from the randomizing either bases or activations. These data demonstrate that hand/forearm muscle synergies derived from various constrained, and perhaps more importantly even unconstrained, behaviors, can be used to form a predictive framework for a wide variety of hand postures.

### **1-G-85 Throwing is not all about timing: adding noise can enhance timing accuracy**

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Accurate target-oriented throwing is a uniquely human behavior that, together with tool use, has been critical in human evolution. Previous studies identified a required accuracy of up to 1ms for the ball release, which appears to conflict with estimates of temporal resolution of the neuromotor system: spike train variability is closer to 10ms. This study aimed to characterize how humans improve their throwing accuracy in the face of this intrinsic variability given these seemingly stringent timing requirements. We also examined whether adding extrinsic noise could benefit their throwing accuracy by increasing 'pressure' on timing precision. A virtual throwing task, inspired by the pub game skittles, served as test bed. Subjects threw a ball tethered to a post to hit a target in a virtual environment. The

ball's trajectory was fully determined by the angle and velocity at release; error was defined as the minimum distance between ball's trajectory and target. The task had redundancy as an infinite number of angle-velocity combinations could achieve zero error, defining a solution manifold. The geometry of the solution space depended on the target location. In Experiment 1, four groups of 10 subjects practiced for 6 days (240 throws per day); each group with a different target location. Based on mathematical analysis of the solution space, we hypothesized that subjects would improve their performance by exploiting the redundancy of the solution space and align their hand trajectory with the solution manifold. To quantify this strategy, two metrics were calculated based on the hand trajectory in the solution space: Timing error quantified the difference between actual ball release time and the release time that would have achieved zero error. Timing window quantified the time during which the hand trajectory was aligned with the solution manifold. Results showed that subjects first decreased timing error, followed by lengthening the timing windows. This pattern was invariant across solution spaces. In Experiment 2, two groups of 10 subjects practiced throwing to one of the target locations for 11 days. From day 3 to 8, noise was added to the time of ball release: at each throw, the angle and velocity measured at ball release was modified by noise. We hypothesized that this added noise would improve task performance, both in terms of timing error and timing window. Results showed that subjects in the noise group indeed performed significantly better than the control group. This hitting success was due to a decrease in timing error. Importantly, this improvement persisted on days 9 to 11 after the noise was withdrawn. These findings demonstrate that humans can overcome their intrinsic variability in timing by creating tolerance windows to allow temporal imprecision without compromising hitting success. As variability was enhanced by adding external noise, humans could improve timing error even further. Importantly, this strategy persisted even without extrinsic noise, indicating beneficial effects of variability in sensorimotor learning. In conclusion, the exquisite skill that humans have evolved for throwing is achieved by developing strategies that are less sensitive to neuromotor noise or unexpected disturbances from environment.

## Poster Session 2

### A – Control of Eye & Head Movement

#### **2-A-1 Use of eye-movements during reproduction of multi-modal self-motion**

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While we move in a 3D environment the combined information from several modalities is usually used to estimate the parameters of self-motion. In the visual modality the global optic flow is an important cue that enables humans and animals to infer the direction and the speed of self-motion. The presence of optic flow information can influence the eye movements of a subject in a two-fold way. On the one hand it elicits automatic eye-movements (similar to optokinetic nystagmus, OKN) that depend on the vector of retinal image motion. On the other hand, top-down driven eye-movements can sample different parts of the visual field to get more accurate information about the optic-flow pattern. Motion information obtained from tactile or auditory modality generally do not require or elicit eye movements, however, it is not clear yet whether this additional sources of information influence the visual intake of information and eye movement patterns. We investigated the eye-movements of six human subjects during a bimodal visuo-auditory distance reproduction task. Subjects sat in front of a large tangent projection screen (70° by 55°). In the first part of each trial (encoding phase) the subjects observed a simulated motion over a plain of random dots that was paired with a sinusoidal sound that coded for



different speeds of motion by a different pitch (higher pitch -> faster speed). In the second part (reproduction phase) they had to actively reproduce the distance covered during the encoding phase using a joystick. In the encoding phase, the self-motion stimulus was always bimodal. In the reproduction phase only the visual information, only the auditory information or a combination of both were provided. The main questions were: 1) Whether there are differences in the eye movement patterns between the encoding and the reproduction phase that reflect the different cognitive processes during the two phases. 2) How the availability of information from different modalities influences the eye-movements. 3) Whether there are parameters of eye-movements that predict the performance in the distance discrimination task. We found that each subject utilized a very restricted part of the stimulus area to obtain information about the simulated self-motion. The dimension of these parts differed between but was highly reliable within the individual subjects. The diameter of this area was typically  $\sim 3^\circ$  and the position was highly correlated on a trial-by-trial basis between the encoding and the reproduction phase ( $r \sim 0.7$ ,  $p < 0.001$ ). Surprisingly this was also the case when during the reproduction phase only auditory information was presented ( $r \sim 0.5$ ,  $p < 0.001$ ). Interestingly, the same was true for the speed of the slow phases of the eye movements. The absolute eye-movement speeds were on trial-by trial basis highly correlated between the encoding and the reproduction phases ( $r \sim 0.75$ ,  $p < 0.001$ ), this remained true (although to a smaller degree) when only auditory information was presented during reproduction ( $r \sim 0.35$ ,  $p < 0.01$ ). We conclude that the subjects at least partly employed reproduction of the oculomotor movement pattern generated during the distance encoding as a strategy for a successful distance reproduction. Supported by DFG-CRC/TRR 135

## **2-A-2 Bilateral subthalamic nucleus deep brain stimulation increases fixation instability: evidence for impaired attention to task set**

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Bilateral subthalamic nucleus deep brain stimulation increases fixation instability: evidence for impaired attention to task set Lisa Chin Goelz<sup>1, 2</sup>, Leo Verhagen<sup>3</sup>, Maya Cottongim<sup>1</sup>, Daniel Corcos<sup>1</sup>, Fabian J.

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Objectives: Patients with Parkinson's disease (PD) exhibit fixation instability compared to healthy controls. Studies in neurologically involved populations have shown that fixation instability is indicative of inattention and may be related to a reduced ability to maintain task set. However, this is yet to be shown in patients with PD. Additionally, PD patients present with greater prosaccade errors during the antisaccade task compared to controls. These errors significantly increase during bilateral (BOTH) deep brain stimulation of the subthalamic nucleus (STN DBS) but not during unilateral (UNI) or during no stimulation (OFF). In order to investigate the effect of STN DBS on fixation instability and to further our understanding of the relationship between fixation instability and attention to task set, we asked the following questions: Does STN DBS affect fixation instability? Is this effect different when attending to different task sets? Is fixation instability during the antisaccade task related to prosaccade errors?

Methods: Ten patients with advanced PD and bilateral STN DBS were tested while off their anti-parkinsonian medication during OFF, UNI, and BOTH on separate days. Each testing session began 3 hours after the appropriate stimulators were turned off for the condition of that day. Patients performed 3 tasks during each stimulation condition: fixation only (FixONLY), fixation prior to prosaccades (FixPS), and fixation prior to antisaccades (FixAS). The order of conditions and saccade tasks were randomized. Fixation instability was quantified using the following measures: number of horizontal

saccades, square-wave jerks, and saccade amplitude. Results: The effect of STN DBS on fixation instability was dependent on task set. STN DBS had no effect for the FixONLY task. For the FixPS task, there was a significant increase in number of saccades during UNI ( $p < 0.0001$ ) and BOTH ( $p < 0.0001$ ) stimulation and a significant increase in square-wave jerks during UNI ( $p < 0.001$ ) and BOTH ( $p < 0.001$ ) stimulation. For the FixAS task, only the BOTH condition significantly increased number of saccades ( $p < 0.0001$ ) and square-wave jerks ( $p < 0.001$ ). There was no effect of stimulation on saccade amplitude across task sets. Finally, only the number of horizontal saccades during the AS task was significantly associated with the prosaccade error rate ( $p = 0.004$ ). Conclusions: The current study shows that STN DBS has a differential effect on fixation instability depending upon task set. Bilateral STN DBS increases fixation instability in the prosaccade and antisaccade task, whereas unilateral STN DBS only increases fixation instability in the prosaccade task. Further, bilateral STN DBS increases fixation instability in the antisaccade task, and this increased instability is related to an increased probability of making a prosaccade error. Our findings suggest that bilateral STN DBS may interfere with attention to task set.

### **2-A-3 Sensitivity to visual gain modulation in head-mounted displays depends on fixation**

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A primary cause of simulator sickness in head-mounted displays (HMDs) is the rendering of visual scene motion that does not match head motion. Agreement between visual scene motion and head motion can be quantified based on their ratio which we refer to as visual gain. We suggest that it is useful to measure perceptual sensitivity to visual gain modulation in HMDs (i.e. deviation from gain=1) because conditions that minimize this sensitivity may prove less likely to elicit simulator sickness. In prior research, we measured sensitivity to visual gain modulation during slow, passive, full-body yaw rotations and observed that sensitivity was reduced when subjects fixated a head-fixed target compared with when they fixated a scene-fixed target. In the current study, we investigated whether this pattern of results persists when 1) movements are faster, active head turns, and 2) visual stimuli are presented on an HMD rather than on a monitor. Subjects wore an Oculus Rift CV1 HMD and viewed a 3D scene of white points on a black background. On each trial, subjects moved their head from a central position to face a 15 deg eccentric target. During the head movement they fixated a point that was either head-fixed or scene-fixed, depending on condition. They then reported if the gain applied to the visual scene motion was too fast or too slow. Gain on subsequent trials was modulated according to a staircase procedure to find the gain change that was just noticeable. Sensitivity to gain modulation during active head movement was reduced during head-fixed fixation, similar to what we observed during passive whole-body rotation. We conclude that fixation of a head-fixed target is an effective way to reduce sensitivity to visual gain modulation in HMDs, and may also be an effective strategy to reduce susceptibility to simulator sickness.

### **2-A-4 Microstimulation in a spiking neural network of the midbrain superior colliculus**

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The midbrain superior colliculus (SC) generates a rapid saccadic eye movement to a sensory stimulus by recruiting a population of cells in its topographically organized motor map. Supra-threshold electrical microstimulation in the SC reveals that the site of stimulation produces a normometric saccade vector with little effect of the stimulation parameters. Interestingly, electrically evoked saccades (E-saccades) have kinematic properties that are indistinguishable from natural, visual-evoked saccades (V-saccades).

These findings support models in which the saccade vector is determined by a center-of-gravity computation of activated neurons, while its trajectory and kinematics arise from downstream feedback circuits in the brainstem. Recent single-unit recordings, however, have indicated that the SC population also specifies instantaneous kinematics. These results support an alternative model, in which the desired saccade trajectory, including its kinematics, follows from instantaneous summation of movement effects of all SC spike trains. But how to reconcile this model with microstimulation results? Although it is thought that microstimulation activates a large population of SC neurons, the mechanism through which it arises is unknown. We developed a spiking neural network model of the SC, in which microstimulation directly activates a relatively small set of neurons around the electrode tip, which subsequently sets up a large population response through lateral synaptic interactions. We show that through this mechanism the population drives an E-saccade with normal kinematics that are largely independent of the stimulation parameters. Only at very low stimulus intensities the network recruits a small cell population with low firing rates, resulting in smaller saccades with abnormally slow kinematics.

## B – Fundamentals of Motor Control

### **2-B-5 Motor fatigability in humans is associated with a shift from mesial to lateral premotor-motor interactions and changes in motor cortex inhibition**

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Motor fatigability describes a performance decrease when tasks are executed for an extended time period. However, the neurophysiological mechanisms mediating motor fatigability are currently not well understood. Here we tested fatigability by instructing participants to perform repetitive finger tapping at maximal speed for 40s. This task is characterized by significant reductions in movement frequency or "motor slowing", which result at least partly from supraspinal processes. We performed a series of experiments applying functional magnetic resonance imaging (fMRI), electroencephalography (EEG), and transcranial magnetic stimulation (TMS) while healthy participants performed either fatiguing (40s) or non-fatiguing finger tapping (10s). In the first experiment, fMRI data was acquired during blocks of fatiguing and non-fatiguing tapping. We found a general increase in BOLD activity within primary motor cortex (M1), premotor cortex (PMC), supplementary motor area (SMA) and cerebellum (Cb) over the course of motor slowing (N = 25, parametric modulation, pFWE < 0.05). Dynamic causal modelling (DCM) further revealed that the increase in BOLD signal resulted from a gradual decrease in self-inhibition of M1 and PMC. This was accompanied by a decrease in effective connectivity from SMA to M1, Cb and putamen, while connectivity from PMC to M1 and SMA increased. In the second experiment, we further investigated the neurophysiological basis of changes in M1 with EEG and assessed spontaneous alpha (8-12 Hz) and beta activity (12-20 Hz). Activity in both frequency bands recovered more slowly after fatiguing tapping compared to non-fatiguing tapping (N = 17, time x tapping interval interaction, p < 0.05), suggesting stronger dis-inhibition of M1. Finally, we measured inhibitory activity directly in the form of short latency intracortical inhibition (SICI) over M1 while participants recovered from blocks of fatiguing and non-fatiguing tapping. Our findings confirmed that motor slowing is accompanied by significant dis-inhibition of M1 (N = 13, time x tapping interval interaction, p < 0.05). Our results suggest that two mechanisms are involved in fatigability during maximal finger tapping: First, fMRI, EEG and SICI data converge to indicate that motor fatigability is associated with dis-inhibiting motor cortex, suggesting a gradual change of inhibitory control at the supraspinal level. One testable

explanation is a decrease in surround inhibition, which might lead to increased co-activation of hand muscles, which ultimately causes motor slowing. Second, our DCM results revealed that dis-inhibition of motor cortex is associated with reduced effective connectivity of SMA, a key area for intrinsic movement generation. Interestingly, a similar shift from mesial to lateral premotor loops and dis-inhibition of M1 has been associated with Parkinson's disease, a disorders characterize by pronounced motor slowing.

## **2-B-6 Experience-Dependent Contributions of Striatal Dopamine to Dexterous Limb Movements**

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Striatal dopamine (DA) has been suggested to influence motor function via dual roles regulating action vigor and reinforcement learning. However, most evidence for these aspects of DA function come from tasks that require no movement (e.g., classically conditioned tasks), simple movements (e.g., lever presses), or innate movements (e.g., locomotion). To determine if and how DA mediates these functions during cortically dependent, dexterous movements, we employed a rat skilled reaching task with real-time high-speed video analysis to trigger optogenetic stimulation of DA neurons during reach-to-grasp movements. DA neuron stimulation during, but not between, reaches progressively impaired performance. Impaired reaches exhibited movement patterns similar to successful reaches, but were characterized by early transitions between reach sub-movements. Once poor reaching patterns were established, rats rapidly transitioned between bad reaches with optogenetic stimulation and good reaches without stimulation. Furthermore, outside of the task, the dopaminergic stimulation induced abnormal movements not present when rats were engaged in the reaching task. Finally, these abnormal movements occurred only in rats with prior experience of DA neuron stimulation. These results suggest that nigrostriatal DA regulates skilled motor performance in an experience- and context-dependent manner, and influences both motor learning and performance. Ongoing studies are directed towards determining how the precise timing of DA signals and behavioral context interact to influence the acquisition and performance of dexterous movements.

## **2-B-7 Separate effects of handedness on prediction and control of hand movement**

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Skilled motor behaviour relies on the brain learning both to control the body and predict the consequences of this control (Flanagan et al., 2003). Prediction turns motor commands into expected sensory consequences, whereas control turns desired consequences into motor commands (Kawato, 1999). Here, our objective was to investigate the effect of handedness on prediction and control of hand movement. We reasoned that if prediction and control are mediated by distinct neural networks they might exhibit different dependence on handedness. To achieve this objective, right-handed participants were tested in two sets of task that were performed either with the right or the left hand. In the first task participants had to track with their eyes a self-moved target whose displacement was driven by means of random hand motion (Landelle et al., 2016). This eye tracking task allowed testing the ability of participants to predict visual consequences arising from own hand actions. In the second task participants had to move a cursor with their hand so as to track an externally moved target (Ogawa & Imamizu, 2013). This hand tracking task allowed testing the ability of participants to control a cursor along a desired trajectory. As expected preliminary analyses show that hand tracking is more accurate with the right hand than with the left hand, as evidenced by a smaller cursor-target distance (-15%).

However our data fail to show a significant difference in terms of eye tracking performance, namely we found a similar eye-target distance when the target is moved by the right or the left hand. Overall these data suggest that, although handedness influences the accuracy of hand control, it does not seem to influence the ability to predict visual consequences of hand movement. We interpret these findings as further evidence that prediction and control of movement are processes mediated by separate neural substrates (Flanagan et al., 2003; Danion et al., 2013). At a more general level, those results provide further evidence that humans exhibit different levels of dexterity with the right and the left hand, but they underscore that the ability to predict visual consequences arising from each hand is identical.

## **2-B-8 Multiple motor memories are formed when implicitly controlling different locations on a tool**

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Skillful manipulation requires forming and recalling memories of the dynamics of objects linking applied force to motion. It has been assumed that such memories are associated with the object per se. However, we often control different locations on an object, such as the left or right edge of a broom when pushing that edge along a wall, and these locations may be associated with different dynamics. We recently showed that multiple memories can be formed when explicitly controlling different visual points marked on an object [1]. Here we asked whether people can form separate memories when these are associated with different control locations that are implicitly defined by the goal of the task. In our task, participants moved a handle, attached to a robotic interface, to control the position of a rectangular object ('eraser') in a horizontal plane. Participants were required to move the eraser straight ahead so as to wipe away a column of particles ('dust'), located on either the left or right, while avoiding an obstacle on the far side of the dust. We found that participants could adapt to opposing dynamics when these were linked to the left and right dust locations, even though the movements required for these two contexts were the same. Two control conditions showed that this learning could not be accounted for by contextual cues or the fact that the task goal required moving in a straight line. These results suggest that people naturally control different locations on manipulated objects depending on the context, and that doing so affords the formation of separate motor memories. [1] Heald JB, Ingram JN, Flanagan JR, Wolpert DM. Multiple motor memories are learned to control different points on a tool. *Nature Human Behaviour*. In Press.

## **2-B-9 Robust developmentally determined spatial muscle synergies revealed in rodent complete SCI and preserved throughout rehabilitation.**

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Motor patterns in legged vertebrates show modularity in young and in adult animals. These can be viewed as comprised of synergies or motor primitives. We do not know if modularity observed in young mammals persists into the intact adult nervous system. Conceivably, during development modular circuit structures might be altered radically by experience and descending pathways. We analyzed hind leg motor patterns, by comparing (1) intact adult rats, (2) the same rats after low thoracic spinal transection, and (3) adult rats whose spinal cords were transected at 5 days after birth, before most postnatal motor development. We used Independent Components Analysis to evaluate modularity. Remarkably, the primitives/synergies of adult injured and neonatal injured rats were not significantly different, despite their radically different developmental histories, experiences of load bearing and reflex stepping capacities. In contrast, intact rats used several synergies that differed significantly from

transected rats. We surmise from these parts of our data that circuits for motor modularity in the spinal cord organize early, before P5, and are largely unaltered by subsequent development, descending pathways and controls, or weight bearing motor experience. This circuit modularity remains available into adult life, but is only fully revealed after complete spinal transection. We next analyzed a larger group of rats, also spinal transected as adults (i.e., equivalent to group 2 above). These rats were divided into three rehabilitation groups: (A) Cage rest; (B) Robot treadmill training; (C) Robot driven epidural stimulation. Rehabilitation (20 minutes per day, 5 days per week) proceeded for 8 weeks. As in prior work with adult spinal transection only group C showed large functional improvements. However, the spatial synergy structures in the three groups remained similar to group 2 and 3 above, and did not alter during rehab. In contrast, the variance contributions (premotor drive power) of the synergies were the likely target of rehabilitation. Taken together these two sets of data suggest a core infrastructure of circuitry for spatial components of premotor drive and muscle synergies is laid down in early development and is preserved into adulthood. Intact skills work around and through this circuitry to create the rich adult repertoire. These circuits are revealed as unchanged after spinal transection and are similar across individuals with different developmental and motor histories. In the complete SCI model, rehabilitation alters strength and coordination of the premotor drives but do not change the basic spatial structures of the synergy distributions to motor pools. The spatial distribution system that was organized and determined in early life is also preserved robustly throughout the different forms of rehab, at least in the spinal complete condition. These studies reveal fundamental features of the mammalian spinal cord structure and its development. The data have impact on our interpretation of circuit analyses in young rodents using genetic methods, and on our understanding and interpretation of SCI and rehabilitation outcomes and designs. Supported by NIH awards from NINDS, NIBIB, and funding from the Craig Neilsen Foundation.

## **2-B-10 Movement shapes sensory feedback: movement-history-dependent changes in muscle spindle encoding and muscle fiber stiffness**

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Sensory feedback is used to guide movement, but movement also shapes sensory feedback from peripheral receptors. For example, muscle spindle Ia afferent encoding of muscle stretch from destabilizing balance or limb perturbations is "movement-history-dependent"; firing is reduced when the muscle has recently been stretched (within 10s). We recently showed that history dependence could be attributed to muscle short-range stiffness (SRS), which is also reduced following stretch. However, it is unclear whether small muscle stretches within the range of natural variability (e.g. postural sway) impact sensory encoding of a perturbation or SRS. If they do, then increasing postural sway or movement variability could impair rapid sensorimotor responses for postural control. Here we determined whether small stretches (e.g. <1% length change in postural sway) modulate muscle spindle firing, and whether this reduction could be attributed to history-dependence in muscle fiber short-range stiffness. We conducted parallel in vitro muscle fiber mechanics and in vivo muscle spindle electrophysiology experiments in rats to characterize the effects of pre-stretch amplitude and inter-stretch interval on history-dependent changes to fiber SRS and spindle Ia afferent responses to stretch. In contrast to prior studies that used relatively large amplitude conditioning and test stretches (>3% length change), we tested muscle spindle and SRS history dependence using conditioning stretches within the small range of natural movement variability (<1%). We hypothesized that conditioning stretch

amplitude and inter-stretch time would interact, where both larger conditioning amplitude and shorter time intervals would reduce Ia firing rate and SRS responses to stretch. Large conditioning stretches (fibers: 0.046  $\mu\text{m}$ /half sarcomere; spindles: 1.67mm) caused significant reduction of SRS and afferent firing at 1ms time intervals, yet both SRS and initial burst amplitude returned to unconditioned levels by 1s and 0.32s, respectively. SRS and initial burst magnitudes were smaller as conditioning stretch amplitude increased. However, both muscle fiber SRS and muscle spindle initial burst were relatively unaffected by conditioning stretches smaller than 0.015  $\mu\text{m}$ /half sarcomere (1.21%) and 0.17mm (0.4%), respectively. We conclude that small amplitude stretches within the range of natural postural variability reduce, but do not eliminate SRS and muscle spindle initial bursts through history-dependent mechanisms. In the context of postural sway, these data suggest normal healthy sway amplitudes do not likely impede robust early reactions to perturbations. However, increasing amplitude of sway/movement variability (e.g. as seen in aging and certain neurological disorders) may lead to balance and general motor control impairment by reducing muscle spindle stretch encoding, and ultimately diminishing and/or delaying sensorimotor responses.

## **2-B-11 Instruction Impedes Learning of a New Controller**

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The use of different strategies or instructions during learning appear to impact later performance. This may be the result of biasing learning to different processes, such model-free vs. model-based reinforcement learning. Here, we set out to create conditions that favored one process over another while subjects learned a novel controller (i.e, a mapping between goals and actions). Our task was adapted from the "grid-sailing task," developed by Fermin and colleagues (2010) to expose model-free and model-based learning. In our variant of this task, subjects navigated a cursor across a grid by pressing keys on a keyboard. The mapping between key-presses and movement of the cursor was arbitrary and differed across subjects. Subjects practiced navigating between a single start-end pair (training phase) and then were tested on multiple, novel start-end pairings (test phase). To bias learning toward model-free or model-based processes, we manipulated the instruction subjects were given about how to solve the task. In the Instruction group, subjects were given the exact sequence of key-presses which would lead them to the target. In contrast, subjects in the No Instruction group were not provided with specific instructions for executing the path, forcing them to explore the mapping between key-presses and cursor movement during training. We hypothesized that the type of instruction can tip the balance between different learning processes, which can be revealed with a transfer test where subjects navigated to a novel set of start-end pairs. Both groups performed above chance in the transfer test. However, the No Instruction group far outperformed the Instruction group, suggesting that they had formed a better model-based controller. Several control experiments confirmed that differences between the groups were not attributable to variability of experience in training, working memory, or explicit knowledge of the controller. Finally, we sought to determine if the newly formed model-based controller could be used to plan out a full route between novel start-end locations. To test this, we trained new groups of subjects and removed feedback of the cursor in the test phase. Unsurprisingly, performance in both groups dramatically declined. Critically, we introduced one trial, testing the position where subjects were originally trained, into the transfer test. While the Instruction group performed similarly well on this trial whether feedback was absent or present, the No Instruction group showed significantly worse performance in the absence of feedback. These results make clear that the controller is limited to a simple state-transition matrix, which maps only the current state to the next

state -- it cannot be used to plan a full path. These results, and a preliminary modeling analysis, are consistent with the idea that instructions bias learning towards a model-free process. Consequently, a flexible, model-based module may be down-weighted.

## **2-B-12 Successfully stopping a movement has global motor effects as evident in a pause of tonic EMG of an irrelevant effector**

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Rapidly stopping action is a common requirement in everyday life. In the lab, it is often studied using the Stop Signal (Logan and Cowan 1984) or Go/NoGo tasks (Drewe 1975). Rapid action stopping appears to have global motor effects. This has been demonstrated by several studies that measured corticospinal excitability with Transcranial Magnetic Stimulation (TMS). When stopping occurs for one effector (such as speech or eyes) there is decreased corticospinal activity for a task-unrelated effector (such as hand or leg) (Badry et al. 2009; Cai et al. 2012; Majid et al. 2012; Wessel et al. 2013). This global motor effect correlates with signals recorded from the subthalamic nucleus (Wessel et al. 2016), and may reflect the operation of a prefrontal-subthalamic nucleus 'hyperdirect' pathway (Nambu et al. 2002; Bari and Robbins 2013) with a broad suppressive effect on basal ganglia output. Yet further investigations of the global suppression are hampered by the method of using TMS to measure corticospinal excitability. This is not convenient for many labs, and also the method requires an exorbitant number of trials to map the temporal profile. Here we tested a novel approach of studying the temporal profile of global motor suppression by measuring electromyography activity (EMG) in a task-unrelated muscle. We asked subjects to perform the Stop Signal task with their right hand while they continuously pressed a squeeze ball between their left thumb and forefinger. We measured EMG activity from the first dorsal interosseous muscle of the left hand using surface electrodes. In accordance with the findings from TMS, and in two separate experiments (each N = 20), we observed a decrease in the task-irrelevant tonic EMG activity for Correct Stop trials compared to both Correct Go and Failed Stop trials. This decrease was quite rapid (~60 ms after the Stop Signal) and transitory, lasting till about the Stop Signal Reaction Time, a metric of the time taken to stop a movement. In addition, we observed that faster RTs had greater EMG activity indicating a greater drive in trials where the subject responded quicker. This probably represents the first evidence that motor planning may be reflected in task-irrelevant muscles as well. This current approach provides a novel method for easily testing whether and when global motor suppression occurs in different task contexts. This is a proxy for a fast stopping process, and possibly a proxy for a hyperdirect frontal-subthalamic circuit with a global impact on basal ganglia output.

## **2-B-13 Stimulus-locked activity in human upper limb muscles and fast online reach adjustments are preferentially evoked by low spatial frequency targets**

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Humans can rapidly correct an ongoing reach movement in response to a sudden change in target position within 100-200 ms after target displacement. To adjust a current movement, visual information about target relocation has to be rapidly transformed into a motor command. We have recently described stimulus-locked responses (SLRs) in human upper limb muscles occurring within 100 ms of visual target onset, even when movements are temporarily withheld or executed in the opposite direction. These observations have led us to hypothesize that both online reach adjustments and the SLR arise from a fast visuomotor system mediated by a common subcortical, tecto-reticulo-spinal



pathway. Very little is known about the visual properties that feed into this fast visuomotor system. To investigate whether the visuomotor system(s) controlling the SLR and online reach adjustments share common visual properties, we studied them following the onset of visual targets composed of perceptually contrast-matched Gabor patches of various spatial frequencies, ranging from 0.56 to 4.44 cpd. We hypothesized that SLRs and online corrective reaches are preferentially evoked by lower spatial frequencies, which are primarily mediated by the magnocellular pathway. In two experiments ( $n = 17$  each) human participants performed either single-step (experiment 1) or double-step (experiment 2) planar arm movements in a robotic exoskeleton while surface electrodes recorded electromyographic (EMG) activity from the clavicular head of the right pectoralis major muscle. During the single-step reaches, movements were generated from a central starting position to a static peripheral visual target presented either to the left or right. In the double-step paradigm, movements were initiated to a central target but required an online correction to a new target on 2/3s of trials. Approximately 70% of participants exhibited detectable SLRs at latencies between 100 and 150 ms in response to low spatial frequency stimuli in both experiments (SLR+). Importantly, our results indicate that both the SLR and online reach adjustments occur progressively later for progressively higher spatial frequencies. Additionally, within the SLR+ group, the number of detectable SLRs decreased with increasing spatial frequencies. Off-line analyses confirmed that these results were not due to concomitant increases in reaction times to higher spatial frequency stimuli. Our data suggest that the SLR and rapid reach adjustments are preferentially sensitive to stimuli composed of low spatial frequencies and support the hypothesis that a common fast visuomotor pathway mediates both the SLR and rapid online reach adjustments.

## **2-B-14 Reward decreases motor fatigability by increasing neural activity within the motor network**

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Reward can motivate individuals to exert high levels of physical effort and thus, invigorate movements. Here, we ask whether reward can modulate motor fatigability and investigate its neurobiological underpinnings by combining behavioural measurements with functional magnetic resonance imaging (fMRI) or electroencephalography (EEG). Fatigability was tested by instructing healthy participants to perform repetitive finger tapping at maximal speed for 40s. Our previous experiments have shown that this task is characterized by significant reductions in movement frequency or "motor slowing". We also observed neural changes during tapping and significant after-effects measured during subsequent breaks, indicating that these changes are at least partly due to supraspinal processes. Here, we report two experiments where we rewarded participants for good tapping performance and investigated (i) whether reward attenuates fatigability and (ii) whether the observed changes are reflected by neurophysiological markers measured with EEG or fMRI. In both experiments, participants performed finger tapping with their dominant index and middle finger followed by short breaks (40s). They executed either fatiguing trials (40s of tapping) or non-fatiguing trials (10s of tapping) while they could either earn a reward (indicated by a visual cue, which appeared either at 20s or 5s respectively) or not. In both experiments, participants ( $n=34$  and  $n=27$ ) exhibited significant motor slowing (mixed-effects model,  $p<0.001$ ) compared to non-fatiguing tapping. Importantly, motor fatigability caused by long tapping was significantly attenuated by reward ( $p<0.001$ ). Using fMRI, we found that fatiguing tapping caused a significant increase of the blood oxygenation level (BOLD) response with a sensorimotor network comprising primary sensorimotor cortex (SM1), premotor cortex, supplementary motor area (SMA), putamen and cerebellum (whole brain analysis,  $pFWE<0.05$ ). Interestingly, this activity was

further increased in rewarded trials and reached statistical significance in bilateral SMA, contralateral SM1, and ipsilateral cerebellum (small volume correction, time\*condition, sphere 8mm, pFWE<0.05). For both rewarded and non-rewarded trials, we observed a gradual decrease of the BOLD response during the break (pFWE<0.005), which took longer after fatiguing than non-fatiguing tapping. In our EEG experiment, we focussed on the recovery period and found that alpha-band power was strongly reduced immediately after tapping but recovered during the break (mixed-effects model, p<0.001) for the electrode overlying contralateral SM1. Recovery of the alpha-rhythm was largest for non-fatiguing tapping, at a medium level for fatiguing un-rewarded tapping and at the lowest for fatiguing rewarded tapping. Our results demonstrated that fatigability can be significantly reduced by reward, which is linked to increased BOLD response in cortical and subcortical motor areas and decreased alpha activity observed over SM1. These results suggest that reward increases the neural drive potentially by disinhibiting motor areas. This is consistent with recent theories proposing that reward has a motivational effect and increases response vigour by overcoming internal costs of movement control.

## **2-B-15 A computational model of afferented muscles reproduces cardinal features of force variability**

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Accurate and precise movement executions are confronted with variability associated with generation of muscle force. Such variability arises from various sources including mechanical properties of muscles and limbs, motor unit properties, proprioceptive feedback, and descending neural commands. Previously, contributions of individual sources have been studied in isolation and in a feedforward manner. However, those factors interact during closed-loop control, which describes nearly all experimental paradigms in which muscle force must be voluntarily controlled. Recently, we showed using a closed-loop simulation of an afferented muscle that neuromechanical interactions among neural noise, mechanical properties of musculotendon unit, proprioceptive feedback and error corrective mechanism suffice to explain cardinal features of involuntary force variability previously observed experimentally. Here, we attempt to extend this observation by incorporating new elements in our model. New elements added to our existing model include stochastic motor unit firing patterns, conversion of neural firing into muscle force, and additional spinal feedback pathways within and across muscles (pathway involved with monosynaptic Ia excitatory feedback, Ia inhibitory interneurons, Ib interneurons, Renshaw inhibitory interneurons, propriospinal interneurons,). Our results show that motor unit properties are important, yet are typically insufficient to explain the majority of force variability or its frequency spectrum. Importantly, we demonstrate previously an unrecognized influence of coordinated activities between two muscles on the amplitude and spectral features of force variability. These results highlight potential importance of such neuromechanical interactions in understanding the generation of force variability in precise and accurate motor tasks and explaining physiological mechanisms of altered neuromuscular control in health and diseases.

## **2-B-16 Two novel electrode systems for ensemble and single-unit recordings from small muscles.**

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Motor control requires the brain to rapidly process sensory signals and coordinate precise patterns of muscle activity. Understanding the learning and control of complex movements therefore requires collecting a large number of parallel recordings within and across multiple muscles. Current

electromyographic (EMG) methods typically rely on non-invasive skin-level surface electrodes or the insertion of fine wires into the muscles. Surface electrodes are unable to record activity from deep or small muscles, and wire electrodes are stiff and tend to injure the muscle at the implant site. Moreover, traditional EMG methods are often unable to isolate spike trains from individual motor units within muscles. To address these limitations, we developed two novel methods to record EMG signals from multiple small (2 mm x 4 mm) vocal muscles simultaneously in songbirds. The first method uses a multi-channel microelectrode flexible array that is sutured to the surface of targeted vocal muscles. The array consists of 16 gold active sites (4x4 grid), where each electrode contact sizes range from 50-200 microns, with inter-contact spacing as small as 50 microns, embedded in 20 microns of photo-definable polyimide. Flexible leads attached to the array are routed under the skin and connected to terminals on an adapter plug cemented to the bird's skull. The high specificity and impedance of each electrode site allows us to isolate spikes from single motor units, which consists of a motor neuron and the muscle fibers it innervates, and multi-motor units. With this method, our lab was able to establish that millisecond-scale spike timing patterns control respiratory muscles and that variations in spike timing significantly alter muscle force output and breathing behavior (Srivastava, et al., 2017). The second method uses a set of carbon nanotube (CNT) fibers, fabricated via a wet spinning process, to record single and multi-motor unit EMG activity. CNT electrodes consist of two single parylene-coated fibers twisted together and coated again. After the tip is inserted under the muscles' fascia tissue, the CNT electrode is secured to the muscle with tissue adhesive. The electrode is routed under the skin and attached to a circuit board cemented to the bird's skull with gold plated electrode attachment pins. The CNT fibers, unlike fine wire electrodes, are strong, extremely flexible, small (14-24 microns) and have low interface impedance. These properties allow us to chronically record from multiple small vocal muscles simultaneously without causing strain on the vocal organ, which could interfere with normal vocal behavior. In current and future projects, the two novel electrode systems will allow us to examine how muscle activity is organized across time and space, offering new insights into how the coordination of activity within and across co-active muscles develop as a skilled behavior is learned.

## **2-B-17 How self-initiated memorized movements become automatic: A replication and validation study of Wu, Kansaku and Hallett (2004) using functional near-infrared spectroscopy (fNIRS)**

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According to Fitts' Theory of Motor Learning, the final stage of learning, termed "automatic", is thought to occur when the motor skill is established and can be performed with little to no attentional demand (Fitts, 1964). Changes in cortical activity associated with automaticity have been evaluated with functional magnetic resonance imaging (fMRI). However, due to the confines of the scanner, only tasks that can be performed in a supine position with no head movement are permitted (Bunce et al., 2008). Functional near-infrared spectroscopy (fNIRS), while similar in principle to fMRI, can not only evaluate gross motor skills but also display the hemodynamic response at a higher temporal resolution. Therefore, the objective of this study was to validate fNIRS as a suitable neuroimaging method by replicating the fMRI protocol and associated prefrontal cortex (PFC) findings as reported by Wu et al. (2004). Half the sample ( $23.2 \pm 2.67$  yrs) of 20 right-handed participants was collected. Participants performed two finger-tapping sequences of different lengths. Sequence-4 (S4) and -12 (S12) consisted of 4 and 12 finger taps, respectively and required the use of the index, middle, ring and pinky fingers. fNIRS was acquired before (pre) and after (post) participants achieved automaticity. After the 'pre' acquisition, participants were given 2-4 hours of practice until they could perform each sequence from memory ten

times in a row with no error, as well as a concurrent secondary task. The motor skill was only then considered automatic. Pre and post consisted of two conditions, rest and active. Each condition was 25-seconds in duration and was repeated five times in an ON-OFF blocked design. Changes in the concentration of oxyhemoglobin (HbO) in the PFC were measured by an 8-channel continuous wave spectrometer. Wavelengths of 850 nanometers were emitted to capture changes in light intensity and were converted to changes in HbO using the modified Beer-Lambert law (Villringer and Chance, 1997). For S4, the paired t-test revealed a trend towards significance ( $t(5) = 2.003$ ,  $p = 0.076$ ) in channel 4, which may correspond to the right, dorsolateral PFC, suggesting a decrease in HbO during post compared to pre. The remaining t-tests revealed no significant differences between pre and post ( $p > 0.05$ ) across the seven channels. However, while not statistically significant, channels 1, 2, 5, 6 and 8 did demonstrate a similar pattern to channel 4, with reduced levels of HbO at post. For S12, the paired t-tests revealed no significant differences between pre and post ( $p > 0.05$ ) across the eight channels. However, upon visual inspection, all eight channels demonstrated a decrease in HbO in post compared to pre. Although, the study lacks statistical power in its present form, the reduced levels of HbO observed may suggest that as the movement becomes automatic, there is a diminished reliance on the PFC. This would be in line with the findings of Wu et al. (2004).

## **2-B-18 Investigating the role of beta oscillations for motor inhibition using brain computer interface**

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**Aims:** The ability to quickly stop an initiated movement is reliant upon effective inhibitory control in the brain. Poor inhibitory control is characteristic of a wide range of motor and psychiatric conditions. The stop-signal task can be used to assay this deficiency. During this task, the participant must cancel an already-initiated motor response. An increase in the amplitude of rhythmic brain oscillations in the beta (15-30 Hz) frequency band are registered in electroencephalography (EEG) recordings accompanying stopping. Recently, it has been proposed that beta activity is causal to stopping behaviour, rather than simply epiphenomenal. Therefore, we investigated if the ability to flexibly modulate the beta rhythm underlays successful inhibitory control. **Methods:** Participants ( $n=24$ ) were divided into four groups, who undertook EEG neurofeedback training. Six were trained to upregulate, and six to downregulate the right frontal beta rhythm. A control group were trained to upregulate ( $n=6$ ) or downregulate ( $n=6$ ) the alpha (8-12 Hz) rhythm. Training occurred over six days. Behavioural performance on the stop-signal task was measured pre- and post-training. **Results:** Participants were capable of learning to modulate the right frontal beta and alpha rhythms. Preliminary results show a strong increase in right frontal beta at a time point corresponding to stop signal reaction time (SSRT). **Conclusions:** To date, we have demonstrated that the neurofeedback protocol is feasible and shows promising results for neuromodulation. Ongoing work aims to investigate if beta training improves SSRT (results pending).

## **2-B-19 The Relationship between Somatosensory Working Memory and Human Motor Learning**

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The capacity to maintain information in sensory working memory concerning previously performed movements, and their success or failure, presumably plays a role in human motor learning. Indirect evidence in support of this idea comes from a recent study in which we found that individual differences in motor learning correlate with changes in functional connectivity between second somatosensory cortex (SII) and BA 9/46v (lateral prefrontal cortex), the latter being known to contribute to

somatosensory working memory (SWM). In the current study, we directly tested the hypothesis that there would be a correlation between proprioceptive SWM and human motor learning. We designed a behavioral task which is a variant of an N-back procedure to assess such working memory. On each trial a robotic device displaced the participants arm in a number of different directions (memory set), and this was followed by a test displacement that was used to assess working memory. On half of the trials, the test direction was one of the items in the memory set, and in the other half it was not. Participants had to indicate whether or not the test movement was from the memory set. As a measure of somatosensory working memory, we computed the proportion of hits minus false alarms as a function of number of movements separating the test item and to-be-remembered item (lag). On a separate day, the same subjects performed a motor learning task in which they made reaching movements to hidden targets and received positive reinforcement when they were successful. To test whether the working memory is domain-specific, we also measured participants visuospatial working memory (VSWM), their digit span test, and their performance in a mental rotation test. Overall, we found that the amount of motor learning was reliably predicted by the SWM and not by any of the other working memory measures, which suggests the involvement of somatosensory system in motor learning. NICHD R01 HD075740, Fonds de recherche du Québec - Nature et technologies (FRQNT)

## **2-B-20 Spinal stretch reflexes exploit musculoskeletal redundancy to support postural hand control**

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Motor behaviour is most efficiently controlled by only correcting disturbances or deviations that influence task success (i.e., the minimum intervention principle). Many experiments have shown that the nervous system generates behaviour that adheres to this sophisticated control scheme, but it is not fully known which neural circuits implement the control laws that produce such behaviour. A wealth of work has indicated that this may be a specialized function of a transcortical feedback pathway that traverses primary motor cortex and other cortical regions involved in the production of voluntary movement. Here we show that, in the context of postural hand control, even the fastest spinal feedback pathway can produce solutions consistent with the minimum intervention principle. In our first experiment, participants placed their hand on a spatial target and we mechanically flexed their elbow - stretching the triceps muscles - and simultaneously flexed, extended or did not change their wrist angle. These perturbations displaced the participants' hand off the target, but critically, the perturbation that yielded the largest hand displacement relative to the target did so with the least amount of elbow flexion. Participants rapidly returned their hand to the target by coordinating rotations of their elbow and wrist - a behaviour consistent with the minimum intervention principle. Notably, we found that the triceps' spinal stretch reflex was tuned to the hand's displacement, and not the amount of elbow flexion. This tuning reflected the amount of elbow extension needed to return the hand to the target. In our second experiment we ruled out the possibility that our initial results simply reflected hardwired connections from wrist afferents to triceps motoneurons. Participants placed their hand on a target and we again flexed their elbow and simultaneously flexed or extended their wrist. Critically, participants responded to these perturbations using two different arm orientations. For one orientation, flexing the wrist moved the hand away from the target, whereas in other orientation, flexing the wrist moved the hand towards the target. Strikingly, the triceps' spinal stretch reflex was again tuned to the hand's displacement from the target rather than the elbow's rotation. In fact, changing the arm's orientation diametrically altered the pattern of the triceps' spinal stretch reflex and did so in a way that was appropriate for returning the hand to its initial location. Taken together, our findings reveal that the

fastest spinal feedback pathway is capable of integrating and modulating feedback from multiple muscles to produce corrective responses that adhere to the minimum intervention principle, forcing a re-evaluation of the how the nervous system derives the sophisticated control laws that support natural motor behaviour.

## C – Posture and Gait

### **2-C-22 Age-related loss of early grasp affordance when viewing a safety handle**

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Introduction: Mere observation of objects in our surroundings can potentiate movement, a fact reflected by visually-primed activation of motor cortical networks [1]. This mechanism holds potential value for reactive balance control where recovery actions of the arms must be targeted to a new support base to avoid a fall. The present study was conducted to test if viewing a wall-mounted safety handle results in automatic activation of motor cortical networks, and if this affordance effect changes with age. We hypothesized that the hand area of the primary motor cortex would be facilitated shortly after visual access to a safety handle versus when no handle was visible, and that this effect would be diminished in older adults (65+ years) compared with younger adults (18-30 years). Methods: Twenty-five young adults and seventeen older adults participated in this study. Transcranial magnetic stimulation (TMS) measured corticospinal excitability in hand muscles directly following access to vision while participants sat in front of a wall-mounted safety handle. Vision was controlled using liquid crystal lenses and TMS pulses were time-locked to occur shortly after the goggles opened (80ms, 120ms, 160ms). Between trials the response environment was unpredictably altered to present either a handle or no handle (i.e. covered). Results: An affordance effect for grasping was evident in the hand muscles of young adults when they viewed a handle versus trials where the handle was covered. This effect was selective both in terms of the muscles activated and the timing at which it emerged. The First Dorsal Interosseus and Opponens Pollicis muscles (synergists in closing the hand) were facilitated 120ms after viewing the handle, but not at earlier (80ms) or later (160ms) points. Abductor Digiti Minimi, which moves the little finger out from the rest of the hand, diminished when viewing the handle across all time points. By contrast, older adults failed to show any corticospinal excitability changes in hand muscles based on viewing the safety handle. Discussion: These findings suggest a rapid engagement of hand muscles suitable to grasp a handle based on vision in young adults. The fact that this affordance effect was present for a safety handle commonly used to regain balance has implications for priming recovery actions suited to our surroundings, even before postural perturbation is detected. The affordance effect observed in younger adults was entirely absent in older adults, suggesting that aging diminishes the ability to quickly put our visual world into automatic motor terms. If indeed the affordance effect helps to prepare compensatory arm responses to avoid a fall, this would suggest that older adults are deficient in this regard. 1. Franca et al., (2012) Corticospinal facilitation during observation of graspable objects: a transcranial magnetic stimulation study. PLoS One, 7(11), e49025.

### **2-C-23 Investigating the redesign of a passive cane via a mathematical model of cane assisted upright balance**

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BACKGROUND AND AIM The ability to predict the performance of assistive technologies, such as a passive-cane, is of great importance for the design of safe and effective tools for fall-prevention in older

adults as well as neurologically impaired individuals. One way of accomplishing this is through model-driven design. A recent development of a mathematical model of cane-assisted balance (Chagdes et al. 2016) can be used to understand how changes in cane design can lead to increased or decreased stability. This abstract presents our initial study investigating the stability of cane-assisted upright balance when cane design parameters are varied. The mathematical model is extended to include the capability of slip and lift detection to evaluate instances when the cane design results in such unwanted behaviors. Furthermore, the model is simulated for two cases that mimic different mechanisms, which lead to instability without a cane: (1) very low muscle stiffness (indicating muscle deterioration) and (2) increased neuromuscular delay (indicating neurological impairment). METHODS Adapting the cane-assisted mathematical model of balance by Chagdes et al. (2016) we suggest a balance strategy which applies corrective torques to the wrists, elbow, shoulder, and ankle joints to attempt to maintain upright balance and cane positioning. The mathematical model is improved by including an ability to identify when the cane slips or lifts. Using this model, a parametric study is performed by varying the cane distance from the feet and the cane length to identify design combinations that lead to a cane slip, cane lift, or human fall. These behaviors, along with design combinations that result in stable balance, are compared in the design parameter space for model parameters mimicking a person with (1) very low muscle stiffness and (2) increased neuromuscular time-delay. RESULTS/CONCLUSIONS The mathematical model predicted that a simple control strategy was able to stabilize cane-assisted upright balance. It was shown through the parametric study that the use of a cane benefited individuals with low levels of ankle stiffness allowing for stable posture when ankle stiffness value was insufficient for stable bipedal balance. The parametric study demonstrated that as stiffness was decreased the range of design combinations resulting in stable balance was also decreased. A similar effect was found when the neuromuscular delay was increased. Furthermore, by comparing the regions of stable cane-assisted balance in the design parameter space we were able to identify a set of ideal design parameters that led to successful balance for each of the mechanisms leading to balance impairment (i.e., decreased muscle stiffness and increased neuromuscular delay). Such a mathematical model can aid in the design of customized passive or active assistive technology for people with different physical properties and impairments; thus, creating the possibility of personalized medicine. REFERENCES [1] Chagdes JR, Freire JPCD, Shukla A (2016) Nonlinear dynamics of upright human balance while using a passive-cane. In: Proceedings of the ASME 2016 Dynamic Systems and Control Conference. Minneapolis, MN.

## **2-C-24 Anticipation of split-belt treadmill perturbations drives adaptation of muscle activity in preparation of heel strike**

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Anticipation of split-belt treadmill perturbations drives adaptation of muscle activity in preparation of heel strike Daniel L. Gregory, Julia T. Choi. Department of Kinesiology, University of Massachusetts Amherst Previous studies have shown interlimb adaptation on split-belt treadmills with varying differences in belt speed (Dietz et al. 1994, Torres-Oviedo et al. 2011). Reactive changes in stance and swing time on each limb are associated with rapid changes in the onset and burst durations of muscle activity (Dietz et al. 1994). Predictive locomotor adaptation, however, is characterized by gradual changes in step-length (SL) and double-support (DS) symmetry, and these parameters show robust after-effects post-adaptation (Torres-Oviedo et al. 2011). Here we sought to examine how predictive mechanisms contribute to the muscle activation pattern during split-belt adaptation. We hypothesized that changes to muscle activity that occur adaptively would be temporally correlated to changes in SL

and DS and show characteristic after-effects post-adaptation. Methods: For this study (N = 10, 6F, 5M), subjects walked on a split-belt treadmill with a 2:1 speed difference for 10 minutes. Electromyography (EMG) was collected from 4 bilateral leg muscles, vastus lateralis (VL), biceps femoris (BF), medial gastrocnemius (MG), and tibialis anterior (TA). EMG signals were amplitude normalized to the peak average during baseline and time-normalized to 100% of the gait cycle. To assess muscle adaptability, baseline speed-matched EMG data were subtracted from all conditions to obtain a difference curve where positive and negative values indicate increased or decreased activation relative to baseline. SL and DS differences were calculated for each stride to measure gait adaptation and regressed with the EMG difference curves across 10% bins of the gait cycle. Results: Initial (strides 1-5) asymmetries in SL and DS difference ( $p < 0.001$ ) returned toward symmetry ( $p < 0.001$ ) and showed robust after-effects ( $p < 0.001$ ). All 4 muscles had significant ( $p < 0.003$ ) initial increases in amplitude during early adaptation which began at terminal swing and ended around weight transfer in the VL, BF, and TA of the slow limb, and early to mid-stance in the MG on the fast limb. These increased EMG amplitudes were reduced or eliminated by the end of the ten-minute period (VL, BF, and TA  $p < 0.05$ , MG  $p = 0.23$ ), were temporally correlated with the changes in SL (slow  $r^2$  VL=0.66, BF=0.57, and TA=0.43, and fast  $r^2$  MG=0.44,  $p < 0.05$ ) and DS (slow  $r^2$  VL=0.61, BF=0.56, and TA=0.43, and fast  $r^2$  MG=0.38,  $p < 0.001$ ), and were matched with significant after-effects (depressed amplitude) post-adaptation ( $p < 0.003$ ). In conclusion, predictive locomotor adaptation is associated with EMG modulations and negative after-effects localized around the step-to-step transition period (just before and during DS), possibly reflecting the anticipatory control of muscle activity in preparation of heel strike. We further hypothesize that sensory feedback during step-to-step transitions provides the "error-signal" that drives split-belt trial-and-error adaptation and to test this, we are currently using short phase-specific speed perturbations to dissociate changes in EMG across phases of the gait cycle.

## **2-C-25 Cerebellar and Parietal Cortex activation predicts walking pattern characteristics during continuous gait adjustments to the split-belt treadmill: An [18F]-FDG PET Study.**

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Background: Gait alterations on a split-belt treadmill (SBT), where each leg is driven at a different speed, highlight the nervous system's ability to quickly adapt the locomotor plan to its environment. However, specific contributions from cerebral and cerebellar regions to this motor adaptation remain unknown. The fact that participants with cortical strokes, hemispherectomy, and even infants prior to independent stepping, have the ability to make changes to their gait cycle within 5 steps of walking on a SBT suggest that a distributed network might be involved. This project aimed to establish if cerebral and cerebellar brain regions increase in activation during continuous gait adaptation to the SBT compared to typical treadmill walking in healthy adults and how the gait pattern influences these changes in activation. Methods: Directly following bolus injection of 18F- fluorodeoxyglucose tracer, 10 healthy adults walked on a treadmill for 30 minutes. In the tied-belt (TB) condition, both belts were maintained at a comfortable speed. On a separate occasion, the continuous adaptation (CA) condition changed the speed ratio between treadmill belts every 15 seconds. Positron emission tomography (PET) images of cerebral glucose metabolism of each condition were compared to assess for clusters with significant increases in metabolism when continuous, unexpected gait pattern changes are required. A multiple linear regression was predicted participants' peak Z value within each significant cluster based on their change in cadence, number of steps taken and step length variability. Results: A significant increase in metabolism during continuous adaptation was found in the left supplementary motor area (SMA), the



right posterior parietal cortex (PPC), the anterior cingulate cortex (ACC) and the left anterior cerebellum ( $p < 0.05$ ). Of these four clusters, participants' peak Z values in the PPC and the Cerebellum could be predicted from gait parameters using multiple regression. The change in cadence, a temporal measure of gait, was the only predictor of peak activation within the PPC ( $R^2 = 0.725, p < 0.01$ ), whereas step length variability, a spatial measure of gait, was the only predictor of peak cerebellar activation ( $R^2 = 0.528, p < 0.05$ ). Peak change in activation within the ACC nor SMA were not related to the gait outcomes measured. There was no evidence of a change in metabolism in the Pre-Frontal Cortex (PFC). Conclusion: Our results suggest that complex control of temporal and spatial aspects of the gait cycle increase metabolism in anatomically separate areas of the brain. This difference in processing of temporal and spatial gait parameters may imply a parieto-cerebellar network could be required for continuous locomotor adaptation. A lack of change in metabolism of the PFC indicates that executive function may not play a substantial role while activation of the ACC independent of gait characteristics signals the need to sustain increased task directed attention in this complex walking task.

## **2-C-26 Auditory inputs contribute to balance control in healthy young and older adults: a simulated hearing loss experiment.**

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BACKGROUND AND AIM: Traditionally, 3 sensory inputs (visual, vestibular, and somatosensory) are associated with the control of balance and have been investigated for their potential contribution to increased fall risk. Recent evidence suggests auditory inputs may also contribute to balance control. Although current evidence reveals an association between hearing loss and balance difficulty, the mechanisms behind how and why hearing loss affects balance are unknown. It is possible that hearing loss taxes cognitive resources. We investigated the contribution of auditory inputs to balance control in healthy young and older adults by simulating hearing loss. METHODS: Twenty healthy young and older adults, cleared of any sensory and neurological deficits participated in the study. Participants completed 1 min standing balance, walking, and responding to 10 surface translation perturbations at  $2\text{m/s}^2$  in AP direction while completing a standardized audiology test (BKB-SIN). The audiology test required the subject to repeat back sentences played through the headphones under normal hearing (control) and simulated hearing loss conditions, randomly assigned. Simulated hearing loss was achieved using a pair of Bose QuietComfort 35 wireless noise-cancelling headphones. Adobe Audition software using a FFT logarithmic curve was used to manipulate sound volume and frequencies of standardized sentences in order to simulate moderate hearing loss to levels documented in literature. Outcomes included: Center of Pressure COP sway variability, number of compensatory steps, COP-COM during first compensatory step after perturbation, performance of auditory task, and self-selected gait speed. Functional Gait Assessment, 6-Minute Walk and Short Physical Performance Battery were also administered. ANOVA was conducted for each of the dependent variables with respect to group and condition of auditory task. RESULTS: Compared to normal hearing, simulated hearing loss resulted in significantly increased COP sway variability significantly and more compensatory steps in response to perturbations in older adults. Preliminary results showed that in response to surface perturbations, the COP-COM distance was an average of 25cm and 15cm in young and older adults, respectively, reflecting the shorter, multiple steps taken by older adults. CONCLUSIONS: Simulated hearing loss negatively impacts postural control particularly in dual-task conditions. The effect is stronger in older adults who have fewer resources to compensate for poor sensory input. Individuals with hearing loss may be at greater risk of falling than

individuals without hearing loss, possibly due to reduced or conflicting auditory information increases the cognitive load and taxes attentional resources particularly in older adults. ACKNOWLEDGMENTS AND FUNDING: Supported by Texas Medical Research Consortium (RI 6042 "Good hearing, Steady feet") and Neurobiology of Aging NIH training grant (T32 AG 020494)

## **2-C-27 Gaze and the control of foot placement when walking in natural terrain**

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Human locomotion through natural environments requires precise coordination between the body and the eye movements that gather the information necessary to guide foot placement. However, little is known about how the visual and locomotor systems work together to support movement through world. We developed a novel system to simultaneously record gaze and full-body kinematics during locomotion over different outdoor terrains. We found that not only do walkers tune their gaze behavior to the specific information needed to traverse paths of varying complexity, they do so while maintaining a constant temporal look-ahead window across all terrains. This strategy allows walkers to use gaze to tailor their energetically optimal preferred gait cycle to the upcoming path in order to balance between the competing demands of efficiency and stability. Thus, gaze and locomotion are intimately linked and reflect the integration of costs, environmental uncertainty, and requirements of the specific task, revealing the structure of the sensorimotor decisions that support successful performance in the face of the varying demands of the natural world.

## **2-C-28 The effects of different levels of midsole cushioning in footwear on mobility performance of females living with multiple sclerosis**

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In neurodegenerative disorders such as Multiple Sclerosis (MS), gait is impaired across a number of dynamic balance domains, resulting in an elevated fall risk, decreased quality of life and increased morbidity. The breakdown of myelin in the nervous system elicits mobility impairments to such an extent that over 75% of MS patients experience difficulty in walking, which is significant as falls have been identified as a major repercussion with more than 50% of middle aged and older adults living with MS suffering an injurious fall. Specific spatio-temporal parameters of gait in persons with MS (PwMS) have been attributed to increased fall risk including stride length and minimal toe clearance, as well as decreased step length, reduced gait speed, decreased cadence, and increased double support. Currently, there is limited research on the impact that different shoe types have on gait in PwMS. Specifically, to our knowledge there is no research available examining shoe constructs (i.e. midsole thickness and contact area) and their influence on gait kinematics in PwMS. Therefore, the purpose of this study was to assess how increased cushion at the midsole affects spatiotemporal measures of gait in females living with MS. To date, data has been collected in five females diagnosed with MS (N = 5; 42 +/- 7 years, 1.66 +/- 0.1 m, 69.13 +/- 17.01 kg) during a two minute walk test under three different shoe conditions; a high cushioned condition using the Hoka One One Clifton 3 (HC), a medium cushioned New Balance 85V1 (MC), and barefoot. Spatiotemporal changes in gait were assessed using Opal wireless inertial sensors (APDM Inc., Portland, OR). Preliminary data demonstrate increased elevation at midswing and increased stride length in HC compared to MC. While not significant in our current, small sample, these results demonstrate strong trends with medium to large effect sizes for both midswing elevation (Cohen's d right leg = 0.479, P value = 0.344; Cohen's d left leg = 0.699, P value = 0.193), and

stride length (Cohen's  $d$  right leg = 0.864,  $P$  value = 0.126; Cohen's  $d$  left leg = 0.828,  $P$  value = 0.138). Data collection and analysis is on-going, and current results indicate the potential for a more densely cushioned shoe to improve gait function in PwMS. Specifically, an increased midsole cushion may increase both stride length and elevation at midswing, each of which are kinematic contributors to falls. Thus, the simple acquisition of a pair of shoes could increase quality of life by reducing fall risk.

## **2-C-29 Dissociation of muscle and cortical response scaling to balance perturbation acceleration**

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Reactive balance recovery engages hierarchically distributed sensorimotor control centers throughout the nervous system, but the role of the cortex is unclear. EEG recordings of cortical activity during reactive balance recovery reveal a robust negative peak of activity (N1) over the supplementary motor area at ~150ms latency. The processes underlying this cortical balance-evoked N1, and its relationship to balance-correcting muscle automatic postural responses (APR) are unclear. Prior studies using averaged responses across trials suggested that cortical and muscle responses during balance recovery share modulation by somatosensory inputs (Dietz 1984b, 1985a/b; Berger 1987; Staines 2001). We hypothesized that the cortical balance N1 monitors somatosensory information driving the simultaneous initial burst (IB) of the muscle APR in translational support-surface perturbations to standing balance, and influences subsequent balance-correcting muscle activity. We tested the dependency of the cortical balance N1 on sensory information by varying perturbation acceleration. Perturbation acceleration has previously been shown to modulate the somatosensory-dependent activation of the IB of the muscle APR (Lockhart 2007), but it is unknown whether the cortical balance N1 shares this acceleration dependency. We predicted that the cortical balance N1 amplitude would scale with perturbation acceleration and correlate to muscle APR activity if they share common sensory origins. Perturbations were unpredictable in timing, direction, and acceleration magnitude. Across subjects, we found much weaker acceleration-dependence of cortical responses ( $R^2=0.022$ ) compared to muscle responses ( $R^2=0.323$ ), with only half of individuals showing acceleration-dependent cortical responses despite acceleration-dependent muscle responses in all individuals. Variation of cortical response amplitudes between subjects ( $R^2=0.528$ ) was much greater than variation within subjects, with larger amplitudes in shorter subjects ( $R^2=0.412$ ). Z-transformed cortical and muscle responses were weakly correlated ( $R^2=0.075$ ), in part due to differences in acceleration-dependence, but also due to a greater reduction in amplitude across trials of cortical responses ( $R^2=0.047$ ) than muscle responses ( $R^2=0.015$ ). Importantly, cortical balance N1 was larger on trials in which subjects took a step to recover balance (two-way ttest,  $p<0.0001$ ), and was correlated with longer-latency muscle activity ( $R^2=0.039$ ). We conclude that the cortical balance N1 shares sensory inputs with the muscle APR IB, but its amplitude is more sensitive to subject-specific factors and recent experience, possibly related to changes in attention or threat assessment, which are known to influence the balance N1. These data additionally highlight a possible relationship between the cortical balance N1 and stepping behavior, suggesting a potential influence of the cortex on longer latency muscle activity and changes in strategy.

## **2-C-30 Leveling the Playing Field: Evaluation of a Portable Instrument for Quantifying Balance Performance**

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Balance is a complex, sensorimotor task where an individual must maintain their center of pressure

within their base of support. Quantifying balance in a reliable and valid manner is essential to evaluating disease progression, aging complications, and injuries in both clinical and research settings. Traditionally, researchers have used force plates to track motion of the center of pressure during a variety of tasks. However, factors such as cost, portability, and availability have limited the potential for objective evaluation of postural stability outside of the laboratory setting. This study compared the "gold standard" for assessing postural stability (i.e., a laboratory-grade force plate) to a more affordable and portable assessment tool (i.e., the Balance Tracking System balance plate) in healthy young adults. Static stability of the participants was assessed in both rigid and compliant surface conditions. Simultaneous collection of data from both systems was achieved through placing the Balance Tracking System directly on top of the force plate. Center of pressure data were used to quantify common postural stability metrics from each device, including: sway area, mean frequency, root mean square, mean distance, mean velocity, and mean path length. Data from each system were time-synchronized during post-processing in MATLAB. Correlations between the center of pressure outcome measures derived from these two instruments were calculated. Additionally, Bland-Altman plots were utilized to go beyond correlations and provide further evidence of agreement between the devices by comparing the bias between each outcome variables' mean differences, assessed by each force plate, within a 95% confidence interval. Based on the results of this study, the measures obtained from the portable balance plate objectively quantified postural stability with high validity on both firm and compliant surfaces. Firm surface measure correlations between devices were all greater than or equal to  $r = 0.493$ . Additionally, in the compliant surface condition, all postural stability metric correlations were greater than or equal to a correlation value of  $r = 0.550$ . While those were the minimum correlations observed, the majority of the metrics in both conditions were correlated at  $r = 0.99$  (sway area, mean frequency, root mean square, mean distance, mean velocity, and mean path length). These results not only demonstrate the high relationship between the devices, but also displayed high agreement between all of the postural stability metrics as assessed by the Bland-Altman plots. Therefore, practitioners and researchers may use the Balance Tracking System as an alternative to the more expensive force plate option for assessing postural stability, whether in the lab, clinic, or field settings to confidently assess.

## **2-C-31 Combined dimensionality reduction and regression to identify correlates of step length asymmetry post-stroke**

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The use of motion capture and instrumented treadmills for gait analyses provides measures of ground reaction forces and segmental kinematics which, when combined, can be used to derive joint kinetics and fully reconstruct the mechanics of locomotor function. Aided by measures of surface electromyography (EMG), these variables can help elucidate the neuromechanical control of locomotion in pathological conditions such as stroke. For example, multiple studies have aimed to identify the mechanisms underlying step length asymmetry in people post-stroke. Results have shown that paretic and non-paretic propulsive forces and spasticity in the paretic plantarflexors are associated with step length asymmetry. Despite the important insights provided by these studies, these analyses require a priori pruning of predictors in order to avoid multicollinearity. Since the spatiotemporal, kinematic, and kinetic variables are all derived from the same patterns of muscle activity, many gait variables are highly correlated. As a result, analyses that rely on multiple regression approaches are limited when assessing gait data given the need for the predictors to be independent. Here, we demonstrate that partial least squares regression (PLSR), which performs simultaneous dimensionality reduction and regression, can

take advantage of the structure among a set of predictor variables and provide a more comprehensive view of the correlates of step length asymmetry post-stroke. PLSR models the relationship between a response variable and multiple, partially-correlated predictor variables by extracting a low-dimensional set of orthogonal latent variables (LVs) that best explain the variance in the response. Here, we used PLSR to model step length asymmetry as a function of sagittal plane joint kinematics and joint moments, peak vertical and fore-aft ground reaction forces, peak impulses and integrated EMG of 12 lower extremity muscles in a sample of 15 chronic post-stroke individuals. The variable importance in the projection (VIP) was computed for each predictor and significant predictors were identified by VIP scores greater than 1, as assessed by significant differences in a t-test, to determine the variables with the greatest contributions to step length asymmetry. On average participants required 6 +/- 2 LVs to model step length asymmetry. The explanatory R<sup>2</sup> of the PLSR models was 0.88 +/- 0.08 and the predictive R<sup>2</sup> was 0.48 +/- 0.25. Across all participants, peak paretic braking force and peak paretic braking impulse had a VIPs > 1 (p=0.035 and p<0.001 respectively). Peak paretic plantarflexion moment and peak knee extension moment also contributed significantly to step length asymmetry (VIP > 1, p=0.007 and p=0.033 respectively). In contrast to previous studies, our results highlight paretic braking, and not propulsion, as a significant correlate of step length asymmetry. This may reflect the use of the paretic limb to actively limit forward progression as a reason for the increased step length asymmetry observed post-stroke. Overall, this study demonstrates that combined dimensionality reduction and regression techniques such as PLSR can identify contributing factors of step length asymmetry among a high-dimensional set of potential predictors.

## **2-C-32 Associations between motor cortex inhibition and gait variability in young and older adults**

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**Introduction:** Interlimb coordination and cortical inhibition diminish with age, posing an inherent risk for gait-related injuries. Levels of inhibition within the motor cortex are significantly associated with coordination of the upper extremities in healthy young and older adults, however, it is unknown if this same association exists for lower extremity control. Thus, this project aimed to identify how motor cortex inhibition contributes to gait symmetry in healthy young (YA) and older adults (OA). **Methods:** Two testing sessions occurred on separate days. Day one consisted of transcranial magnetic stimulation to assess motor cortex inhibition via the cortical silent period (cSP). The cSP was measured while participants maintained a submaximal isometric voluntary contraction of the vastus medialis oblique during knee extension for two minutes. Concurrently, a stimulation was given every 7-10 seconds to elicit a minimum of twelve cSPs. Each cortical hemisphere was tested independently. Day two consisted of three walking conditions: a normal (self-selected pace) 6-minute walk, a dual-task (DT; self-selected pace) 2-minute walk, and a fast 2-minute walk. Phase coordination index (PCI), which incorporates the assessment of both accuracy and consistency of gait cycle generation, was the primary outcome measure and was assessed via wireless inertial sensors during over-ground walking. **Results:** Twenty-nine healthy adults participated in the study; 14 YA and 15 OA. The cSP duration was statistically different between the YA and OA for the right motor cortex (p=0.045) with no statistical group difference for the left motor cortex (p=0.21). There was a main effect of group, demonstrating a larger PCI for OA compared to YA (p=0.01). Additionally, there was a main effect of condition indicating a greater PCI during DT (p<0.001) and fast walking (p<0.001) in comparison to normal walking. No significant PCI difference was found between the DT and fast walk conditions. Linear regressions for the YA revealed significant positive relationships between the left hemisphere cSP and the normal (r=0.70,

$p=0.01$ ) and fast ( $r=0.79$ ,  $p=0.001$ ) walking conditions with non-significant relationships between the right hemisphere and the three walking conditions. Although not significant for the OA, a negative correlation between the left hemisphere cSP and normal walk PCI was observed ( $r=-0.45$ ,  $p=0.10$ ). Conclusions: The current results indicate that motor cortex inhibition is significantly related to gait coordination in YA when measured using PCI. Specifically, these findings indicate that less motor inhibition is associated with more symmetric gait in YA, whereas in OA greater motor inhibition is related to more symmetric gait. Taken together, these results suggest that cSP may be an important neurophysiologic marker of symmetric gait function and may undergo a fundamental shift in cortical control with advancing age, thus providing a neural marker when analyzing clinical populations with impaired mobility.

## **2-C-33 Dynamic balance control during obstacle negotiation in individuals with post stroke hemiparesis**

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Obstacle negotiation is required for safe mobility, yet one third of individuals post-stroke fail this task (Said et al., 2005) which leads to a higher incidence of falls (Said et al., 2013). To maintain dynamic balance, whole-body angular momentum (H) must be regulated through foot placement and muscle force generation. Improper foot placement and diminished muscle forces can result in higher H and potential loss of balance. We have previously reported that among a variety of walking adaptability tasks, obstacle negotiation had the highest H in the mediolateral direction, particularly during the trailing limb single-stance phase (Vistamehr et al., 2017). This study identifies differences in the underlying mechanisms of regulating H between individuals post-stroke and healthy controls (HCs) by comparing foot placement and muscle activations and their association with H. Kinematic and bilateral surface EMG data from 7 lower extremity muscles were recorded from 15 individuals post-stroke and 10 HCs during obstacle negotiation. Data recorded during the trailing limb single-stance phase were analyzed. Mediolateral balance was quantified using the peak-to-peak range of frontal plane H (HR). Frontal plane H is partially regulated by foot placement, which determines the mediolateral and vertical moment arms from the whole-body CoM to the stance foot CoM. Muscle activation was quantified by average EMG amplitudes, normalized by the mean peak amplitude during self-selected walking recorded in the same session. Between-group differences were identified using paired t-tests. Associations between HR, foot placement and muscle activations were identified using Pearson's correlations. Individuals post-stroke had significant balance control deficits (HR was 62% higher relative to HCs,  $p=0.001$ ). The mediolateral moment arm was wider (40%,  $p=0.003$ ) for the paretic leg compared to HCs and was correlated with a higher HR ( $r=0.67$ ,  $p=0.001$ ). A wider moment arm during single-stance creates a destabilizing moment away from base of support and towards the swing leg that may compromise dynamic balance. The vertical moment arm was also higher in these individuals and was correlated with a higher HR ( $r=0.50$ ,  $p=0.01$ ) and requires greater balance control from the stance (paretic) leg muscle output. However, paretic leg soleus activation was lower compared to HCs (35%,  $p=0.004$ ) and was inversely correlated with HR ( $r=-0.35$ ,  $p=0.08$ ). Soleus is a major contributor to the regulation of H during walking (Neptune and McGowan, 2016). Thus, the lower soleus activation and correlation with the higher HR suggests impaired soleus activity may present a challenge for individuals post-stroke to maintain balance during obstacle negotiation. In addition, medial hamstring activation

was higher (40%,  $p=0.057$ ) in both paretic and nonparetic (correlated with HR ( $r=0.43$ ,  $p=0.03$ )) legs than in HCs, which could reflect a compensatory strategy for decreased soleus activity (Hall et al., 2011). Overall, poor balance control during obstacle negotiation post-stroke was associated with more lateral paretic foot placement, elevated body CoM, and lower soleus activation in the paretic leg. Rehabilitation targeted at improving these parameters may help improve dynamic balance control post-stroke.

## **2-C-34 Control of intersegmental dynamics during perturbation of accurate stepping during locomotion**

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Natural movements require coordinated actions at multiple joints to be successful. How this coordination is achieved is not fully understood. Kinetic analysis of multi-joint arm movements revealed that substantial part of this coordination may result naturally (passively) from mechanical interactions between segments of the limb (Dounskaia 2010). This observation, however, was obtained from experiments in which movements were restricted to the horizontal plane, and gravity was not a factor. Locomotion is the one of the most frequent motor activities, and gravity is a critical component. In this study, coordination between forelimb joints was investigated during locomotion in the cat. Unperturbed and perturbed accurate stepping along a raised horizontal ladder was investigated. In the unperturbed condition, all crosspieces of the ladder were spaced equally, 25 cm apart. Perturbations were achieved by displacing one of the crosspieces 5 cm toward to or away from the cat, requiring the cat to adjust the step length to land on the crosspiece. The crosspiece could be displaced at three different time points along the cat's progression, manipulating the time the cat had to adjust the length of the step. Joint kinematics and kinetics were analyzed for the steps bringing the forelimb to the unperturbed or displaced crosspiece. The focus was on the roles of active muscle torque, passive gravitational torque, and interaction torque in the rotation of each joint. We found a consistent joint control pattern during the swing phase of the step in all conditions. The movement was initiated with an active elbow flexion and mainly passive shoulder flexion. This was followed by a period of predominantly passive rotations in both joints. Halfway through the movement, muscle torque started causing active deceleration of the shoulder flexion, while the elbow continued to move mainly passively. The wrist rotated predominantly passively, with the muscle torque contributing only at the very beginning and end of the motion to stabilize the joint against high interaction torque. This pattern of control was largely preserved when the cat had to adjust the step to the displaced crosspiece. Changes in the step length were accomplished predominantly by a change in the speed of shoulder rotation during the last quarter of the swing motion. The influence of the timing of the crosspiece displacement on the muscle torque contribution to the movement was largely limited to large steps that were made on a short notice. We conclude that the pattern of joint control during locomotion exploits gravity and the limb's inter-segmental dynamics, and that this pattern is maintained during step adaptations to changes in the environment. We discuss these findings in relation to previous results regarding the control of locomotion and suggest that the observed joint control pattern may simplify neural control of locomotion while enabling flexible responses to environmental disturbances.

## **D – Integrative Control of Movement**

### **2-D-35 Functional brain activity during motor control and pain processing in chronic jaw-pain**

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Changes in brain function in chronic pain have been studied using task-based paradigms that deliver acute pain-eliciting stimuli or assess the brain at rest. These data point to the idea that regions both within and beyond traditional pain processing networks are altered in chronic pain, with regions of the motor network often implicated. Although motor disability occurs with many chronic pain conditions, few studies have directly assessed brain activity during motor function in individuals with chronic pain. Here, we used chronic jaw-pain as a model and assessed brain activity during a precisely controlled grip force task and during a precisely controlled pain-eliciting stimulus on the forearm. For each task, we used a machine learning analysis to identify regions whose activity maximally separated the jaw-pain group from controls while minimizing within group variability. Activation within difference regions was then used for a classification-analysis to examine the effectiveness of the tasks in distinguishing the groups. We report three novel findings. First, although the parameters of grip-force production were not different between groups, the jaw-pain group showed increased activity in prefrontal cortex, insula, and thalamus. Second, although stimulus intensity and pain perception were not different between the groups, the jaw-pain group showed lower activation in rostral regions of the inferior and middle frontal gyrus. Third, classification accuracy was higher for the motor task as compared to the pain task. Our findings suggest that a motor task offers an alternative approach for studying altered brain function in chronic jaw-pain.

## **2-D-36 The influence of kinesthetic motor imagery on goal-dependent modulation of the long-latency stretch response**

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Mechanical perturbations to the upper-limbs elicit short (SLR; 25-50 ms) and long-latency (LLR; 50-100 ms) responses in stretched muscle (Hammond et al. 1956). While the SLR is relatively immutable, the LLR has received a great deal of attention for the reason that it modulates based on the intention/goal of the performer. For example, instructing participants to compensate against a perturbation results in a large LLR compared to trials with the instruction to not-intervene (e.g. Crago et al. 1976). On compensate trials, a voluntary response appears continuous with the LLR and it is a long-standing matter of debate whether goal-dependent LLR modulation results from excitability changes along one or more of the contributing pathways (Hammond et al. 1956), or alternatively whether the modulation is simply an artefact of a hastened voluntary response superimposing onto the end of the stretch response (Crago et al. 1976). It was recently suggested that a distinction between the reflexive and voluntary mechanisms responsible for goal-dependent LLR modulation may be difficult because both responses engage common supra-spinal circuitry (Scott 2004). The LLR reflects the first volley of activity through the neural circuits that are later engaged by the voluntary response (Pruszynski et al. 2008; Scott 2004). The purpose of the present study was to determine whether the overt execution of a voluntary response is a prerequisite for goal-dependent LLR modulation to occur. In order to test this, kinesthetic motor imagery was used. This form of imagery has been shown to activate many of the same CNS structures as the physical execution of the imagined response, without actually executing the movement (Jeannerod 2001). Participants (N=10) always received a large wrist extension perturbation and were instructed to "not-intervene with the perturbation, but imagine yourself compensating against the perturbation as fast as possible and the feeling that this produces". Kinesthetic imagery trials were compared to standard not-intervene and compensate conditions. As expected, no changes to the SLR response were observed between any conditions ( $p = .364$ ) and the LLR was significantly increased (by 67.8%;  $p = .007$ ) on compensate trials compared to not-intervene. On imagery trials, we observed a non-



significant trend towards an increased LLR (8.3%;  $p = .093$ ) compared to the not-intervene condition. However, we also found that the voluntary response "leaked out" (a significant increase in voluntary epoch activity compared to a participant's not-intervene trials) on 37.0% of imagery trials. When these trials were omitted from the analysis, the LLR on imagery trials was comparable in magnitude to the not-intervene condition ( $p = .804$ ). Thus, it would appear that even though superimposition of a hastened voluntary response cannot account for all changes to the LLR, the overt execution of a voluntary response is still required for goal-dependent LLR modulation to occur. This research was supported by NSERC

## **2-D-37 Contributions of action selection and execution to spatiotemporal interference in a bimanual rhythmic-discrete task**

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Simultaneously performing bimanual movements leads to inter-manual interference. For example, when producing a discrete movement using one arm while moving the other rhythmically, rhythmic movement transiently speeds up after discrete movement initiation. Such inter-manual interference can occur at the level of motor execution, planning, and can be modulated by cognitive processes. This study aimed to assess the degree to which parameters of motor execution and action selection contribute to spatiotemporal interference during bimanual rhythmic-discrete movements. Experiment 1: If discrete and rhythmic movements interfere at the motor execution level, then discrete movements that require greater neural control and greater transcortical cross-talk would lead to greater spatiotemporal modulation of rhythmic movement. To test this hypothesis, subjects ( $N=8$ ) performed a rhythmic-discrete bimanual coordination task similar to Wei et al. (2003) consisting of rhythmic flexion-extension elbow movements in the horizontal plane using dominant hand (period: 1.45 s; amplitude: 40°) while responding to a visual imperative signal using a discrete movement of index, middle, ring, or little finger (10 trials per finger; total 40 trials per subject). Movements by the less independent fingers (middle and ring; Häger-Ross & Schieber, 2000) were expected to lead to greater spatiotemporal modulation of rhythmic movement. Spatiotemporal interference was quantified as phase and amplitude shift of the rhythmic movement cycle immediately after discrete movement initiation in comparison to pre-discrete response cycles. Results showed similar phase advance of the rhythmic movement for all fingers ( $M = -15.5^\circ$ ,  $SE = 6.0$ ). However, amplitude of the rhythmic movement decreased to a greater extent when the discrete movement was performed by the ring finger ( $M = -2.8^\circ$ ,  $SE = 0.6$ ) as compared to the other digits ( $M = -0.6^\circ$ ,  $SE = 0.5$ ), providing support for the hypothesis of execution-level interference between rhythmic and discrete movements. Experiment 2: If bimanual discrete and rhythmic movements also interfere at the level of action planning, then additional action selection constraints on the discrete movement would lead to greater spatiotemporal modulation of the rhythmic movement. Subjects ( $N=15$ ) performed a task similar to E1, but now a single discrete response had to be selected from either 2 or 4 possible alternatives (Hick-Hyman law). Results showed phase advance ( $M = -7.6^\circ$ ,  $SE = 2.8$ ) and amplitude decrease ( $M = -1.1^\circ$ ,  $SE = 0.6$ ) of the rhythmic movement immediately after discrete movement regardless of the number of possible response alternatives. There was also no differential modulation of the rhythmic movement period or amplitude prior to discrete response in any of the conditions. Overall, these studies suggest that spatiotemporal interference between rhythmic and discrete movements occurs at the motor execution, but not planning level. Action planning for the discrete movement does not affect the execution of the concurrent rhythmic movement. These findings

are consistent with the theory that rhythmic and discrete movements are two motor primitives and do not share common planning processes.

### **2-D-38 Probing sensory signals in motor cortex using a virtual balancing task**

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Multisensory processing is vital for activities of daily living. Behaviors such as walking or manipulating an object require that we tailor our actions to the environment in an ongoing manner, using sensory information to guide them. Yet, by design, many tasks used in neurophysiology laboratories do not incorporate ongoing sensory-guided action. To understand the neural mechanisms by which sensory feedback is integrated into neural commands for movement, we adapted the Critical Stability Task (CST) from the human performance literature (Jex et al., 1966). The CST is a prolonged motor control task for which sensory feedback is crucial, wherein subjects interact with an inherently unstable virtual system and must generate continuous sensory-guided actions to balance it at an equilibrium point. The difficulty of the CST is determined by a single parameter, which allows us to quantitatively establish the limits of performance for different sensory feedback conditions. In our version of the CST, adapted for monkeys, the animals must maintain a drifting cursor at the center of a monitor by making continuous hand movements, or by issuing neural commands to a brain-computer interface (BCI) that moves the cursor. The CST confers three experimental advantages: 1. it allows us to observe as skill learning develops over weeks and months. 2. Because we can use non-visual feedback, the CST enables us to directly quantify cross-modal sensory integration in the control of ongoing action. 3. It enables us to evaluate how sensory signals impact behavior in an ongoing manner. Additionally, the CST can potentially be used to assess the presence of sensory signals in primary motor cortex, and to quantify their strength. We hypothesize that primary motor cortex would exhibit a strong sensory response during a motor task that requires ongoing sensory feedback. We have trained three monkeys to perform the CST using visual and vibrotactile feedback under hand control. One monkey also performed the CST using visual feedback under BCI control. We present behavioral data for all monkeys, as well as multi-electrode neural data recorded while one monkey performed the CST.

### **2-D-39 Reach velocities index word learning in virtual reality**

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Little is known about how motor learning interacts with concurrent high level cognitive processes. We developed a gamified word learning experiment in virtual reality to explore sensorimotor grounding of language. This method offers a potential bridge from theories of sensorimotor learning to theories of high level cognition. Participants learned novel object names by manipulating virtual objects with the use of handheld controllers. The controllers were visually represented to participants as virtual hands. The six novel objects resembled potion bottles with visually distinct shapes and colors. The objects were arranged on either side of a large cauldron occupying the center of the virtual space. Participants heard one of the novel words, then grasped one of the potions and tilted it over the cauldron to pour the ingredient. They received feedback indicating whether the potion was correct or incorrect and continued until a performance criterion was met (about 100-200 trials). We recorded hand movements and correct/incorrect trials. To analyze the relationship between word learning performance and the underlying motor dynamics, we identified, for each subject, the first run of 9 consecutive correct trials. We consider this the point where participants had sufficiently learned the object names. The trials were

split into 'early' (those before the identified run) and 'late' (the remainder) sets. For each trial, we calculated the velocity of the 3-dimensional motion trajectory and applied a peak detection process. We selected the final velocity peak for each trial, excluding peaks with a magnitude less than 2.5 cm/s. This selection corresponded to the reach from the potion to the cauldron, which we verified through manual inspection of the trajectories. We analyzed subjects' peak velocities for each trial, as well as the average velocities for early and late trials aligned to the final peak. We found that the average velocity was greater for late than early trials. We also found that peak velocities tended to increase over time but this increase was greatest for the early trials. Few subjects showed an increase in late trials. This was supported by separate linear regressions fit to the early and late trials of each subject, which showed greater peak velocity slopes for early trials than late. In summary, changes in the velocity profile of reaching movements offer a motor correlate to word learning. We observed motor learning as participants learned object labels, with little evidence of motor learning once the labels were acquired. This suggests that motor learning in naturalistic experimental conditions could offer an index of higher cognitive processes, such as language learning.

## **2-D-40 Change in temporal aspects of movement affect slips of the pen**

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Slip of the pen is a common type of mistake in our daily life. Unintentional error in action, such as slip of the pen, is called action slip. Action slip is defined by the absence of fault in memory. It has been said that action slip occurs when people perform many simple skilled action automatically, and they do not explicitly monitor the feedback from each action. In other words, it has been proposed that action slip is caused by lack of attention or open-loop control of action sequences that originally require closed-loop control. Slips of the pen can be induced by an experimental approach called Rapid Repeated Writing (RRW). RRW requires participants to write one character repeatedly as fast as possible for a few minutes. During RRW, some people mistakenly write different characters from what they intend to write. Some notice their mistake by themselves, but some do not until an experimenter points it out. It has been shown that slip of the pen occurs during either RRW of Japanese phonetic characters (Hiragana) and that of Chinese characters (Kanji). Previous studies proposed that wrong activation of motor representations result in slip of the pen. They hypothesized that repetitive movement in RRW activates not only a motor representation of writing movement for intended character but that for different character, and the improper activation leads to slip of the pen. Though the hypothesis has been considered to be reasonable, the studies only focused on the static aspects of the errors such as similarity in shapes of characters. Therefore, it remains unclear about dynamic change in motor sequences when improper representations are activated. The present study thus aimed to investigate how kinematic aspects of writing movements change just before slip of the pen occurs. In this study, we hypothesized that slight discrepancy between motor command and sensory feedback that caused by loss of rhythm in automatic movement leads to slips of the pen. In the experiment, 10 participants performed two-minute RRW of one Hiragana character for five trials. Writing time per character and interval time between characters were calculated as temporal aspects of writing movement. These two indices were compared between three periods: the beginning of a trial, the period just before slip of the pen occurred, and the end of a trial. As a result, slips of the pen was observed in 6 participants. The one-way ANOVA showed that there was no significant effect of the period on writing time per character, whereas interval time between characters was longer in the period just before slips of the pen and the end of a trial than in the beginning of a trial. In conclusion, the present study reported for the first time

that temporal changes in writing movement are related to the occurrence of slips of the pen, and widening discrepancy between online visual feedback and motor commands may contribute to a trigger of unintentional motor sequences.

## E – Disorders of Motor Control

### **2-E-41 Deep brain stimulation in essential tremor: tremor and dysmetria in the upper and lower limb**

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Essential tremor (ET) is one of the most common movement disorders in humans. The hallmark symptom of ET is a 4 to 8 Hz action tremor of the upper limbs. Deep brain stimulation (DBS) can reduce tremor amplitude and improve quality of life. However, it remains unknown whether DBS improves tremor and accuracy of goal-directed movements with the upper and lower limb. Here, we test whether DBS reduces upper and lower limb tremor and dysmetria (movement error) in ET patients. Nineteen ET patients treated with DBS ( $70.1 \pm 8.1$ , 7 women) and 10 healthy (HC) aged match controls ( $68.0 \pm 6.2$ , 8 women) performed ballistic goal-directed movements with the wrist and ankle joint. ET performed the session twice, once with DBS on and once with DBS off (counterbalanced order). We quantified the tremor and dysmetria of the ballistic goal-directed movements. When DBS was switched off, ET exhibited greater tremor and dysmetria than healthy controls for both the wrist and ankle joints (all  $P < 0.05$ ). Turning on the DBS, reduced the tremor amplitude of the wrist ( $P = 0.04$ ) but not the tremor of the ankle ( $P = 0.66$ ) during ballistic goal-directed movements. In contrast, DBS did not reduce dysmetria for neither the wrist ( $P = 0.3$ ) nor ankle ( $P = 0.08$ ). Our findings suggest that although DBS can reduce the tremor of the upper limb, it has no significant effect on lower limb tremor or upper and lower limb dysmetria.

### **2-E-42 Deep brain stimulation in a patient with dystonia modulates spatiotemporal control within hands, but not between hands: a case study**

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Dystonia is characterized by involuntary, aberrant contractions of muscles causing twisting movements and/or abnormal postures. Deep brain stimulation (DBS) is used to treat dystonia and other movement disorders and mitigate symptoms. The purpose of this study was to determine the time course of motor performance changes when DBS was turned off, and back on, in a dystonia patient implanted with a DBS. We tested a 23-year-old male participant with primary generalized dystonia (DYT1 mutation) affecting primarily lower limbs, but also upper limb movements. The participant had previously undergone surgery to implant a DBS device with electrodes bilaterally stimulating the globus pallidus pars interna (GPi). Five healthy right-handers served as controls. Participants used a bimanual KINARM endpoint robot to trace circles (10 cm diameter), one for each hand, displayed approximately at shoulder width on a horizontal screen in front of them; hand locations were represented by a cursor on a screen. One trial included tracing a circle 15 times with their right hand, their left, and both hands, using in-phase coordination. For the first five circles, the circling pace was cued by an acoustic stimulus at 1 Hz. After this, the stimulus stopped and participants continued circling at that rate; only the ten uncued movements for each unimanual, and the bimanual condition were analyzed. In the first block, participants performed ten baseline trials. The next two blocks had 40 trials each; the dystonia participant performed block two with DBS off (~58 min), and block three with DBS back on (~56 min).

The fourth block served as a ten-trial post-test. We recovered the following spatiotemporal measures from the trajectories, across each trial: within hand, we obtained movement frequency deviation, defined as the difference between movement and the target frequency, and spatial variability defined as standard deviation of the Euclidean distance between the hand trajectory and the circle template, serving as proxy for circularity. Between hands (in the bimanual condition), we measured relative tangential angle (RTA), and uniformity, a measure of dispersion of RTA. Preliminary results showed that during baseline, all participants moved slightly faster than 1 Hz in both uni- and bimanual conditions. The controls continued to do so in the other blocks, whereas the dystonia participant slowed down to slightly less than 1 Hz during the DBS off block, and gradually increased speed once DBS came on again. His spatial variability was higher than that of controls; this was pronounced in the bimanual condition, particularly affecting the left hand. RTA and uniformity were unaffected by DBS status, and not different from the control participants. These findings suggest that DBS may help recover central temporal and spatial control mechanisms, likely mediated by basal ganglia-cerebellar-thalamocortical loops. They also indicate that between-hand coordination, at least during a stable attractor state, appears to remain intact in dystonia.

## **2-E-43 Modular muscle stimulation improves neuromuscular control in post-stroke subjects**

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Background: Reaching task control entails coordinated activation of a selected group of muscles with a stereotyped time sequence [1], which is best described as a muscle synergy representation of the motor module. The muscle synergy is disrupted after cerebral lesion such as in stroke. However, the motor module can reorganize in order to compensate for the disruption in muscle coordination. Examining reaching movements in individuals following stroke may shed light to the alteration in neural control underlining the abnormal organization of motor module, and may relate quantitatively the degree of impairment of motor module to functional abnormality [2]. We hypothesize that if the muscles are stimulated during performing the reaching movement in such a way that muscle activations are similar to the normal pattern of muscle synergy, the motor module may be transformed from the altered organization towards the normal pattern before lesion. Methods: 8 subjects with post-stroke hemiparesis and 9 age-matched normal subjects were recruited to participate in this study. The hemiparetic subjects were divided into sham and stimulation groups. All subjects performed front reaching (FR) and lateral reaching (LR) movements. EMG data from normal subjects generated a baseline pattern of muscle synergy for comparison. The hemiparetic subjects in the sham and stimulation groups carried out a training session of movements in one hour per day in consecutive 5 days. The stimulation pattern was based on the baseline muscle activation from a healthy subject. Performance of movements in kinematics and muscle synergy patterns was compared before and after the 5 days of training. Results: Of the 6 patients of the stimulation group, 2 patients of the sham group, after their training, preliminary results indicated that the average of synergy similarity was increased in both groups in two tasks. However, the improvement was found significant only in the FR task of the stimulation group for the vector similarity index. The kinematic performance of P/D (peak velocity of hand/movement duration) also showed general improvement in the two tasks of both groups. The improvement in kinematics was significant in LR task of the stimulation group. Correlation analysis indicated that the variation of P/D was strongly correlated to similarity of time profile in task of forward reaching. The accuracy of reaching (error of endpoint variability) had a significant correlation with the vector index of similarity. The improvement in Fugl-Meyer score was positively correlated to that of the

vector index of similarity. Conclusions: Results support the positive effect of modular muscle stimulation on the improvement of neuromuscular control in hemiparetic subjects. The FES strategy and results will have an impact on the longitudinal rehabilitation of patients following stroke. References: [1] S. Li et al., "Coordinated alpha and gamma control of muscles and spindles in movement and posture," *Front. Comput. Neurosci.*, vol. 9, Oct. 2015. [2] S. Li, C. Zhuang, C. M. Niu, Y. Bao, Q. Xie, and N. Lan, "Evaluation of Functional Correlation of Task-Specific Muscle Synergies with Motor Performance in Patients Poststroke," *Front. Neurol.*, vol. 8, Jul. 2017.

## **2-E-44 Abnormal antagonist activation during reactive balance is associated with Parkinson's disease and age**

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**BACKGROUND:** Abnormal antagonist leg muscle activity could indicate increased muscle cocontraction and serve as a useful tool for clarifying the mechanisms of balance impairments in Parkinson's disease (PD). Prior studies showed that PD patients demonstrate earlier, longer, and larger antagonist muscle activation in automatic postural responses. The generalizability of these findings is limited by participants being selected for postural difficulties and minimal tremor or by small sets of muscles and perturbation directions. Our objective was to test whether antagonist activation was abnormal in a group of PD patients not selected on phenotype. We also ran secondary analyses to test the effect of age. **METHODS:** We used baseline measures from a longitudinal study of exercise-based rehabilitation to compare antagonist activation in 31 people with PD (H&Y 1-3; UPDRS-III 32±9; age 68±9; Fullerton Advanced Balance Scale [FAB] 29±6) and 13 age-matched participants without PD (age 64±9; FAB 33±3). PD patients exhibited significantly worse balance on the FAB ( $p=0.006$ ). EMG from 11 leg muscles was recorded during balance responses to support-surface translations in 12 directions. Because antagonist-agonist cocontraction is challenging to assess using EMG signals, we quantified antagonist activation across perturbation directions with a muscle modulation index (MMI) adapted from the literature. MMI for each muscle was computed as  $100 \times [\text{maximum} - \text{minimum}] / \text{maximum}$ , using maximum and minimum EMG activation levels across directions. For each muscle, we expressed associations between PD or age and the presence of low MMI as odds ratios (OR).  $\text{OR} > 1$  indicate strong associations between PD (or age) and low modulation. Linear mixed models tested for associations between PD or age and MMI. **RESULTS:** We found abnormal antagonist activity in a broader sample of PD participants, muscles, and perturbation directions than previously studied. Taken together, our results suggest abnormal antagonist activity was more strongly associated with PD than age. PD was associated with low MMI (OR:  $2.03 \pm 1.02$ , range 1.24-4.02; statistically significant in 1/6 muscles, tibialis anterior [ $p=0.001$ ]). Age was also associated with low MMI (OR:  $2.79 \pm 1.67$ , range 1.21-5.69; statistically significant for biceps femoris long head, soleus, and tibialis anterior [ $p=0.003$ , 0.033,  $<0.001$ ]). Linear mixed models identified significant associations between MMI and PD ( $p=0.039$ ) but not age ( $p=0.098$ ). **CONCLUSION:** Antagonist activity is abnormal during automatic postural responses in a broader range of people with PD. This activity may be a mechanism of balance impairment in PD and thus a potential target for rehabilitation. MMI might serve as a marker of improving balance, even before clinical scores improve.

## **2-E-45 Motor strength or motor control: What matters in chronic stroke?**

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Background: Walking and driving are crucial activities for reintegration in the community following a stroke. Motor recovery remains incomplete several years after stroke contributing to residual impairments in these activities. Whether impairments in walking and driving in chronic stroke occur due to the deficits in motor strength or motor control remains unclear. Therefore, the objective of this study was to determine the contribution of motor strength and motor control to functional performance related to walking and driving in chronic stroke survivors. Methods: Chronic stroke survivors (N=21, age =  $65.04 \pm 13.72$  years, time since stroke =  $4.79 \pm 4.66$  years, Fugl-Meyer Assessment Lower Extremity Score =  $27.61 \pm 4.85$ ) and healthy controls (N=21, age =  $68.59 \pm 8.53$  years) performed four tasks that involved ankle dorsiflexion and plantarflexion; 1) Maximum voluntary contractions (MVC), 2) Visuo-motor tracking task (sinusoidal target, frequency 0.3 Hz.), 3) simulated driving task that required driving on a winding road and responding as fast as possible to an unexpected stimulus by pressing the brake pedal and 4) over-ground walking for 10 meters at self-selected speed. The motor strength was determined as the highest of the maximal force obtained from the three MVC trials. Motor control ability was quantified by measuring the motor accuracy (root mean square error, RMSE) and motor variability (standard deviation, SD) on the visuo-motor tracking task. Functional performance was determined a) on simulated driving by the reaction time measured as the time elapsed from stimulus presentation to the application of peak force on the brake pedal, and b) during over-ground walking task by the stride length variability measured as the coefficient of variation of the stride length. To examine the group differences on motor strength, motor control, simulated driving and over-ground walking tasks, we used independent t-test. To determine the contribution of motor strength and motor control in walking and driving tasks, we performed a multiple linear regression with motor strength (MVC during ankle dorsiflexion and plantarflexion) and motor control (RMSE and SD) as the predictor variables and driving reaction time and stride length variability as the criterion variables. Results: Compared with the control group, the stroke group showed significant a) decrease in plantarflexion strength and b) increase in RMSE, SD, driving reaction time and stride length variability. The multiple regression model revealed that motor accuracy (RMSE) was a significant predictor of the driving reaction time ( $R^2 = 0.221$ ,  $p < 0.05$ ). Further, motor variability was a significant predictor of the stride length variability ( $R^2 = 0.331$ ,  $p < 0.01$ ). Most importantly, the motor strength on dorsiflexion or plantarflexion did not predict driving reaction time or stride length variability. Conclusion: These findings demonstrate that the deficits in motor control (reduced accuracy and increased variability) rather than motor strength predict residual impairments in driving and over-ground walking in chronic stroke survivors. Therefore, rehabilitation interventions should focus on assessing and improving motor control to enhance functional outcomes in chronic stroke survivors.

## **2-E-46 Cortical dynamics within and between parietal and motor cortex in essential tremor**

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Essential tremor (ET) is a disorder of the cerebello-thalamo-cortical network or the inferior olive-cerebellar network. Recent fMRI-studies have shown that in areas within the parietal and the motor cortices, abnormal activation occurs in ET subjects while performing visually-guided movement tasks and that their tremor exacerbates with increases in visual feedback. Despite the above knowledge, how neuronal oscillations and directionally-specific connectivity relate to the magnitude of this visually-induced tremor in ET remains unexplored. Here, the goal was to examine how the magnitude of tremor in ET during a visually-guided pinch-grip force production task consisting of low and high visual feedback

conditions relate to the cortical oscillations at parietal and motor cortex, and the directionally-specific connectivity between these cortices. The study consisted of 24 ET subjects (mean/sd age = 66.04/11.56 years) and 17 age matched healthy controls (mean/sd age = 62.94/8.64 years). For the ET-group, the mean disease duration was 24.26 years (sd = 20.67) and their mean FTM-TRS score was 37 (sd=18.40). For controls the mean FTM-TRS score was 0.50 (sd = 0.96). The two groups showed significant difference in FTM-TRS score but no significant difference in MoCA scores. We simultaneously measured cortical activity and tremor at low and high visual feedback conditions while subjects produced visually-guided pinch-grip force. Per subject, cortical sources of oscillations were localized using an EEG-based source localization procedure, and were grouped into domains using measure projection analysis. For each subject per condition, we established the event related spectral perturbation (ERSP) at each domain, and directional connectivity estimates between each pair of domains. The ERSP-plots and the connectivity estimates were examined across groups and conditions. To examine the association between the cortical oscillations and connectivity and the worsening of tremor from low to high visual feedback, we performed a multi-linear-regression analysis. For this analysis, the tremor magnitude during each trial was defined as the sum of power of force in the 4-12 Hz band. Our analysis yielded domains in ipsilateral and contralateral motor cortices, and ipsilateral parietal cortex. There were three notable findings: (1) by altering the visual feedback level, the ERSP activity in 4-12 Hz and 12-30 Hz frequency bands at all three domains could be modulated for both groups. However, an impaired ERSP modulation in ET subjects was detected at contralateral motor cortex with a significantly diminished desynchronization at the high visual feedback condition. (2) For the ET-group, the bidirectional connectivity strength in 12-30 Hz between the superior parietal cortex and the contralateral motor cortex was significantly blunted relative to controls. (3) The worsening of tremor from low to high visual feedback was directly associated with the ERSP modulation in the 4-12 Hz across feedback conditions at contralateral motor cortex. Our findings provide new evidence to support the hypothesis that ET is a network level disorder involving abnormal cortical oscillations within the visuomotor system and diminished connectivity between parietal and motor cortices.

## **2-E-47 Oculomotor movements affect reaching movements in stroke survivors**

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Background. Activities of daily living, such as driving and walking, require fast oculomotor movements (saccades) to gather visual information that guides motor planning and execution. Most stroke survivors experience chronic difficulties performing these daily activities. We have previously shown that stroke survivors with mild motor impairments and no visuospatial neglect make a greater number of saccades than age-matched controls during planning and initiating arm movements (reaching). The excessive number of saccades result in relatively worse overall motor performance by the stroke survivors. However, the precise nature of the interaction between the oculomotor and limb motor processes relationship remain unclear. Objective. Here, using robotics and eye-tracking, we investigate whether saccades interfere with speed and smoothness of reaching movements in stroke survivors. Methods. We examined saccades and reaching in stroke survivors and healthy controls who performed the Trail Making Test (TMT), a neuropsychological test of visuomotor processing and executive function that relies on organized patterns of saccades to guide reaching movements. Results. Compared to age-matched controls, stroke survivors made a greater number of saccades during reaching movements. In both controls as well as stroke survivors, most of these saccades were closely followed by a transient decrease in reaching speed. Furthermore, in stroke survivors, the number of saccades made during



reaching were strongly associated with reduced speed and smoothness of reaching movements and with greater difficulty performing daily activities (measured using Stroke Impact Scale). Conclusions. These results indicate that post-stroke neural damage produces interference between eye and limb movements that may cause deficits performing motor skills. This also suggests that clinical assessments and treatments for post-stroke impairments of visual search could facilitate improvements in motor performance.

## **2-E-48 StartReact reveals differential reticulospinal control of muscle activation and inhibition during gait initiation in patients with corticospinal degeneration**

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**BACKGROUND AND AIM** - Corticospinal lesions cause impairments in voluntary motor control. Recent findings from StartReact paradigms suggest that some degree of voluntary control may be taken over by a compensatory pathway involving the reticulospinal tract. StartReact is the accelerated release of a preprogrammed motor program by a startling acoustic stimulus (SAS), presumably conveyed by the reticulospinal tract. Patients with corticospinal lesions have delayed simple reaction times, yet their SAS-induced reaction times are completely normal compared to healthy individuals (1). As previous studies mainly focused on isolated single joint movements, the question remains whether the reticulospinal tract can also be utilized for controlling whole-body movements. To test this notion, we applied the StartReact effect during gait initiation in healthy controls and in patients with retrograde axonal degeneration of the corticospinal tract (Hereditary Spastic Paraplegia, HSP). **METHODS** - We included 12 patients with 'pure' HSP and 12 healthy controls. They stood upright in front of a LED display with each foot on a separate force plate. As soon as the visual imperative stimulus was presented, the participants had to perform three consecutive steps. In 25% of the performed 16 trials, a SAS was presented simultaneously with the imperative stimulus. We determined latencies of tibialis anterior (TA), rectus femoris (RF), anticipatory postural adjustment (APA) and step onsets, as well as soleus (SO) offset. **RESULTS** - Without SAS, we observed an overall delay in HSP patients compared to controls, varying between 32 ms in SO offsets and 130 ms in step onsets. Administration of the SAS accelerated TA and RF onsets in both groups, but more so in HSP patients (SASxgroup,  $p < 0.05$ ), resulting in (near-)normalized onset latencies. In the healthy controls, the SAS also accelerated SO offsets, but an opposite effect was observed in HSP patients (64 ms delay in SAS-trials vs 32 ms in non-SAS trials; SASxgroup,  $p < 0.05$ ). The SAS also accelerated APA and step onsets in both groups, yet it did not normalize these onsets in the HSP patients (23 ms and 153 ms delays with SAS; SASxgroup,  $p > 0.115$ ). **CONCLUSIONS** - The (near-)normalization of TA and RF onset latencies with SAS that we observed in the HSP patients confirms previous findings. For SO deactivation, however, no such effect was found, which may underlie the persisting delays with SAS in APA and step initiation in these patients. This defective muscle deactivation may be due to the reticulospinal tract having indirect inhibitory (as opposed to direct excitatory) projections onto motoneurons (2), or by self-sustained firing of motoneurons overriding the inhibitory commands (3). Future studies in patients or animals with corticospinal lesions should clarify the mechanisms of inhibitory reticulospinal control. **REFERENCES** - 1. Nonnekes et al. (2014). 2. Peterson et al. (2010). 3. Heckmann et al. (2005)

## **F – Adaptation & Plasticity in Motor Control**

### **2-F-49 Uncontrolled manifold analysis reveals structure of variability in lip-jaw kinematics during speech production**

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The articulatory system influences sound pressure level (SPL) during speech. Increasing SPL is associated with increased jaw opening and increased upper and lower lip displacements. Mouth opening (MO = distance between upper and lower lip) increases to increase SPL via lip radiation in part. However, the robustness of the MO - SPL relation, and whether it persists regardless of how individuals are cued to increase SPL is unknown. Since cues can differ in their naturalness and cognitive load, individuals may develop different motor goals and exhibit different behaviors across cues. Given the salience of cueing in basic research and treatment of articulation disorders, we aim to examine whether the cue used to elicit increased SPL influenced the control of articulatory targets for MO. Nineteen young adults (11 women), aged 20-30 years participated in the study. They repeated the sentences "Buy Bobby a puppy" and "You buy Bobby a puppy if he wants one" fifteen times, one time per breath, under four SPL conditions: comfortable loudness and pitch (COMF), while targeting 10 dB above comfortable (10dB), at what they felt was twice their comfortable loudness (TAL), and in background noise (70 dBA) (NOISE). These conditions are a mix of internal (TAL) and external cues (10dB, NOISE), and the NOISE condition mimics a naturally experienced cue to increase SPL. The "Buy Bobby a puppy" section was extracted from the peak MO velocity in "Buy" to the peak MO velocity in the second syllable of "puppy" for all sentences. The repeated trials for a given condition were time aligned using the lip closure instants for stop consonant "p" and "b". We performed the uncontrolled manifold analysis on the vertical positions of the upper lip, jaw, and the lower lip relative to the jaw. This analysis partitions the variance in these variables and yields the variance that does not affect MO (Vg), the variance that affects MO (Vb), and a measure of stability (DV) of the MO at compatible time instants across multiple trials. The stability is greater when the lips are closed than when they are open (DVclosed: 0.89 +- 0.03, mean +- SE); DVopen: 0.69 +- 0.02; F(1,18) = 103.89; p<0.01). This is consistent with the idea that since lip closure is critical to the acoustic realization of stop consonants, MO is highly controlled, but MO is less critical to the acoustic realization of vowels. The stability is lower if the sentence is embedded (DV-NotEmbedded: 0.83 +- 0.03; DV-Embedded: 0.77 +- 0.02; F(1,18) = 4.416; p=0.05). Adding movement goals before and after the target sentence reduces stability, which is consistent with previous work. Vg and Vb are highest for the NOISE condition, and significantly higher than COMF. Prior analyses of MO variability revealed no differences across these conditions. This novel finding suggests that the NOISE cue leads to a relaxation of the constraints on the articulation, but in ways that maintain the MO - the critical variable for sound production.

## **2-F-50 Neural and behavioral sensorimotor adaptation changes in astronauts during spaceflight**

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Sensorimotor adaptation refers to movement control adjustments in response to mechanical or sensory perturbations. While postural and locomotive changes from long duration spaceflight have been well documented, the extent to which long duration spaceflight affects sensorimotor adaptation remains unclear. It may be that the ongoing adaptation to microgravity interferes with other sensorimotor adaptation tasks. Here, we examine whether a six-month International Space Station Mission influences the behavioral and neural correlates of sensorimotor adaptation in a preliminary sample of eight astronauts; data collection is ongoing. Astronauts used a joystick to move a cursor to targets presented

on a screen under normal cursor feedback and 45° rotated feedback, a task known to produce an adaptive response. They performed the task up to three time-points before spaceflight, at three time-points during spaceflight, and up to four time-points post spaceflight. Functional MRI was acquired during the task for the pre and post spaceflight sessions. Preliminary behavioral analyses revealed that the average rate of adaptation during the adaptation blocks was similar across all time-points. That is, astronauts showed no evidence of savings across multiple experiences completing the task. Moreover, average direction error was largest for after effects during flight, followed by post flight. Preliminary neuroimaging analyses showed flight-related brain activation changes in frontoparietal regions and the right cuneus during early adaptation. The left posterior-medial frontal lobe, left inferior frontal gyrus, and right anterior cingulate cortex exhibited activation changes across time points during late adaptation. Finally, the right middle frontal gyrus, right precuneus, and right cerebellum (lobules IV-V) showed changing activity across time points during after effect trials. Given that the largest spaceflight effects were on the after effect trial performance, it may be that spaceflight interacts with implicit components of adaptation as well as savings. Further analyses will include assessing the remaining time-points for a total sample of 13 astronauts. We will also examine correlations between brain and behavioral changes from pre to post flight during different phases of sensorimotor adaptation. Supported by NASA NNX11AR02G and NSBRI SA02802.

## **2-F-51 Age-related differences in brain activity and changes in deactivation during visuomotor skill learning**

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The age-related changes in neural mechanisms of visuomotor learning, and especially from learning visuomotor tracking tasks, are unclear. Our previous systematic review and meta-analysis showed that changes in TMS outcomes (excitability and short-interval intracortical inhibition) are not related to behavioral changes in visuomotor performance (Berghuis et al 2017). In the current study, we use fMRI to examine the age-related changes in brain activity immediately and 24h after visuomotor practice with the dominant right hand. Furthermore, correlations between parameter estimates and motor learning were analyzed. Healthy older (n=16, 7F, mean age 62.6 years) and healthy young (n=17, 10F, mean age 25.5 years) adults performed a pre-test, training session and a post-test of a visuomotor tracking task on Day 1 and a retention test on Day 2. The task consisted of experimental (zig-zagged template) and control tasks (monotonically increasing or decreasing line). fMRI was acquired during the test-moments (Siemens Allegra, 3T, 279 volumes per test). Older (error: 14.5°) in comparison with young adults (error: 9.7°) performed the experimental task more poorly at the pre-test but practice improved both age-groups' performance to a similar extent from pre- to post-test (young: 26%, old: 25%) and post-test to retention (young: 7%, old: 1%). fMRI results showed that older adults activate similar areas as young during task execution but they activate bilateral subcortical areas, left pre- and post-central gyri, frontal, temporal and parietal areas to a greater extent. Averaged across age-groups, brain activity in right occipital and parietal areas decreases from pre- to post-test and increases back to pre-test levels at retention test. From post-test to retention, there was more brain deactivation in bilateral precuneus, left temporal, frontal and occipital areas in young adults, whereas in older adults, there was no change or a trend for less brain deactivation in these areas. In left pre-/post-central gyrus and left inferior frontal gyrus in older adults, preliminary correlation analyses showed a trend that a generally higher

brain activation is related to worse performance. Furthermore, the opposite direction of correlation in young and older adults between left pallidum/thalamus and left calcarine/precuneus activity with motor skill acquisition supports the compensation hypothesis. In conclusion, the higher brain activity does not help older adults to perform the skill as well as younger adults but older adults may use this overactivation as a compensatory strategy to learn the task at a similar rate to those in young adults.

## **2-F-52 Motor cortex changes associated with multisensory perceptual learning**

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Spatial realignment of visual and proprioceptive estimates of hand position is necessary both to keep estimates in register over time and compensate for perturbations. If such perceptual learning affects perceived hand position in a common sensorimotor map, and thus motor planning with that hand, we might detect neurophysiological changes in the motor system after visuo-proprioceptive realignment. We focus on M1, as this motor execution area is linked to processes that may have substrates in common with visuo-proprioceptive recalibration: motor adaptation and proprioceptive training (Hirano et al 2015, Mattar et al 2013, Wong et al 2012). We hypothesize M1 excitability change after subjects are exposed to misaligned but not veridical visuo-proprioceptive information, and that changes are specific to M1 representation of the misaligned hand. Expt 1. In two sessions each, 32 healthy adults experienced misaligned or veridical visuo-proprioceptive information about their static left index finger in a matching task with no performance feedback or knowledge of results (Block & Bastian 2011, 2012). TMS over M1 representation of misaligned index finger (FDI) was used before and after the matching task to compute the I/O curve, area under which represents M1 excitability. A multilevel model of area under the I/O curve suggests a negative association between the misaligned session and proprioceptive realignment ( $\beta = -1.50$ ,  $p < 0.001$ ), and a positive association between the misaligned session and visual realignment ( $\beta = 0.49$ ,  $p = 0.05$ ). I.e., subjects who realigned proprioception more than vision had decreased M1 excitability, while subjects who realigned vision more than proprioception had increased M1 excitability (Munoz-Rubke 2017). These patterns are absent from the veridical session, and unrelated to motor performance in the matching task, as the index finger of interest performed the same action--touching a stationary tactile marker--in both sessions. Expt 2. If misaligned information about the index finger is presented, would changes to M1 excitability be limited to that finger, or extend to the entire effector (including biceps and forearm)? The former might suggest a role for subject's locus of attention (on their misaligned finger position), while the latter might suggest that the brain generalizes perceptual learning to any motor representation that might be involved in finger positioning; i.e., the whole arm. We repeated Expt 1 in a new group (N=24), again measuring M1 representation of the misaligned index finger (FDI), with the addition of 4th finger muscle ADM, forearm muscles (ECR and FCR), and biceps. While results in misaligned finger FDI reproduce those of Expt. 1, no other muscles show significant associations with realignment. These results suggest visuo-proprioceptive realignment is associated with physiological change in the motor system, consistent with a common sensorimotor map for multisensory and motor control. M1 changes are related to the modality being realigned, suggesting a modality-specific neural mechanism such as modulation of somatosensory cortex or dorsal stream visual areas that impact M1. The effect is limited to the misaligned finger, suggesting somatotopic specificity related to the perceptual perturbation.

## **2-F-53 Does prior stance slip-perturbation training augment or mitigate the recovery response to a novel stance trip-perturbation in chronic stroke survivors?**

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**Background:** Evidence suggest that chronic stroke survivors, demonstrate a potential for acquiring reactive adaptations to external perturbations. However, there is limited evidence on generalization of such motor adaptation to different contexts. For example, the influence of sensorimotor adaptation when exposed to a diametrically opposite types of perturbation is unknown. Thus, the aim of this study was to examine whether prior slip training would mitigate (interfere) or enhance (generalize) the recovery response to an unexpected novel trip perturbation in chronic stroke survivors. **Methods:** 29 community dwelling stroke survivors were assigned to either training group (n=13) or to control group (n=16) which only experienced a single novel unannounced backward trip-like perturbation (TC). The training group received an initial block of 8 slip-like stance forward perturbations (S1-S8) followed by a novel backward trip perturbation (T1). ActiveStep (Simbex) motorized treadmill was used to induce perturbations during standing. Body kinematics was recorded using the 3D Motion analysis system. The following variables were computed and analyzed: Falls, number of steps, center of mass (COM) stability, its position and velocity relative to the base of support, step length and trunk angle. The COM stability was calculated as the shortest distance from the COM motion state to the backward computational threshold of the feasible stability region and normalized to the length of this region. Such a measure would allow a uniform scale for comparison of stability during opposing perturbations. Higher values of stability (>1) indicate greater forward instability and lower values (<0) greater backward instability with value between 0 and 1 being optimally stable. Paired t-tests were used to compare parametric variables between S1 -S8 and T1. Independent t-tests were used to compare outcomes between T1 and TC. Nonparametric tests were used to compare the falls and number of steps. **Results:** The training group demonstrated significant adaptation to the repeated slips from the 1st to last trial with reduced number of steps, and a longer 1st compensatory backward step length to position their COM anteriorly, resulting in a significant increase in reactive stability and thus, decrease in fall rate ( $p<0.05$ ). These rapid adaptive changes were positively transferred to the recovery response from the novel trip (T1) in which participants demonstrated lesser falls and number of steps, with a longer compensatory forward step, a more posterior COM and decreased trunk flexion than the control group, resulting in the training group having lesser forward instability ( $T1<TC$ ;  $p<0.05$ ). **Conclusion:** The results indicate that the training group performed better than the control group, on exposure to an unexpected novel trip. The results suggest that chronic stroke survivors can accurately adapt to repeated slip perturbation training and furthermore, demonstrate generalization to an opposing trip perturbation.

## **2-F-54 Eye movements represent explicit learning in hand movement adaptation**

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Recent studies suggested that motor adaptation consists of two learning components: explicit and implicit. While total adaptation is the combination of these two components, measuring the relative contribution of each remains a challenge. Recent visuomotor rotation adaptation studies have measured the explicit learning by asking subjects to verbally report their aiming direction (explicit intention). Here, we examined whether the explicit component can be assessed from the subjects' eye movements. We used the same task design which was previously used to obtain continuous verbal reports of aiming direction, with the addition of eye tracking to assess subjects' eye movements during the adaptation. Each subject participated in two experimental sessions. Half of the subjects did a first session with verbal report and a second without, and the other half did the non-reporting session first.

We found that the eye movements followed a general pattern where the eye initially fixates the origin of the reaching movement and then, after target appearance saccades to the target. During the rotation block, the eyes saccade again towards the direction the hand moved to correct for the rotation. In early rotation trials, this eye movement falls quite close to the point the hand reaches to. However, in the late rotation trials, the eye movement is somewhere between the hand position at the end of the reach and the original target. During the reporting sessions, we found that in most trials the eye fixation just before movement onset was very close to the reported aiming direction. There was a close match between the learning curve of the reporting and the learning curve of the eye movements. Strikingly, the eye movements during the non-reporting sessions showed the same basic pattern seen during reporting: a rapid rise early in the rotation phase followed by a gradual decline over the course of the learning set, as expected for explicit learning. While the implicit knowledge implied by the eye movements was much greater than the implicit knowledge demonstrated when subjects return to aim towards the target during washout, these two implicit components were highly correlated across subjects, suggesting that the eye fixation at movement initiation may provide a measure of explicit adaptation.

## **2-F-55 The fast and slow adaptive processes are malleable based on prior experience**

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Movement errors can be caused by changes to the environment and our body. By analysing properties of movement errors, we can uncover underlying characteristics of motor adaptation such as learning and retention. Two well-defined behavioural phenomena in adaptation tasks are savings and spontaneous recovery. Savings is the ability of prior learning to speed up subsequent relearning. Spontaneous recovery is a rebound of behaviour toward the initial/previous level of adaptation. Short-term motor adaptation (e.g., over a period of minutes) is believed to be supported by two separate processes, each with distinct timescales, one fast and one slow, that operate simultaneously. The fast process responds strongly to error, learns quickly, but has poor retention. The slow process has better retention but is less sensitive to errors and thus learns more slowly. This work aims to broaden our understanding of how learning and forgetting contribute to our ability to adapt our movements. Here we tested the hypothesis that repetition of the same motor task influences properties of the fast and slow processes (fast & slow learning rates, and fast & slow retention) differently than when switching to a novel motor learning task. Healthy adult participants grasped the handle of a robotic manipulandum and performed reaches to virtual visual targets while the hand and arm were occluded. Participants completed one of two experiments, each of which was divided into two sessions, separated by a 5 minute session break. In the first session participants adapted their reaches to a viscous (velocity-dependent) force field (FF). In the second session participants reached in the same FF as in the first session (Experiment 1, n=54) or in the opposite FF (Experiment 2, n=46). The experimental sequence was null field (no force) trials, FF adaptation, FF reversal, and finally a series of channel trials. During FF adaptation we probed learning using randomly interspersed channel trials in which the path of the robot handle was constrained to a straight line. In Experiment 1, in which participants experienced repetition of the same perturbation, we found an increase in learning rate both in the fast and slow processes that resulted in savings. In Experiment 2, in which participants experienced a novel perturbation in the second session, we observed a statistically reliable difference in the fast process retention parameter. Given that the sequence of trials within a session included a brief FF reversal, the FF in session 2 was not completely novel and this difference could reflect spontaneous recovery. Our work suggests that the

fast and slow learning adaptive processes are malleable depending on previous experience with a motor task.

## **2-F-58 Muscle activation during index finger tapping at preset and freely chosen rates**

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Muscle activation increases with increased preset index finger tapping rates [1]. We tested whether the same occurs during the phenomenon of repeated bout rate enhancement, which is characterized by an increased tapping rate in the 2. of two consecutive bouts of freely chosen finger tapping [2]. For the present study, healthy individuals participated in two experiments. In Exp A (n=21), two 3-min tapping bouts were performed at freely chosen rates. The bouts were separated by 10 min rest. In Exp B (n=11), two 1-min tapping bouts were performed at preset rates of 150 and 168 taps/min, respectively, in counterbalanced order and separated by 2 min rest. A metronome was used for tapping in Exp B. Tapping was performed with the right hand's index finger. Surface electromyography (sEMG) was recorded from the extensor digitorum communis (EDC) and the flexor digitorum superficialis (FDS) muscles of the right forearm. Root-means-square envelopes of the sEMG signals were calculated across the entire duration of the bouts. In Exp A, rates in the 1. and 2. bout were 155±52 and 175±59 taps/min, respectively ( $p<.001$ ). In Exp B, rates in the 1. and 2. bout were 151±1 and 169±3 taps/min, respectively ( $p<.001$ ). In Exp A, the sEMG activity for EDC and FDS did not change significantly ( $p=.122$  and  $p=.723$ , respectively). In Exp B, sEMG activity for EDC increased by 15.1±22.0% from the low to the high rate ( $p=.013$ ), while no significant difference was found for FDS ( $p=.104$ ). The data concerning sEMG from Exp B with preset rates support previous findings [1]. For comparison, the results from Exp A with freely chosen rates - namely that the increased rate was not accompanied by changes in muscle activation - was a novel finding. It has been suggested that the magnitude of sEMG activity reflects descending neural drive [3]. Thus, it could be speculated that the increase in sEMG activity in EDC during tapping with an increased preset rate in Exp B reflected a larger descending neural drive for EDC. Further, perhaps the increased rate during the phenomenon of repeated bout rate enhancement, in the 2. bout of Exp A, occurred as a result of an excitation of the rhythm generating part of the spinal central pattern generator, which might be involved in the control of tapping rhythm [4]. The latter might cause an increased rate, without increased descending neural drive. In conclusion, the present study confirmed previous findings of increased muscle activation of EDC at an increased, preset, finger tapping rate. For comparison, muscle activation of EDC did not change at an increased rate during repeated bout rate enhancement where the rate is freely chosen. Regardless of tapping condition, there was no significant effect of rate on muscle activation of FDS. References: 1. Schnoz et al. 2000 Eur J Appl Physiol 83: 207-14. 2. Hansen et al. 2015 J Mot Behav 47: 365-73. 3. Arabadzhev et al. 2010 J Electromyogr Kinesiol 20: 223-32. 4. Finkel et al. 2014 J Comp Neurol 522: 3437-55

## **2-F-59 Multiple measurements of aftereffects in a visuomotor adaptation task**

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The present study investigated the development of aftereffects in a visuomotor rotation task by multiple measurements. Previous studies have used aftereffects as a measure reflecting the degree of acquisition of a new internal model. Therefore, if aftereffects are observed in a catch trial, one is regarded to successfully adapt a new visuomotor environment. However, considering the idea that we retain multiple internal models at the same time and flexibly switch them for an upcoming situation,

aftereffects may reflect not only the achievement of acquisition but also switching efficiency. To address this question, we measured aftereffects multiple times in the time course of visuomotor adaptation. In the experiment, participants carried out a visuomotor rotation task, in which they continuously followed a randomly moving dot with a mouse cursor as accurately as possible. In adaptation trials, visual feedback of the mouse cursor was rotated by 150 degrees. We manipulated the measurement times as an independent variable; in the time course of the adaptation task, catch trials were introduced once, twice, or four times in separate experiment groups (C1, C2, and C4 groups, respectively). We compared aftereffects in the last catch trial that was conducted at the same timing across the groups. Based on the assumption that the switching efficiency improved as a function of the experience of catch trial, we predicted that the aftereffects in the last catch trial in the C4 group is smaller than those in the C1 and C2 groups. In the C4 group, aftereffects are predicted to decrease after an increase in the time course. The results in general are consistent with our prediction, supporting the idea that aftereffects reflect not only the results of adaptation but also switching efficiency.

## **2-F-60 Downregulation of primary sensorimotor missing hand cortex activity is a correlate rather than a driver of phantom limb pain relief**

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Following arm amputation individuals generally report experiencing vivid, and often painful sensations of their missing limb (phantom limb pain, PLP). PLP is notorious for being difficult to treat, in part due to an incomplete understanding of its underlying mechanisms. Traditionally, PLP is thought to originate from reorganisation in the primary sensorimotor cortex triggered by input loss. We recently challenged this prevalent view of maladaptive cortical reorganisation, by showing a positive association between chronic PLP and maintained activity in the primary sensorimotor missing hand cortex during phantom hand movements, providing new possibilities for PLP treatment. Here we took advantage of preserved phantom hand motor control to design a new PLP treatment. To influence information processing of peripheral missing hand signals that were previously implicated with PLP, we instructed amputees to execute phantom hand movements during a single twenty-minutes session of non-invasive brain stimulation, via anodal (1mA) transcranial direct current stimulation (tDCS) over the primary sensorimotor missing hand cortex (hereafter intervention stimulation). We tested fifteen upper-limb amputees suffering from chronic PLP in a within-participants, double-blind, counterbalanced, and sham-controlled design. Subjective PLP ratings and functional MRI scans were obtained prior to, during, and post brain stimulation. Subjective PLP ratings were also obtained in the week subsequent to each stimulation session to assess potential lasting stimulation effects. While PLP was significantly increased in the sham stimulation condition immediately after brain stimulation, a common occurrence during phantom hand movement, task-concurrent intervention stimulation averted this PLP increase. Importantly, we observed significant PLP relief ninety minutes following task-concurrent intervention stimulation. This stimulation-induced PLP relief lasted at least one week, while no lasting PLP changes were observed in the sham condition. PLP relief associated with reduced phantom hand movement activity in the primary sensorimotor missing hand cortex after stimulation. This observed correlation is highly consistent with our previous evidence linking worse PLP to increased activity in this area. Importantly, reduced activity in the primary sensorimotor missing hand cortex was only observed after stimulation, suggesting it may be a correlate of PLP relief rather than its driver. We next explored which brain areas during stimulation predicted the subsequent downregulation of activity in the primary



sensorimotor missing hand cortex. We found that activity changes during intervention stimulation in several pain-related areas, including the insula and secondary somatosensory cortex, predicted both the subsequent reduction in primary sensorimotor cortex activity and PLP relief. The insula is known to be a key area in encoding the sensory aspects of pain and its modulation. Yet, the role of the insula in PLP has remained largely unexplored. Together, our findings suggest that processing in the primary sensorimotor cortex, an area often suggested to be involved in PLP and other neuropathic pain conditions, may be a correlate of the experienced pain rather than its cause.

## **2-F-61 Motor adaptation to novel field dynamics is not associated with proprioceptive acuity in older or younger adults**

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During normal healthy ageing there is a deterioration in motor control which is characterized by increased reaction times, movement duration and kinematic variability. This is thought to be due to a multi-factorial process of general sensorimotor system decline, yet the extent to which proprioceptive sensory loss contributes to age-related motor impairments is not well understood. Last year, we reported an active, multi-joint reaching task to estimate systematic (bias) and variable (uncertainty range) proprioceptive errors in older and younger adults, before correlating them with performance on a rapid target-based reaching task. Although physically inactive older adults had larger biases, there were no associations between performances on the 2 tasks for either age group. Following this, we were interested to see whether this was also true for motor tasks which place greater emphasis on utilizing proprioceptive feedback for performance. In this experiment, we therefore examined the relationship of dynamic proprioceptive acuity with sensorimotor reach adaptation to a velocity-dependent force-field in a group of older and younger adults. To further isolate the contribution of proprioception to adaptation, we also included an additional sub-group in each age range who adapted with limited visual feedback of the perturbation. We hypothesised that baseline uncertainty range would predict adaptive performance (lateral deviation at peak velocity and adaptation index), and that this would be strongest when vision of the perturbation was occluded. Since there is evidence to show increased reliance on visual feedback for motor control with advanced age, we also predicted the greatest extent of age-related impairment in motor adaptation would occur when visual feedback was occluded. We partially replicated the effect of physical activity on proprioceptive bias from our previous experiment, in that baseline bias was larger for physically inactive participants, but this was regardless of age. We also found that adaptive performance was similar between age groups and visual feedback conditions. Critically, we did not find that baseline proprioceptive uncertainty range was associated with motor adaptation in either age group or visual feedback condition. We suggest that the lack of age effects on adaptation gives support to the notion that age-related motor impairments are highest in tasks which require explicit cognitive resources (since these are reduced in force-field adaptation paradigms, especially in the absence of visual feedback). Furthermore, while the motor task certainly involves proprioceptive feedback, movements were discrete and relatively fast which suggests limited use of on-line feedback control. Further investigation may therefore look to examine the association of proprioceptive acuity and continuous on-line movement control with advanced age. This work was funded by the MRC-ARUK Centre for Musculoskeletal Ageing Research (CMAR)

## **2-F-62 Role of somatosensory cortex in consolidation of motor learning**

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There has been recent interest in the idea that motor learning does not occur in isolation but rather that motor learning involves changes to sensory systems and sensory networks in the brain as well. As an example, previous studies of sensorimotor adaptation have shown that motor learning is associated with a systematic change in the sensed position of the limbs. Consistent with this finding, neuroimaging studies have found learning related changes in both sensory and motor areas of the brain. The neuroplasticity that is seen in sensory systems following motor learning could be driven by corticocortical connections between motor and somatosensory cortex such that motor outflow during learning causes the changes in somatosensory cortex. Another possibility comes from motor learning studies in rats which suggest that plasticity in somatosensory cortex could be a result of its role in processing sensory error information during motor learning. However, it is unknown whether these learning related changes in somatosensory cortex play any role in the consolidation of motor memories developed through motor learning. We test the hypothesis that somatosensory cortex contributes directly to the consolidation of motor memory by using inhibitory transcranial magnetic stimulation. Participants perform a motor learning task which involving force-field adaptation. Immediately following adaptation, we apply continuous theta-burst transcranial magnetic stimulation (cTBS) to suppress activity in primary somatosensory cortex (S1) with the goal of blocking motor memory consolidation. Subjects return to the laboratory 24 hours later to test for memory retention. It is seen that stimulation of somatosensory cortex following adaptation greatly reduces retention. Sham TMS to S1 does not interfere with retention, nor is the interference following stimulation of S1 due to the spread of current from S1 to motor cortex (M1). This is shown by applying cTBS stimulation directly to M1 at a level equal to that due to current spread from S1. These results suggest that primary somatosensory cortex is involved in the initial consolidation of motor memories developed during learning.

## **2-F-63 Motor exploration in children and adults when learning a novel motor task**

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In spite of its theoretical and practical importance, the question of how children and adults learn a novel motor task from scratch is still poorly understood. Specifically, the issue of motor exploration, which has been proposed as a key step to learning novel skills, has been incredibly hard to study in the lab because studies of motor learning predominantly use variations of well-learned tasks in which little or no reorganization of coordination is required. To overcome this limitation, we used a recent paradigm called a 'body-machine interface' in which movements of the body are mapped to the control of an external object. In our case, participants had to learn to move a screen cursor to different targets by motions of the shoulder and torso. We examined how children (9-yr and 12-yr olds) learned this task compared to young adults (18-25 yr), with a specific emphasis on the exploratory strategies used during learning. Participants wore inertial measurement units (IMUs) on the shoulder and torso, and we mapped these angles to the position of a cursor on the screen. The mapping was obtained by extracting the principal components during an initial "dance" phase where participants were asked to make random movements, and was therefore non-intuitive. Participants performed center-out reaching tasks with the screen cursor, and learned the task over 5 days (1160 total reaches). We quantified task performance based on the movement time (i.e. how long they took to reach the target). We also examined exploration strategies using principal components analysis to understand how these exploration strategies changed with learning, and if they were different between age groups. Results showed age-related differences in task performance early in learning - children took longer movement

times compared to adults early in learning. However, with extended practice, they caught up to the adults by the end of 5 days of practice. Analysis of the exploration strategies showed that children and adults showed similar distribution of variances in their principal components by the end of practice. These results suggest that while children take longer to reach the same performance level as adults on a novel task, their exploration strategies seem to be similar to those in adults after extended practice.

## **2-F-64 Explicit learning during visuomotor adaptation constitutes of two distinct components: explicit reportable knowledge and explicit control**

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**Objective** Multiple processes operate during adaptation to visuomotor rotations. Explicit aiming strategies and implicit recalibration are two of them, and constitute dissociable and relatively independent learning processes. Various methods have been used to dissociate explicit from implicit learning, with the most recent approaches employing trial-by-trial reporting and process dissociation, a measure derived from cognitive psychology and adapted to the field of motor learning. While closely related, the former seems to measure the awareness of the perturbation a subject can report, while the latter targets the explicit control a subject has over his movements. The aim of the present study was to dissociate subjects' awareness of 'what they can report' from 'what they can control' and to, this way, show that different components of explicit learning exist. **Methods** We conducted two experiments, in which subjects performed baseline and rotation blocks of fast center-out reaching movements using a robotic manipulandum. The first experiment comprised two experimental groups, the consistent reporting group and the intermittent reporting group. Dissociation trials were interspersed throughout the blocks in both experiments. The second experiment was designed to enhance explicit control by alternating between washout and adaptation blocks. Besides this, the protocol was equivalent to group 2 in experiment 1. **Results** The reporting group showed better performance during adaptation with a higher asymptote (group 1: 59.45°, group 2: 53.87°;  $p < .01$ , CI = 1.93 - 9.24). Comparing the two measures of explicit learning, process dissociation revealed more explicit control in the consistent reporting group as compared to the intermittent reporting group (group 1: 31.88°; group 2: 10.88°;  $p < .001$ , CI = 16.20 - 25.86). Taken together, reporting seems to lead to more explicit control, while the intermittent reporting shows the opposite effect. We did not succeed in increasing subjects' explicit control in our second experiment. However, regression analysis of the beginning of the washout blocks showed an increase in slopes throughout adaptation. Moreover, we found that subjects were unable to aim straight towards the target during exclusion trials after washout indicating a fast build-up of implicit knowledge. This contrasts subjects' ability to re-aim during adaptation within the first four trials. These results provide evidence for an implicit process that operates on a faster time scale than the cerebellar-based slow component. **Conclusions** Consistent reporting improved subjects' performance to the visuomotor rotation. Moreover, it enhanced subjects' ability to control adaptation more than their ability to report strategy. The time course of explicit learning in the intermittent groups did not reflect the typical time course as seen by previous studies. In our second experiment, we confirmed the findings of previous studies providing evidence for two implicit processes that operate on different timescales. Our results indicate an internal structure of explicit learning that is not well captured by state-space models.

## **2-F-65 Temporally labile motor adaption is implicit rather than explicit in nature**

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In visuomotor adaptation tasks, human participants readily change their behavior to compensate for imposed perturbations. This response has a labile component which decays over seconds, and a stable component that endures for much longer (Sing et al., 2009). Visuomotor adaptation can also be divided into implicit and explicitly declarable strategic components (Taylor et al., 2014). Here we asked whether the temporally-labile adaptation resulted from implicit or explicit learning by carefully measuring the temporal decay for visuomotor memory at multiple time points for both implicit and strategic learning (n=19). Participants made verbal reports of aim changes while trained to asymptotic performance with a 30° visuomotor rotation, for 200 reaches to a single target. They were then exposed to 7 different randomized inter-trial time delays of 3, 6, 10, 20, 30, 60 and 90 seconds. Each time delay was tested 8 times, with 9 re-adaptation trials following each exposure, allowing full asymptotic adaptation to be recovered before the next delay was imposed. We observed a decay of the adapted state that increased rapidly over the first 10 seconds and appeared to asymptote by 30s. The observed decay curve displayed an exponential time course with a time constant of just over 10 seconds. At 90sec, the longest inter-trial interval we tested, we observed a decay of  $15.0 \pm 6.1\%$  of the total adaptation (95% CI). When we dissected the overall adaptation into implicit and explicit components, we found  $14.7 \pm 5.2\%$  decay for implicit learning but only  $0.3 \pm 2.5\%$  decay (not significant) for explicit learning. In fact, we observed no significant temporally-labile component of explicit aiming over any of the delay intervals, indicating that the temporally-labile adaptation is implicit rather than explicit. Moreover, upon repeating this experiment with a smaller 15° rotation (n=17), we measured a similar  $11.5 \pm 6.0\%$  (95% CI) decay for implicit adaptation but only  $1.3 \pm 1.3\%$  (not significant) for explicit aim. Our findings show that explicit strategies are stable over at least 90sec, which is consistent with the performance of declarative memory in other task contexts (Ebbinghaus, 1885). Implicit sensorimotor adaptation, on the other hand, has both temporally-labile and temporally-stable components. The dissection of visuomotor memories into implicit and explicit components and into temporally labile and stable parts may greatly aid in future attempts to understand the neurophysiological mechanisms of sensorimotor adaptation.

## **2-F-66 Distinct neural signatures of reward and sensory prediction error in motor learning**

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Adaptation of motor output to changing environments occurs by multiple distinct processes. In sensory error based learning, it is thought that the nervous system predicts the sensory consequences of motor commands, and that sensory prediction error drives learning when sensory information violates these predictions. In reinforcement learning it is thought that the brain predicts the subjective value of actions, and that reward prediction error drives learning when the outcome differs from that which is expected. Actions that produce better than expected outcomes are reinforced while actions that produce worse than expected outcomes are deterred. We recorded EEG activity to identify and dissociate the neural correlates of reward prediction error and sensory prediction error during two different sensorimotor learning tasks designed to isolate each response. In both tasks, we measured neural activity in response to feedback that was provided only at movement endpoint, to avoid confounding neural activity related to movement execution. We observed sensory error based learning in a visuomotor rotation task, in which feedback was provided in the form of a cursor that indicated reach angle at movement endpoint. During randomly selected trials, the feedback was rotated around the starting position of the reach to induce sensory prediction error. Participants adapted their reaches on a trial by trial basis to compensate for these perturbations. In a reward learning task, binary reward

feedback indicated whether each reach was successful or unsuccessful without revealing hand position at movement endpoint. Reward was delivered probabilistically according to reach angle, and participants adapted their reaches to produce reach angles that resulted in higher reward probability. We found that a fronto-central event related potential called the feedback related negativity specifically encoded reward prediction error during reward based learning, but did not occur during the sensory error based learning task. These findings suggest that the feedback related negativity is specific to processing reward prediction error. A more posterior component called the P300 was elicited by endpoint cursor feedback during the visuomotor rotation task, and its amplitude was modulated by the size of the visuomotor rotation. Furthermore, we observed a positive correlation between behavioural learning rate and P300 amplitude during the visuomotor rotation task, such that participants who exhibited a larger P300 amplitude tended to adapt to a higher proportion of imposed errors. These findings suggest that the P300 reflects a neural process related to visuomotor adaptation driven by sensory prediction error. Our results reveal a dissociation between well characterized EEG signatures of error processing in two distinct motor learning processes.

## **2-F-67 Neural adaptation in response to change in the musculo-skeletal system: A new primate model.**

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The musculoskeletal system can change over time or by injuries. After limb amputation or traumatic injury, subcortical as well as somatosensory and motor cortical areas are reportedly subject to substantial reorganisation accompanied by a compensatory motor plan. Although surgeons routinely modify the human body (e.g. tendon transfer for restoration of wrist and finger extension following radial nerve injury, control of a myoelectric prosthesis after amputation, etc.) only little information is available about cortical and subcortical adaptations to this physically modified body and its underlying mechanisms. Recent studies have shown that motor commands together with sensory feedback, can counteract the maladaptive reorganization of sensory-motor cortices in amputees (i.e. phantom pain), thus inspiring new rehabilitation techniques, based on motor imagery or targeted muscle and sensory re-innervation. In changing a primate's body using tendon cross-union of two forearm muscles we seek studying the physiological adaptations on cortical and subcortical level as well as the time course of those changes occurring within and between cortical structures. Eventually, we hope that the information gained leads to improvements in current and novel rehabilitation programs and will furthermore foster our understanding of cortical and subcortical plasticity. For this objective, we aimed to establish a tendon-transfer model using the forearm muscles of macaque monkeys and evaluate the adaptation of their neural control by means of behaviour and EMG (electromyographic) measurement. We trained monkeys to perform a simple grasping task. Behavioural observations and chronic EMG recordings from different forelimb muscles were used to evaluate the grasp performance. Subsequently, we surgically cut the tendon of one extrinsic finger flexor (Flexor digitorum profundus, FDP) and one wrist-elbow flexor (Brachioradialis, BRD), both at wrist level. The distal end of BRD was then joined with the FDP tendon. The monkeys fully recovered, fed themselves at day 1 post-surgery and soon performed a precision grip using BRD successfully as finger flexor. Furthermore, movement and hold times recovered within weeks. Lastly, recorded EMG's revealed continuous changes in the activity profile stabilising after some weeks and resembling the profile of an extrinsic finger flexor. In subsequent experiments a tendon cross-union was performed between the Extensor Digitorum Communis and Flexor Digitorum Superficialis. We observed continuous changes in EMG activity profiles of muscles

including those which were not part of the cross-union. EMG amplitude was reduced and time of peak activity adopted a new equilibrium e.g. between original and early adaptation. Since the tendon-transfer model is less invasive and keeps the central and peripheral nervous system intact, we believe this is a superior model to study how the intact CNS adapts in response to change in the musculoskeletal system.

## **2-F-68 Not all solutions are created equal: Stability influences the exploitation of redundancy**

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Although it has been well established in several tasks that humans exploit the redundancy around a specific motor solution, the factors governing the use of this redundancy are still not well understood. An important aspect that has received little attention is the concept of 'stability' of a motor solution - the ability to maintain a solution in the presence of perturbations. Here, we examined how the stability of a solution affects the exploitation of redundancy and subsequent learning of a novel solution. The task used was a bimanual shuffleboard task, where participants held a bimanual manipulandum (KINARM) and made a discrete throwing motion to slide a puck towards a target. The task was redundant in that the distance traveled by the puck was determined only by the sum of the left and right hand velocities (with a perfect score achieved at  $VR + VL = 1.5$  m/s). Participants performed the shuffleboard task in two conditions - (i) in the 'unconstrained' version of the task, participants were free to use any solution they desired, and (ii) in the 'constrained' version of the task, we put an obstacle around the desired solution and controlled the horizontal position of the puck, so that only a certain range of velocities allowed the puck to go through the obstacle. We refer to these solutions in terms of % contribution from each hand- so a '50-50' solution would correspond to  $(VR, VL) = (0.75, 0.75)$  m/s, a '60-40' solution would correspond to  $(VR, VL) = (0.9, 0.6)$  m/s etc.. We manipulated prior learning in 3 groups ( $n = 12$  each): (i) a 'naïve' group that learned 55-45 from the start, (ii) a 'stable' group that learned 50-50 before switching to 55-45 and (iii) an 'unstable' group that learned 60-40 before switching to 55-45. Participants performed the prior task for 1 day before switching to the criterion task on Day 2. Our main variable of interest was the distribution of variability in the task and null space. Results showed that the more unstable solutions (55-45 and 60-40) showed greater distribution of variance along the null space compared to the 50-50 group. Moreover, with learning, both the 55-45 and 60-40 solutions reduced their null space variability. When examining the learning of the novel 55-45 task, the 50-50 group showed much greater difficulty adapting to the 55-45 solution compared to the 60-40 group initially in learning. This was also accompanied by an increase in the null space variability. However, by the end of day 2, there were no significant effects of group in either the task or null space variability. These results show that stability of prior coordination patterns play an important role in the use of redundancy, and highlight the fact that learning does not occur on a 'blank slate'. Further understanding of the role of stability has important implications not only for theoretical models of learning, but also in rehabilitation where the goal is to sometimes alter well-established maladaptive coordination patterns.

## **2-F-69 Force field generalization and the internal representation of motor learning**

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The act of motor learning leads to a memory, or representation, of the information needed to produce the new motor behavior. This representation allows us to produce the movement again at a future time, and to generalize this information to new untrained circumstances. So for example, to examine the

representation of a newly learned force field we often do the following: subjects learn to move in the force field in a single direction, and are then tested in unpracticed directions. The assumption is that their performance in these unpracticed directions is a direct read-out of the newly learned representation (e.g. an estimate of its strength), and how it varies across reach directions. As such, each test movement should differ from the learned movement only in direction. The findings from force field generalization studies, however, have not lead to a clear depiction of the underlying representation. The ability to generalize quickly degrades with increasing changes in reach direction, though the evidence is limited and not clear if it holds for all learning directions. There is evidence that ability to generalize may be asymmetric, with performance varying whether reach directions are to the left or right side of the learned movement. Finally, it is not clear how changes in limb impedance across testing directions influence the results. To address these issues, we ran a force field adaptation experiment with eight groups of subjects each training one of eight standard reach directions, and then generalizing in the remaining seven directions. Thus we could compute the standard generalization curves for all directions, characterizing the extent to which generalization degrades as the test direction varies. As previous work has found, generalization degraded quickly for all training directions. We found strong asymmetries in these curves that varied in magnitude and direction across the training directions. These findings were inconsistent with previous explanations based on representations that shift with motor errors. Using the generalization curves to fit Gaussian-like representations did not help explain these asymmetries. To correct for changes in limb impedance we then computed new generalization curves characterizing the extent to which generalization to the same testing direction changes as the training direction varies. As before these new generalization curves degraded quickly and were inconsistently asymmetric. However, using these new curves to fit Gaussian-like representations did explain the asymmetries. The underlying representations are symmetric, and centered on the training directions. However, the widths are largely proportional to the errors experienced in each training direction. These variations in the representation's width give rise to the asymmetries observed in the generalization curves. Overall our findings highlight the importance of controlling for changes in limb dynamics and the effects they have on learning.

## **2-F-70 Short-term memory maintenance by motor memory retrieval**

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Recent studies have demonstrated that motor memory monotonically decays with passage of time with a time constant of ~20 sec (Hadjiosif et al., MLMC 2014, Zhou et al. JNP 2017). In the case of declarative memory, however, temporal decay of short-term memory can be prevented by repeating memory retention, indicating the memory retrieval plays an essential role to maintain the memory (i.e. maintenance rehearsal, Craik & Watkins, 1973, J. Verb. Learn. Verb. Behav.). Previously, we have reported the similar phenomenon in the motor memory domain (Sasaki and Nozaki, SfN 2016). Specifically, after adapting reaching movements to a velocity-dependent force fields (FF), two consecutive force channel (FC, Scheidt et al., JNP 2000) trials were performed to examine how the motor memory quantified by the force exerted against the FC changed from the 1st to 2nd FC trial. We found that the motor memory was maintained up to 8 sec before starting the monotonic decay. Notably, this maintenance effect was likely to result from the motor execution (i.e., memory retrieval) rather than motor adaptation in the 1st FC trial, because the memory update in the 1st FC trial was negligible. This result led us to hypothesize that the motor memory retrieval contribute to the short term maintenance of motor memory. In the present follow-up study, we examined the motor memory

retrieval was effective for memory maintenance even after the temporal motor memory decay already started. Participants performed 200-trial training session consisting of 160 FF trials and 40 FC trials to acquire the motor memory. FC trials were randomly interleaved in one-fifth probability. In the test session after this training session, participants repeated an 8-trial test set 35 times. Each test set consisted of 6 FF trials followed by 2 consecutive FC trials. Inter trial interval (ITI) between the 2 FC trials varied from 3 sec to 20 sec, so that we could evaluate how the motor memory changed with passage of time. ITI was fixed at 4 sec for other trials, but ITI between the 6th FF trial and the 1st FC trial were 8 sec in 30 sets out of 35 sets. After 8 sec from the 6th FF trial, we supposed that time-dependent decay already started. Assuming that motor memory retrieval induces short term memory maintenance effect, like memory rehearsal in declarative memory, the motor memory measured by the 2nd FC should not follow monotonic decaying pattern with ITI. Indeed, we observed that the amount of motor memory did not show monotonic decay, even when ITI between the 6th FF trial and the 1st FC trial was increased to 8 sec. Current computational framework for motor learning assumes that motor memory recall induces inevitable decay (i.e., FC trial induces trial-dependent memory decay; Smith et al., PLoS Biol. 2006, Ingram et al., Curr. Biol. 2013). Thus, our study provides a new insight into the function of motor memory recall; motor memory retrieval by motor execution contributes to short-term memory maintenance.

## **2-F-71 Aim-based generalization shapes local dual adaptation to opposing cursor rotations**

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Humans performing skillful movements can switch between environments requiring different sensorimotor transformations. Acquisition of this ability has been investigated in dual adaptation experiments where participants practice different visuomotor transformations in alternation. Behaviorally, dual adaptation can occur by formation of separate visuomotor maps or by local shaping of a single visuomotor map as long as the centers of local generalization are spatially separate. Evidence in favor of local learning comes from Woolley and colleagues (2011), who found that dual adaptation was possible when training to different regions of the workspace. Notably, the critical factor here was not the direction of the movement per se, rather only the visual direction of the target, suggesting a target-based representation. More recent findings suggest that generalization centers on explicit aiming strategies (Day et al., 2016; McDougale et al., 2017), a possibility not previously considered. To tease these possibilities apart, we contrasted target-based with aim-based generalization in a series of dual adaptation experiments while assessing implicit and explicit learning. Participants in all experiments performed a center-out reaching task in a single physical workspace. Visual workspace alternated between the left and right half of the screen and cued opposing cursor rotations. We tested generalization to 9 targets in each visual workspace. In experiment 1, practice was to the same straight ahead target under opposing 45° rotations. Explicit shifts generalized broadly across directions and were specific to the visual workspace. Aftereffects displayed identical, bimodal generalization patterns in both workspaces with the signs and locations of modes consistent with local, aim-based generalization in the common physical workspace. Experiment 2 had opposing 60° rotations matched to two targets 45° apart so that aiming strategies should cross over during the course of training, for which case aim-based generalization predicts interference. Consistent with this prediction, aftereffects were absent. This catastrophic interference should be overcome if the spatial overlap of opposing strategies is minimized during learning. To test this, in experiment 3, we provided participants with ideal strategies at the onset of training and found that aftereffects recovered whose pattern was consistent with aim-based



generalization. This indicates that separate aiming strategies rather than visual targets are key for implicit dual adaptation within a single visuomotor map. An important methodological implication is that peak aftereffects after dual adaptation will not be found at the visual target location. What's more, these results suggest that dual adaptation can be rather complex, as the time course of aiming strategies shapes local learning. Finally, it is more likely that separation of visual workspaces cues different aiming strategies and not separate visuomotor maps.

## **2-F-72 Motor imagery of different future movements can engage distinct motor memories**

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Mentally rehearsing a motor skill can lead to improvements when performing the same skill. Here we show a powerful and complementary role, in which mental imagery of movements after actually performing a skill allows learning that is not possible without imagery. We leverage a well-studied motor learning task in which subjects reach in the presence of a dynamic (force-field) perturbation (Shadmehr and Mussa-Ivaldi 1994). When two opposing perturbations are presented alternately for the same physical movement, there is substantial interference, preventing any learning (Gandolfo et al., 1996; Howard et al., 2015). However, when the same physical movement is associated with follow-through movements that differ for each perturbation, both skills can be learned (Howard et al., 2015; Sheahan et al., 2016). Here we show that when subjects perform the skill and only imagine the follow-through, substantial learning occurs. However, without such motor imagery there was no learning. In contrast to previous studies of mental practice, here imagery is not a mental rehearsal of the skill itself. That is, all subjects actually make the initial movement in the field, but the mental imagery is of a future movement (the follow through) separate from this skill. This suggests that the act of imagining different future movements, even though subjects know they will not be performed, allows two motor memories to develop for the same physical state of the limb. We have previously suggested that the key to representing multiple motor memories is to have each associated with a different neural state, rather than physical state of the body (Sheahan et al., 2016). Our results suggest that imagining different future movements may lead to distinct neural states from the start of the movement. Indeed our results converge with recent electrophysiological work in non-human primates, demonstrating that covert BMI-controlled reaches acquire similar initial neural states during motor preparation as do physical reaches to the same targets (Vyas et al 2018). Our results show that mental imagery can have a profound effect on skill acquisition even when the skill is always performed, and suggests that motor imagery may evoke different neural states for the same physical states, thereby enhancing learning (Churchland et al., 2012; Sheahan et al., 2016).

## **2-F-73 Motor practice under variable cortical activities fosters the stability of motor memories**

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Humans can learn new motor skills through trial and error, producing a memory that will be recalled the next time. However, this memory is temporary, and the skill gets close to the baseline with the passage of time. Thus, a fundamental issue in motor learning is how to better retain the memories. Previous studies that examined familiar tasks such as ball throws revealed the advantage of variable practice over constant practice in retention of motor memory (Kerr and Booth 1978; Shea and Kohl 1991). These studies insisted that the benefit might arise from the stronger schema of motor task constructed by variable practice (Schmidt 1975), but no mechanistic explanation has been proposed. Here, in a series of

two experiments and a computational model, we demonstrated that variable practice facilitates learning of novel dynamics [force field (FF)] and the neural underpinnings of this facilitation. In experiment 1, 50 participants performed 110 reaching movements under a velocity-dependent curl FF while holding a robotic manipulandum. They were divided into five experimental groups. One group had a single visual target to be reached, which was shown 10 cm forward from the start of the movements. In the other groups, 11 visual targets uniformly distributed in the range of  $\pm 2.5^\circ$ ,  $5^\circ$ ,  $10^\circ$ , or  $20^\circ$  from the front target were used for the training (10 reaches for each target). Following the FF learning, all participants performed 50 reaching movements to the front target in a channel in which errors were absent. The results showed that decay of motor memories, quantified using the force exerted against the channel in the last 10 trials, was least when the target position varied within  $\pm 5^\circ$ . The amount of memory at the end of FF learning and the learning rate was not different between the groups. A model incorporating selective improvement in the retention indicated that variability of corticomotor neurons being active during learning would mediate the stability of the memory. Thus, in experiment 2 we empirically validated this prediction by manipulating cortical activation patterns using transcranial direct current stimulation (TDCS) while participants engaged in FF learning. Twenty-four participants were enrolled in one of two experimental conditions. One applied four different TDCSs to the motor cortex in which current flowed anterior-to-posterior, posterior-to-anterior, medial-to-lateral and lateral-to-medial directions relative to the central sulcus during FF learning. The other used one of the four TDCSs throughout the learning period. The results fitted to our model prediction. Decay of motor memories, tested during sham TDCS, was less in the participants who were exposed to FF with multi-pattern TDCSs. We supposed that cortical activity of reaching movements varied by externally applied four different electric fields and therefore a motor memory was tagged to multiple cortical activation patterns. Variability in cortical activities during motor learning might allow to create robust memory representation and to well retain than one created under single activation pattern.

## **2-F-74 Role of the Corpus Callosum in mediating interlimb transfer of motor skills: Insights from neurological patients.**

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When we learn a motor skill, learning can generalize to another scenario involving, for example, a different motor task or a different limb. The generalization of motor learning across limbs, known as interlimb transfer, has been well demonstrated by research on short-term sensorimotor adaptation. Despite a large body of work, the neural mechanisms underlying interlimb transfer remain unclear (Criscimagna-Hemminger et al. 2003; Perez et al. 2007). Among the various theoretical models, many of them highlighted the corpus callosum (CC) as a key brain structure mediating interlimb transfer (Parlow 1989, Ruddy and Carson 2013). Here we studied sensorimotor adaptation and interlimb transfer in neurological patients with lesions of the CC. According to the callosal access model, we hypothesized that impaired interlimb transfer would be observed in CC patients as compared to healthy matched controls. We used a confirmed prismatic perturbation procedure to assess interlimb transfer in a reaching task: the dominant arm was exposed to the prismatic perturbation before subsequent testing of the unexposed non-dominant arm looked to examine interlimb transfer. Preliminary data from one patient with CC lesions following a ruptured brain aneurysm indicates a reduced level of interlimb transfer compared to controls, despite normal prism adaptation. While more controls and patients with CC lesions have to be examined, our preliminary data support the idea that the CC contributes to interlimb transfer of motor skills (Taylor and Heilman 1980). Acknowledgments "This project has

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## **2-F-75 Comparing visuomotor adaptation and mirror-reversal learning using system identification techniques**

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New motor skills can be learned via adaptation, where an existing control policy can be adapted in service of a new task, or via de novo learning, where a new control policy must be built from scratch. Although both types of learning are ethologically important, de novo learning has been relatively understudied in comparison to adaptation. A previous study has suggested that adaptation and de novo learning occur via two separate mechanisms (Telgen et al. 2014), but the results were limited by the use of step perturbations. While step perturbations can provide insights into the control policies participants use to solve motor tasks, other system identification approaches have been developed which can more comprehensively characterize the state of motor learning. Here, we use system identification to compare visuomotor adaptation and mirror-reversal learning. Participants were asked to track a target as it moved along a sum-of-sinusoids trajectory under either a 90 degree visuomotor rotation or a mirror-reversal along a diagonal axis. The compensation for both mappings across different stages of learning was highly frequency-dependent. Generally, tracking of low frequency components of movement was better than high frequency components. At low frequencies, performance in the mirror-reversal and rotation conditions was comparable. However, participants had more difficulty performing at high frequencies under the mirror-reversal than the rotation. The frequency-dependent differences in compensation between the two conditions were further apparent in the angle of compensatory movement and the response latency. Our results demonstrate that the frequency spectrum of movements affects the ability to compensate for visuomotor perturbations. For this reason, system identification may provide a more flexible and powerful approach to characterize motor performance than simple step perturbations.

## **G – Theoretical & Computational Motor Control**

### **2-G-76 A history-dependent model of muscle spindle sensory encoding for sensorimotor control research**

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Here, we introduce a new model of muscle spindle sensory encoding based on history-dependent forces in muscle fibers to facilitate more realistic simulations of normal and impaired sensorimotor control. Motor control research often overlooks history dependence in muscle spindles, defined as the reduction of muscle spindle sensitivity caused by movement in the muscle prior to stretch. History-dependent muscle spindle function is hypothesized to affect both conscious proprioception and automatic motor responses to perturbation, but is difficult to test directly. Simulations could help reveal the role of prior movement in modulating muscle spindle responses to perturbation, but current models of muscle spindle function lack history-dependence, assuming a unique relationship between muscle spindle firing

and muscle stretch kinematics. We recently showed that muscle spindle stretch responses have a nonunique history-dependent relationship with imposed kinematics, but are uniquely related to pseudolinear combinations of history-dependent eccentric muscle force and its first time derivative, yank. History-dependent muscle fiber forces can be reproduced by simulating muscle cross-bridge cycling kinetics, but not in phenomenological, e.g. Hill-type, descriptions of muscle contraction often used in muscle spindle models. We hypothesized that history-dependent muscle spindle spiking responses could be predicted by simulating cross-bridge population cycling kinetics in conjunction with a conductance-based model neuron. As hypothesized, our model is capable of generating muscle spindle responses to a ramp-hold perturbation classically described by initial bursts, dynamic response, and rate adaptation. Ours is the first model capable of producing history-dependence, i.e. changes in the dynamic response and initial burst based on the prior movement of the muscle. Surprisingly, our model predicted several features of muscle spindle firing that we did not anticipate. By varying relative sensitivities of the model neuron to simulated intrafusal force and yank, we produced a large set of spiking response phenotypes spanning experimentally-observed ranges of initial burst amplitudes, dynamic responses, and degrees of rate adaptation observed in the classical muscle spindle literature. The model also exhibited an emergent fractional power relationship between dynamic index and imposed stretch velocity, a hallmark characteristic of muscle spindle primary afferent responses to stretch. Our neuromechanical muscle spindle model maybe provide a multiscale framework for simulating both history-dependent and classically-observed firing behaviors across a wide range of perturbations and movements. Such a model could be used to simulate the effects of muscle activation level and changes in neural dynamics on muscle spindle firing, which are known to be altered in both normal and impaired sensorimotor control.

## **2-G-77 Generalization of the dynamical systems modeling approach to capture interactions between premotor and primary motor cortex and their influences on kinematic features.**

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Investigating what neurons in different motor regions encode during movement provides insight into the complex sensorimotor control system. A recent approach to studying neuronal activity during movement is to construct a dynamical systems model (DSM), wherein the state vector consists of firing rate signals for different populations of neurons in a given motor region, and the output is the movement trajectory. This approach allows for the populations to influence each other in a dynamical manner, which in turn generate movement. However, the DSM approach has primarily been used to model single regions and in short time periods where no external event (e.g. visual cue, movement onset) occurs. To capture long time periods, a different DSM is constructed in each time period that modulated with a different external event. Here, we expand the DSM framework to allow for a single model to characterize neural dynamics (i) over the entire trial during which multiple events occur and (ii) between multiple brain regions. The multiple events are modeled as exogenous inputs entering the motor regions, PM and M1, whose firing rates are in general coupled and evolve dynamically to generate kinematic output. We apply our general DSM approach to neuronal data captured in two nonhuman primates executing a reach-to-grasp task, and demonstrate the model's ability to reconstruct population activity in both PM and M1 simultaneously in addition to kinematic trajectories.

## **2-G-78 Joint control during arm movements performed during activities of daily living**

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The ultimate goal of human movement control research is to understand how natural movements performed in daily activities, are controlled. Natural movements require coordination of multiple degrees of freedom (DOF) of the arm. Here, we examined patterns of arm joint control during daily functional tasks, which are performed through rotation of the shoulder, elbow, and wrist with the use of seven DOF: shoulder flexion/extension, abduction/adduction, and internal/external rotation; elbow flexion/extension and pronation/supination; wrist flexion/extension and radial/ulnar deviation. Analyzed movements imitated the following 8 activities of daily living: moving an empty soda can from a table and placing it on a shelf set to 3 different heights, bringing the can to the mouth as for drinking, combing hair, turning a book page, bringing the right hand to the left side of the chest, and brushing teeth. Kinematic and kinetic analyses were conducted. The studied kinematic characteristics were displacements of the 7 DOF and contribution of each DOF to hand velocity. The kinetic analysis involved computation of 3-dimensional vectors of muscle torque (MT), interaction torque (IT), gravity torque (GT), and net torque (NT) at the shoulder, elbow, and wrist. Using a relationship  $NT = MT + GT + IT$ , we assessed the role of active control and the passive factors (gravitation and inter-segmental dynamics) in rotation of each joint by computing MT contribution (MTC) to NT. MTC was computed using the ratio of the signed MT projection on NT to NT magnitude. Despite the variety of joint movements required across the different tasks, 3 patterns of shoulder and elbow coordination prevailed in each movement: 1) active rotation of the shoulder and predominantly passive rotation of the elbow; 2) active rotation of the elbow and predominantly passive rotation of the shoulder; and 3) passive rotation of both joints. Analysis of wrist control suggested that MT mainly compensates for passive torque and provides adjustment of wrist motion according to requirements of each task. An exception was tooth brushing during which different subjects used different joint control strategies. A reason for this exception could be that the instruction was to move the brush horizontally back and forth in front of the mouth, which differed from the movement typically used for tooth brushing. We conclude that the 3 shoulder-elbow coordination patterns during which at least one joint moves largely passively represent joint control primitives underlying performance of well-learned arm movements, although these patterns may be less prevalent during non-habitual movements. We discuss that the advantage of these control primitives is that they require minimal neural effort for joint coordination, and thus increase neural resources that can be used for cognitive tasks.

## **2-G-79 Learning to move in a switching environment: a jump Markov model of motor adaptation**

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The dynamics of our sensorimotor environment can change in a discontinuous manner, such as when we grasp an object, put on ski boots or enter a swimming pool. To cope with such abrupt transitions, a person could learn multiple models of their environment, each associated with different parameters, and switch between these models whenever the environment switches. To detect a switch in the environment, two sources of information can be used: sensory cues (e.g., the visual geometry of an object) that are informative of the context (i.e., the dynamics of an object), and sensory cues that arise from movement in the environment (e.g., the perturbed state of the limb). The former are typically referred to as contextual cues and are available prior to movement onset, whereas the latter result from perturbations in the environment and are observed during a movement. Importantly, because the link between sensory cues and dynamics may not be known a priori, a person must be able to learn new associations between sensory cues and contexts. We formalize the above problem statement in a novel

jump Markov linear (JML) model of motor adaptation. A JML model (also known as a switching state-space model) combines a hidden Markov model (HMM) with multiple linear dynamical systems (LDS) to model systems with multiple operating modes. Here the operating modes represent contexts and each mode is associated with an LDS that models how perturbations in the environment evolve and are observed. At each point in time, only one mode is active, and over time the system switches (or jumps) between modes. We hypothesize that motor adaptation involves online estimation of the states (i.e., the perturbations inferred by each LDS) and parameters (i.e., the parameters of each LDS, the mode transition probabilities and the probabilities of cues given contexts) of a JML model of the environment. To test this model, we use a robotic interface to generate different dynamic contexts (e.g., clockwise and counterclockwise force fields) which can switch on a trial-by-trial basis. We confirm two predictions of the model. First, we show that the effectiveness of contextual cues is not constant but can change as participants learn to associate cues with contexts. Second, we show that participants use information available after movement onset -- the observed perturbation -- to partition learning between multiple context-specific memories, enabling more effective reduction of interference than contextual cues alone. The JML model provides a normative framework for understanding motor adaptation in non-stationary environments that are associated with unfamiliar contextual cues.

## **2-G-80 Cortical posture memories minimize work**

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The real-time control of the human movement system is extraordinarily complex, drawing on almost every subsystem in the forebrain, but the motor cortices have the most prominent role in specifying planned movements. In this role one of the most fundamental constraint they have to deal with is the bandwidth needed to control the musculo-skeletal system of 300 degrees of freedom (DOFs) and 600 muscles. The slowness of neural circuitry dictates that the cortex must communicate with the spinal cord with abstractions, which must be planned ahead of execution time. The exact representation of the motor cortical areas is still a subject of debate, but one prominent hypothesis is that of a kinematic plan in body coordinates. Object-centered kinematics as a control signal is attractive for a number of reasons. Studies by Graziano suggest that the cortex codes for complete task-centered posture changes[1]. Cisek has shown data that suggest that the cortex codes competing for movements separately as action potentials before the choice point[2]. Also, such kinematic data is easily coded in terms of posture basis functions. To study kinematics in whole-body movements, a previous experiment set out to explore the strategies for choosing movements by having subjects complete large-scale tracing tasks in the virtual environment and then measuring their postures with a PhaseSpace motion capture device. The unexpected finding was that different subjects used almost the same posture sequences to complete the traces. The match between subjects was so close that we set out to test whether there was a common principle used to generate the tasks and this poster reports on calculations that suggest a principle is the cost of the movement. A 50 DOF human dynamic model was built to solve the joint torques needed for a movement given a kinematic plan. It allowed the cost of a sequence of posture changes to be computed during the task. First, the model was constrained to repeat the movements that the subjects made. Next, the model was constrained to trace curves that were slightly perturbed versions of the original. The dynamic model integrated the equations of motion and consequently computed the cost of the movement, thus we were able to compare the work needed for individual tracings with that of slightly perturbed curves. The result was that each of the perturbed tracings was more expensive than the original, supporting the conclusion that what the motor cortex is committing

to memory is trajectories with the lowest cost. [1]Aflalo, Tyson N., and Michael SA Graziano. "Relationship between unconstrained arm movements and single-neuron firing in the macaque motor cortex." *Journal of Neuroscience* 27.11 (2007): 2760-2780. [2]Cisek, Paul. "Making decisions through a distributed consensus." *Current opinion in neurobiology* 22.6 (2012): 927-936.

## **2-G-81 Markerless tracking of user-defined anatomical features with deep learning**

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Quantifying behavior is crucial for many applications in neuroscience. Videography provides easy methods to observe animals, yet extracting particular aspects of a behavior can be highly time consuming. In motor control studies, humans or other animals are often marked with reflective markers to assist with computer-based tracking, yet markers are intrusive, especially for smaller animals, and the number and location of the markers must be determined a priori. Here we provide a highly efficient method of markerless tracking in mice based on transfer learning with very few training samples (~ 200 frames). We demonstrate the versatility of this framework by tracking various body parts of mice in different tasks: odor trail-tracking (by one or multiple mice simultaneously), and a skilled forelimb reach and pull task. For example, during the skilled reaching behavior, individual digit joints can be automatically tracked from the hand. Remarkably, even when a small number of frames are labeled, the algorithm achieves excellent tracking performance on test frames that is comparable to human accuracy.

## **2-G-82 Parametric versus discrete working memory representations in sensorimotor learning**

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Recent research has revealed that sensorimotor learning involves more than just a single, implicit error-based learning system: Strategic learning processes occur alongside implicit ones, and these processes appear to be related to both higher reaction times and better performance. The explicit "reportability" and increased reaction time related to strategic learning are highly suggestive of "controlled" processing (Cohen et al., 1990). According to classic models, working memory is fundamental to controlled processing for managing, manipulating, and retaining information. Spatial working memory ability correlates with performance in visuomotor learning (Seidler et al., 2012), and appears to support explicit strategies (Christou et al., 2016); however, it remains unclear what specific working memory operations underlie strategies in visuomotor adaptation tasks. We broadly classify working memory strategies into parametric versus discrete operations: Parametric working memory strategies are useful when the task itself is parametric, requiring subjects to learn novel spatial or temporal relationships which could rely on mental imagery or simulation. However, these operations significantly slow processing time. In contrast, discrete strategies are possible when the number of task-relevant associations (e.g. S-R pairs) does not tax working memory capacity. Discrete strategies act like a look-up table, placing significantly less burden on processing time. To test for these two broad classes of working memory strategies, we created conditions that would preferentially favor either parametric or discrete operations in a visuomotor rotation task. In a 2 X 2 design, we show that the complexity of the learning environment (i.e. number of targets) determines which strategy is recruited, with lower complexity leading to a discrete working memory strategy, and greater complexity leading to a more expensive parametric

strategy. The latter was evidenced by the apparent mental rotation of an intended movement direction during motor preparation: Reaction times were a linear function of rotation size, consistent with classic visual mental rotation (Shepard and Metzler, 1971). Additional experiments further elucidated these putative working memory strategies using a forced response time task. Depending on the complexity of the environment, time pressure produced either intermediate movements between the target and goal, or a bimodal distribution of responses with a mode at each goal location. The former is consistent with a parametric operation, such as mental rotation, whereas the latter is consistent with a discrete operation, such as a look-up table. These results reveal how two classes of working memory operations can be leveraged as effective strategies in motor learning.

## **2-G-83 Interactions of balance control and locomotion in cats walking on a split-belt treadmill**

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In the past, dynamic stability of human locomotion in the frontal plane has been investigated using an inverted pendulum model and notion of the extrapolated center of mass. It is not known whether a similar approach could be applied to a quadrupedal locomotion. The goal of this study was two-fold: (1) determine if the frontal plane dynamics of the cat center of mass (COM) during split-belt locomotion could be accurately described by an inverted pendulum model and (2) examine if the model can explain previously obtained experimental results. We developed a mathematical model of the balance control system based on an inverted pendulum model whose dynamics was controlled by shifting the pendulum pivot point at the time instances when the COM approached the limits of dynamic stability, i.e. stability thresholds. These thresholds were computed using Bayesian inference based on experimental data obtained in different experimental conditions. The data included 3D full body cat kinematics and ground reaction forces recorded during split-belt locomotion with different speeds in control conditions and with the fore- and hind paws on the same side of the body anesthetized. The inverted pendulum model described the experimental dynamics of the cat COM in the frontal plane with high accuracy. The model revealed a mechanism of controlling dynamic stability in the frontal plane. According to this mechanism, when the COM is approaching the threshold of dynamic stability on one side of the body, the animal lifts the contralateral limbs, and the gravitational force reverses the direction of COM movement so that the margin of dynamic stability increases. This mechanism produces frontal plane oscillations of the COM during locomotion that are synchronized with transitions between specific locomotor phases. The developed model helped explain why the COM shifts towards the slower belt during split-belt walking. This happens primarily due to the medial shift of the stability threshold on the fast side of the area of support. This results in a reduction of the amplitude and the period of the COM oscillations in the frontal lane. Furthermore, anesthesia of ipsilateral paws leads to a shift of the COM towards the anesthetized paws caused by symmetric shift of both thresholds in the direction of the anesthetized side. This result is interpreted as an illusion of an increased stability on that side due to reduced tactile perception of the anesthetized paws.

## **2-G-84 Hypermetria after exposure to visuomotor delay in a virtual game is caused by unaware adaptation of movement planning**

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Sensory feedback delays inherently exist in the sensorimotor system due to information transmission and processing, and we must take them into consideration to enable successful interaction with the



world. However, the underlying mechanisms of these compensation mechanisms are not clear. A recent work showed that an experience with a visuomotor delay between the hand and paddle movements during a virtual game of pong leads to hypermetric movements in a subsequent blind reaching task. This suggests that the brain does not represent the actual time lag to compensate for the delayed feedback but rather approximates the delayed dynamics using current state information. Here, we investigated if the effect that was observed during action is also associated with a perceptual bias. Following a delayed pong game, participants were asked to perform blind reaching movements towards a target while imagining an invisible cursor, and a subsequent location assessment task. In the latter, participants were asked to assess the location of the imagined cursor at the end of the reaching movement relative to the location of a marker that was presented on the screen and was shifted with respect to the actual location of the hand. We found that participants performed hypermetric reaching movements, but reported that the invisible cursor reached the target. This result suggests that they were unaware of the hypermetria, and therefore, their perception was biased towards the target. In a second experiment, we examined whether the adaptation to the visuomotor delay affected movement planning or its execution. The experiment was similar to the first experiment except for the blind reaching task; this time, movements were performed without a visible target being presented, but towards a location that was freely chosen by the participant. This enabled us to examine whether the existence of the target, which drives an internal visually-dominated planning process, is important for the hypermetric reaching movements and the perceptual bias. Strikingly, the removal of the target cancelled the hypermetria in the reaching movements. Moreover, participants reported that the invisible cursor was located at the hand position. The combined results suggest that the observed hypermetria is a result of an unaware adaptation of movement planning. Understanding the way externally-induced delay between the sensory modalities influences our action and perception sheds light on the processes that underlie sensory integration and movement control, and it may help in understanding different pathological conditions that are characterized by delayed information transmission. Moreover, it can be important for designing, developing, and controlling systems that contain inherent delays, such as teleoperation and surgical robotics. This study was supported by the BSF and the Helmsley Charitable Trust through the ABC Robotics Initiative of Ben-Gurion University of the Negev, Israel.

## **2-G-85 Action selection under conflict: replacement versus suppression of competing response options**

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In our daily activities, we often need to withhold an automatic, habitual response in order to carry out a desired action. For example, when an object falls from the kitchen counter, we may automatically want to catch it, unless the object is a knife, in which case we ought to avoid it. It has been proposed that an automatic response is always prepared but can be supplanted by a more appropriate action prior to response initiation (Haith et al., 2017). Alternatively, it has been suggested that the prepotent response might be actively inhibited, allowing the correct response to be generated when ready (e.g. Ridderinkhof, 2002). To dissociate between these possibilities, we used a task in which participants were provided with an arbitrary cue (a colored 'X') instructing them which of four potential directions to aim a reaching movement to (e.g. blue = left). During the 'conflict' condition, this cue was presented in a spatial location that was sometimes incongruent with the instructed direction, creating a conflict. Participants (N=9) first performed the reaching task with the spatial and then the color mapping (204 trials each). They were then exposed to the conflict condition (408 trials), in which a colored symbol

would appear in one of the four spatial locations, with a spatial-color onset asynchrony of 200ms. Participants were instructed to ignore the spatial information, and respond according to the color mapping. We examined the relationship between RT and the probability of each particular response being generated (spatial, color, or other) responses for each participant. At very low RTs (200-400ms), we observed a high probability of movements erroneously generated towards the spatial location of the stimulus. As RT increased, the probability of selecting the correct response increased. Contrary to the action-replacement hypothesis, however, this increase did not directly mirror the decrease in the probability of a prepotent, spatial response. Instead, the probability of selecting either of the other two responses increased, such that the distribution of responses transiently became uniform across all four directions. This pattern is consistent with some form of suppression, rather than replacement, but was not entirely consistent with the theory of response inhibition, which would have led to a diminished reduced probability of generating the spatial response relative to other responses. By contrast, we found that all responses were equally likely during the period immediately prior to the correct response being selected. This suggests that instead of suppressing specific actions, selection of the correct action under conflict may depend on suppression of the entire stimulus-response mapping. This is consistent with the idea of "task set" as suggested in the task-switching literature.

## **2-G-86 Objects without boundaries: generalization between visual statistics and physical affordances**

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The concept of objects is fundamental to cognition and is defined by a consistent set of sensory properties and physical affordances. Although it is unknown how the abstract concept of an object emerges, most accounts assume that visual or haptic boundaries are crucial in this process. Using a novel visuo-haptic statistical learning paradigm, we tested the alternative hypothesis that boundaries are not essential but simply reflect a more fundamental principle: consistent visual or haptic statistical properties. We created an inventory of artificial "objects", each object defined as a unique pair of unfamiliar shapes. In two experiments, separate groups of participants experienced a sequence of visual scenes, each consisting of several of these objects. For one group, the objects could only be identified based on the consistent visual co-occurrence of their constituent shapes across scenes, while for the other group by the physical effort required to pull the scenes apart as simulated by two robotic interfaces. Crucially, for both groups, we controlled for all other information that could segment objects such as boundary cues. Therefore, we isolated purely statistical learning in the visual or haptic domain. We then examined how the information extracted from visual or haptic statistics affected performance on both a visual familiarity and a haptic pulling test, thus measuring within-modality learning as well as across-modality generalisation of statistical information. Within-modality tests showed that participants learned the visual or haptic associations between the shapes. Critically, despite the absence of explicit boundary cues, participants showed strong generalisation, predicting object properties in the other modality in which they had no prior experience. Across participants, we also found a strong positive relationship between within- and across-modality performance suggesting that variability in performance on both tasks is due to the same underlying cause: differences in how well participants learned the inventory. Furthermore, a within-participant test showed that the particular pairs a participant regarded as the true objects of the inventory in one modality were also the ones that they treated as the true objects in the other modality. Thus, the positive relationship in performance we found in the two modalities could not be attributed to generic (e.g. attention-based) sources of

modulation. Our results demonstrate that unified object-like representations arise from the mere observation of statistical contingencies. This provides evidence for the primacy of statistical determination over edges or boundaries in the emergence of multisensory object representations.

## **2-G-87 Learning expands the planning horizon in finger sequence tasks**

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Theories of action selection and motor planning have focused on mechanisms that underlie the preparation of single movements. However, many everyday skills involve the production of complex sequences of movements. The dynamic interplay between selection and execution of sequences of actions is currently not well understood. Using an explicit finger sequences task, we investigate to what degree information regarding upcoming actions can be utilized by the nervous system to plan multiple actions into the future and how this ability is influenced by learning. We trained 13 healthy right-handed adults over five days to produce 14-digit sequences of key presses, indicated by visually presented numbers between 1-5 (numbers 1-5 assigned to fingers thumb-pinky). On every trial, participants were shown only a fixed number of digits ahead of their current press (viewing window). The window size varied between 1 (next digit revealed with pressing the current digit - serial reaction time task / SRTT) to 14 (full a-priori knowledge of the sequences). Trials contained a mixture of fully random sequences, and sequences that were composed of 6 reoccurring 3- or 4-digit segments. The effective planning horizon was defined as the point at which larger window sizes did not lead to better performance. Our results clearly indicated that participants selected/ prepared multiple actions into the future. On day 1, where the effect of learning is minimal, participants performed significantly slower for window size 1-3, compared to a fully visible sequence. This suggests that information regarding up to 3 digits ahead was used to improve performance. For random sequence, the effective planning horizon then increased from 3 on the first day to 4 on the last day of training ( $p=0.003$ ). This indicates that part of the general improvement in performance in the sequence production task results from a better ability to utilize more information and preplan more movements. From day 2 onward, participants were significantly faster in reoccurring compared to random sequences ( $p=0.005$ ). However, participants showed no significant difference in performing random and reoccurring sequences on window size 1. This indicates that information about upcoming presses is necessary to exhibit the benefits of learning. At the same time, performance for reoccurring sequences became less dependent on window size. Specifically, unlike random sequences, the effective horizon size stayed the same (window size 3) in reoccurring sequences, even though the performance was getting faster. This indicates that the upcoming presses in reoccurring sequences could be recalled from memory, which removed the need for explicit visual information. Finally, we show that the observations of this study can be successfully modelled using an extension of a simple drift-diffusion model (DDM) of decision making to encompass ability to preplan multiple actions into the future.

## **2-F-88 What are the fMRI signatures for plasticity during motor sequence learning?**

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An important aspect of many motor skills is the ability to produce complex sequences of movement. While behavioural improvements in sequence tasks are easily observable, the underlying neural processes remain elusive. Numerous functional magnetic resonance imaging (fMRI) studies have set out to illuminate these brain-related changes, but there is very little agreement about the neural changes

that occur during sequence learning. Existing studies have reported both fMRI signal increases and decreases (Steele & Penhune, 2010, *Journal of Neuroscience*; Karni et al., 1995, *Nature*), changes in the fine multivariate patterns (Wiestler & Diedrichsen, 2013, *eLife*), changes in measures of repetition suppression (Wymbs & Grafton, 2014, *Cerebral Cortex*) and changes in functional connectivity measures during task performance (Bassett et al., 2015, *Nature Neuroscience*). The overall aim of this study was a) to design a longitudinal fMRI motor learning study and re-test a number of reported findings in the literature, and b) to test a specific set of new hypotheses regarding multivariate pattern changes. To assure that this is performed in a principled manner, we pre-registered our design including our predictions on Open Science Framework. We employed a longitudinal study with a within-subject design. Participants were trained to perform six 9-digit sequences on a piano-like device over a period of 5 weeks. To examine the evolving changes in brain representation during learning, they underwent MRI scanning four times (1st scan before any training, 2nd after a week, 3rd and 4th after five weeks). During the scanning sessions, participants executed the 6 trained sequences, as well as 6 other, untrained sequences. In scanning sessions 1-3, participants performed both trained and untrained sequences at a regulated speed, while in the last session they execute the sequences as fast as possible. This contrast allowed us to assess whether learning-related neuronal representations are also expressed when the speed of execution is controlled. One of our pre-registered aims was to examine the stability of sequence-specific pattern across learning. We predicted that early in learning the specific pattern of activity for each of the trained sequences will change substantially, but that they will stabilize later in time. In other words, we expected the correlation between sequence-specific activity patterns would show low correlations across session 1 and 2, and increased correlations between session 2 and 3. This effect was predicted to be specific to trained sequences, with untrained sequence-specific patterns demonstrating more stable correlations across all sessions. Our results from the first 12 subjects indicate that premotor and superior parietal areas demonstrate such learning-induced plasticity. Comparing the patterns across scans 3 and 4 revealed that similar sequence-specific patterns are recruited when the sequence is executed at maximal speed or a slow, controlled pace. These results suggest that stability of sequence-specific pattern across time might be a good metric for cortical plasticity in learning, independent of the execution speed.

## **2-F-89 Selection, preparation, execution: breaking down elements of skill learning**

Giacomo Ariani<sup>1</sup>, Jörn Diedrichsen<sup>2</sup>

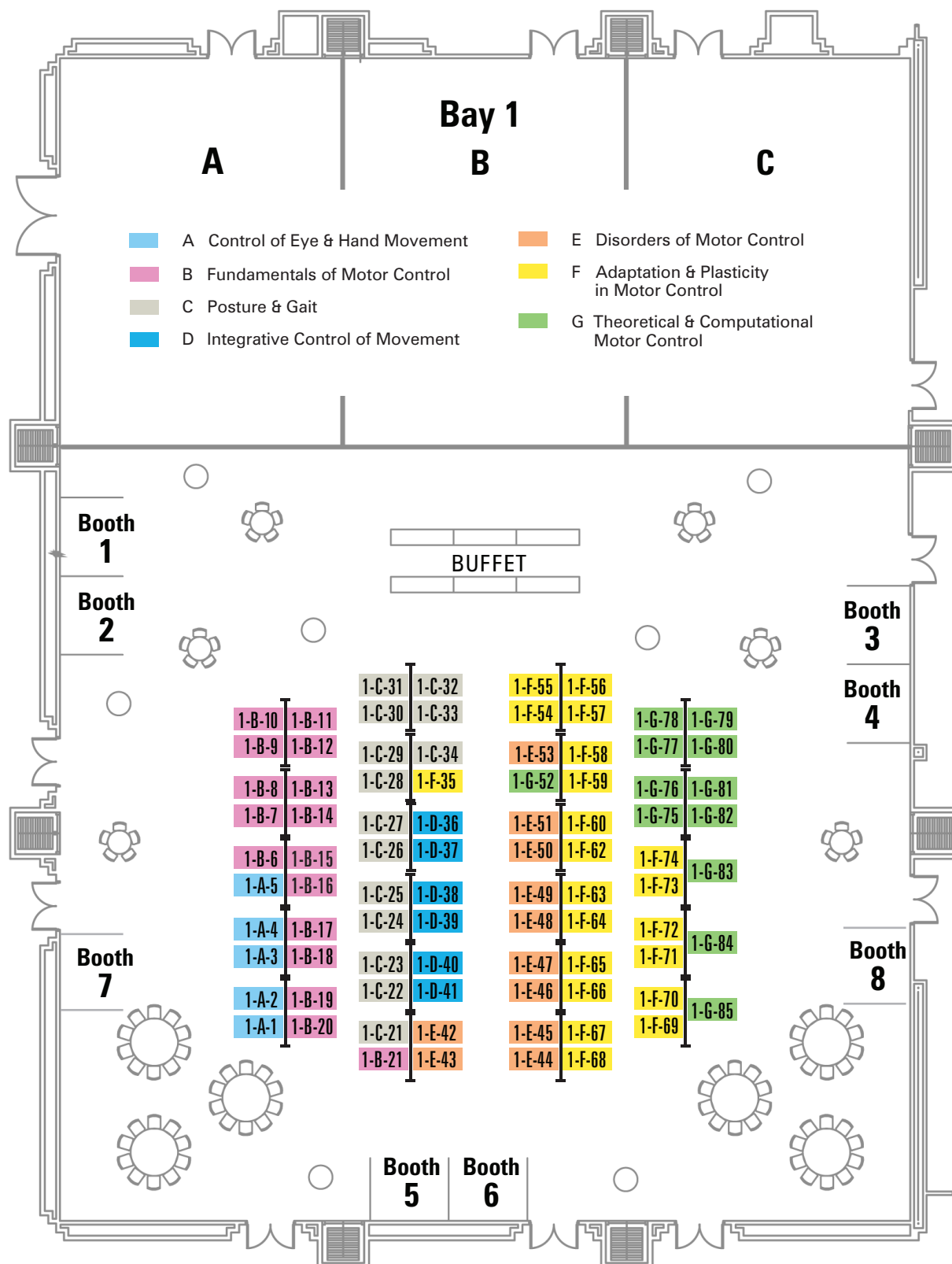
<sup>1</sup>*The Brain and Mind Institute*, <sup>2</sup>*University of Western Ontario*

Systematic behavioral training improves performance in complex motor tasks such as the discrete sequence production task. However the precise mechanisms behind such behavioral improvements are still poorly understood. Here we aimed at breaking down elements of skill development by investigating the role of action selection, motor preparation, and sequence execution in motor sequence learning. We used a sequence production task in which five finger presses were cued by five visually presented numbers (e.g., 1 = thumb, 5 = little). Participants had always full explicit knowledge of the sequences to be executed, which then had to be produced as fast as possible (speed/accuracy trade-off). Over the course of 4 days, participants were trained on 10 sequences (10 blocks per day, each sequence presented 40 times). Each day, participants were also tested on 80 untrained sequences (2 blocks per day, each sequence only presented once). On the 4th day, participants performed the trained sequences 337 ms faster than the untrained sequences ( $p < 0.001$ ). Using a forced reaction time (RT) task (e.g., Haith et al., 2016) we also manipulated how much time participants had to prepare each sequence. This allowed us to separate the processes occurring during sequence preparation from those occurring during

sequence production. Participants were trained to press the first finger of the sequence synchronously with the 4th tone of a series of four regularly paced tones (800 ms apart). To measure the speed of single action selection, on a subset of trials we required participants to press only the first finger in the sequence. Preparation time varied from 600 to 200 ms before the 4th tone. The preparation time to reach 80% finger selection accuracy improved from 492 ms on the first day to 394 ms on the last day of training. This speed-up of action selection constitutes one of the main factors for the improvements in both trained and untrained sequences. To assess the role of motor preparation in sequence learning, we also required participants to produce the full sequence, with the informative cue presented 2400, 1600, 800, or 400 ms before the 4th tone. At the end of training we found evidence that trained sequences could be more quickly selected and prepared than untrained sequences. A preparation time of 2400 ms allowed participants to execute untrained sequences more quickly. For trained sequences, a preparation time of 800 ms appeared to be sufficient for full preparation (interaction  $p=0.019$ ). We also found that participants were faster in producing trained rather than untrained sequences regardless of the preparation time given on each trial, even for the longest preparation times ( $t=9.43$ ,  $p < 0.001$ ). In a successive control experiment on the same set of participants, we corroborated that these findings held even when mixing trained and untrained sequences within the same block. These findings indicate that the motor execution of trained as compared to untrained sequences has improved. Overall, our results indicate that faster performance in the discrete sequence production task can be attributed to a combination of 1) general speed-up of action selection, 2) faster preparation of learned sequences, and 3) better execution of well-trained sequence elements.

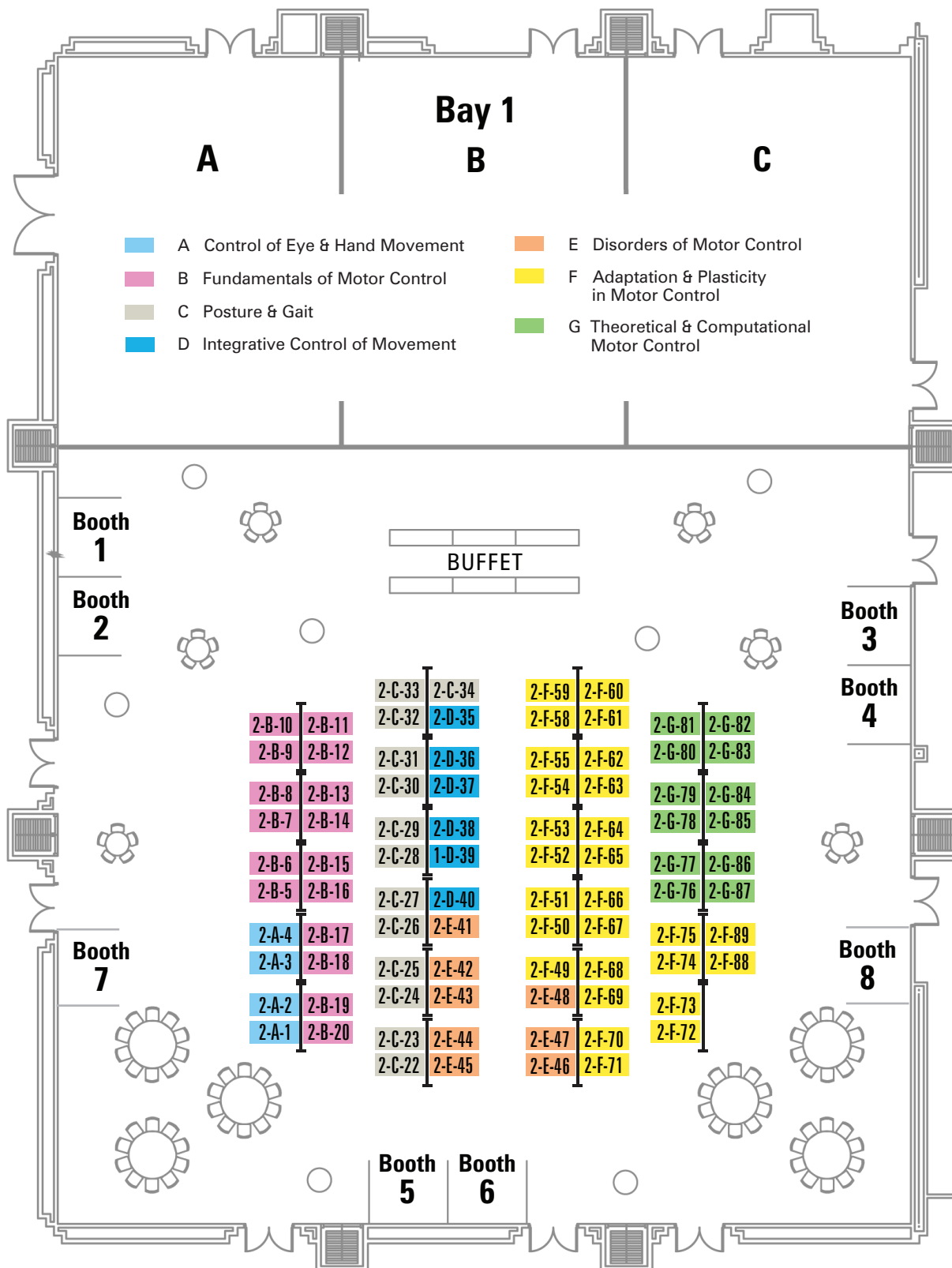
# Poster Session 1 Floor Plan • Tewa Room

Tuesday May 1 & Wednesday May 2 8:00 – 17:00



# Poster Session 2 Floor Plan • Tewa Room

Thursday May 3 & Friday May 4 8:00 – 14:45





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