



Society for the  
**Neural Control of Movement**

# NCM 23<sup>RD</sup> Annual Meeting

## NCM Posters

Authors, Titles, Affiliations  
& Abstracts • Sessions 1 & 2



**Satellite Meeting**  
**April 15 – 16, 2013**

**23rd Annual Meeting**  
**April 16 – 20, 2013**

**El San Juan Hotel & Casino**  
A WALDORF ASTORIA HOTEL

San Juan **Puerto Rico**

## 2013 At-A-Glance Satellite and Annual Conference Schedule

El San Juan Hotel & Casino, Puerto Rico



Society for the  
**Neural Control of Movement**

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## Session 1 Posters are listed by theme.

### A - Adaptation & Plasticity in Motor Control

#### 1-A-1 Incomplete adaptation as a combination of learning and forgetting

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Humans can easily handle changes in intersensory mappings, for instance those induced by wearing prism glasses. However, adaptation to a new inter-sensory mapping is generally incomplete when subjects have to rely on terminal feedback. Recent models of adaptation involve a combination error-based learning and forgetting of the new mapping. These models do predict incomplete adaptation due to a balance between learning and incomplete retention. Here we test whether perturbing this balance by scaling the feedback leads to a change in the level of adaptation. Here, we test adaptation to a ten-degree egocentric visual rotation in a 3D position matching task. We perturb the balance by scaling the feedback errors: learning will be proportional to the scaling factor, while the retention (forgetting) remains unaffected. As predicted, we found that adaptation is closest to complete in the magnified feedback condition and most incomplete in the reduced feedback condition. This is direct evidence that incomplete adaptation can be explained by a combination of learning and forgetting.

#### 1-A-2 Speed and crank resistance affects coactivation of knee muscles during cycling movements

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Introduction: We study electrical activities (EMG) of thigh muscles during cycling movements of healthy people to define stimulation patterns for functional electrical stimulation (FES) driven cycling of spinal cord injured patients. During cycling knee muscles have different roles: the extensors are the main power generators while flexors are regulating the movement. For fine control the flexors generate torque not only during knee flexion but during extension as well. This study examines the coactivation of thigh muscles during cycling with different speeds and loads. Methods: Able bodied individuals (41) executed cycling movements under 6 conditions [fast and slow cycling in load condition low (1), moderate (2) and high (3)]. Each subjects made at least 10 cycles in each condition. Surface EMGs were recorded with sampling frequency of 1000Hz from quadriceps and hamstrings muscle groups. After filtering (4th order Butterworth) and smoothing (RMS) the signals, coactivation of the muscles was quantified by a coactivation rate (CR) in each cycle the subjects made. A muscle was considered active at a certain moment if its actual EMG amplitude exceeded the 35% of its maximal EMG value. Data were time normalized for 100 equal time units. CR is defined as the number of units in which both muscle groups are active out of the 100 units in a cycle. (Thus CR is the time of coactivation in percentage of total movement time.) For each condition the mean CRs across cycles were computed, so each person has 6 mean coactivation rates (MCR). Results: The MCRs are significantly ( $p < .05$ ) higher during fast cycling than slow cycling and also in load condition 1 than 3 and in load condition 2 than 3. There is no significant difference between the MCR-s in load conditions 1 and 2 in either speed. Discussion: Increased cycling speed is

associated with increased coactivation of the thigh muscles. However if cycling is executed against higher resistance (load) than muscle coactivation is decreased. This supports that besides raising of the muscle's power (EMG) there is another mechanism in the nervous system to raise cycling performance: changing the coactivation of the muscles. This change may reflect the adaptation of neural control to altered external conditions. Such change in coactivation may be applied in artificial stimulation patterns when FES driven cycling is planned to be generated with increased pedaling speed or against higher crank resistance. Supported by TAMOP-4.2.1.B-11/2/KMR-2011-0002 and a HAESF grant (to JL).

#### 1-A-3 Changes in kinematics when learning to use a pair of pliers with different transformations

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<sup>1</sup>University Medical Center Groningen

Making goal-directed actions with a tool implies that movements of the body are transformed to movements of the new end-effector, the tool. Tool properties determine how bodily movements translate to end-effector movements. Most studies on tool transformations today addresses relatively simple pointing movements. The current paper examines how reaching and grasping are coordinated when participants learn to act on new affordances when objects have to be picked up with a novel pair of pliers. We manipulated the location of the hinge on the pair of pliers; when the hinge was located close to the digits the beak opened faster than the digits, whereas a hinge far from the digits decreased beak opening speed relative to the digits. This implies that depending on the location of the hinge reaching and grasping should be coordinated differently. We studied how this coordination changed over the learning to use a pair of pliers and how this learning differed over different pair of pliers. Three groups of 10 participants each (all university students) picked up a small cylinder with a pair of pliers for 100 times on two consecutive days. The pair of pliers was always 20cm long. One group had the hinge at 5cm from the fingers, one group at 10cm, and one group at 15cm. We measured kinematics of the beak. We analysed standard prehension measures, such as hand opening time and hand closing time. Interestingly, the grasping pattern with a pair of pliers showed a plateau phase, which is remarkably different from non-tool grasping showing a clear peak in the grasp profile. Importantly, for all pair of pliers this plateau time decreased over repetitions of trials, but the plateau time was longer for the 15cm pair of pliers. The open time was smaller for the 5cm pliers whereas the closing time was smaller for the 15cm pair of pliers. The results showed that the location of the hinge determines how hand opening and hand closing are coordinated; if small hand movement results in large movement of the beak, then hand open time is shorter. Also, plateau time is shorter when large hand movement has small beak movement as an effect. The findings can be interpreted as that over learning the hand movement is adjusted so that the grasping pattern of the beak of the pliers matches a grasping pattern of a natural grasp as close as possible. This implies that the movement of the beak of the pliers is controlled, indicating that the tool is incorporated in the body schema. Moreover, the learning continued over the whole experiment, suggesting that adaptation processes are continuously at work.

#### 1-A-4 Cerebellar damage degrades motor and perceptual aftereffects following walking adaptation

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Healthy adults can learn a new walking pattern on a split-belt treadmill when one leg is driven to move faster than the other.

Subjects initially take asymmetric steps, but learn to restore stepping symmetry within ten minutes. When the treadmill belts are subsequently returned to the same (i.e. tied) speeds, subjects walk with the opposite asymmetry (i.e. motor aftereffect), indicating that a new walking pattern has been learned and stored. We recently found that young healthy adults also have a robust perceptual speed aftereffect following split-belt adaptation—they feel like the leg that was moving faster during adaptation is slower in the post-adaptation period. This decays throughout the post-adaptation on a similar timescale as the motor effect. Furthermore, there appears to be a correlation between the amount of perceptual aftereffect and the amount of motor learning. This suggests a relationship between changes in the motor and sensory systems after motor learning. However, it is also possible that the motor and perceptual aftereffects arise from different mechanisms. Motor aftereffects are thought to be cerebellum-dependent since cerebellar damage abolishes them. More specifically, this has been thought to be due to loss of a forward model housed within the cerebellum that can make predictions about how motor commands will move the body (e.g. Miall et al. 2007). In this framework, the perceptual aftereffect would be expected to occur as a part of this cerebellum-dependent recalibration of a forward model (e.g. Synofzik et al. 2008). However, it is also possible that perceptual changes could be due to a separate, use-dependent learning mechanism (e.g. Diedrichsen et al. 2012) that would be caused here by walking at a given speed for extended periods of time. It is known that perceptual judgments of speed change can change after simply walking, running or hopping on a regular treadmill (Anstis 1995). This type of mechanism may rely more on sensory cortices rather than cerebellar structures (Block and Bastian 2012). Here we asked if motor adaptation is required for perceptual aftereffects in split-belt walking. We addressed this by testing whether people with cerebellar damage have normal perceptual aftereffects despite having degraded motor aftereffects. Our preliminary results show that, compared to age-matched controls, cerebellar patients have reduced or absent motor and perceptual speed aftereffects following split-belt adaptation. Thus, our findings demonstrate that perceptual aftereffects are linked to the motor aftereffects during walking adaptation and are not likely to be due to a separate sensory mechanism. Supported by NIH HD040289.

## 1-A-5 Neural synchrony in speech motor learning

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What are the neural correlates of motor learning? Presumably, as we learn a task coordinated activity emerges over distributed network of brain regions. The degree of coordination over the network can be a useful measure of learning. It is hypothesized that neural synchronization is such a measure of coordinated network activity that supports motor learning. We studied phase synchronization patterns of event related potentials (ERPs) in a speech motor learning task in which auditory feedback was altered in real-time as subjects repeatedly uttered a consonant-vowel-consonant word. The auditory feedback alteration was such that it lowered the first formant frequency of the vowel sound. We also recorded continuously EEG signals throughout the speech motor learning task. The ERPs were extracted and aligned at the onset of vocalization and were used to compute phase coherence between the theta and the gamma frequency bands. We observed emergence of significant phase synchronization following motor learning. Our results suggest that phase synchronization patterns provide a window to the coordinated network activity that underlies speech motor learning.

## 1-A-6 Motor learning by observing: A resting-state fMRI study

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Recent research has demonstrated that motor learning can be achieved not only through direct, firsthand experience, but also by merely observing another individual learning to move. These findings demonstrate that neural representations of novel environments can be acquired through observation. When we observe the actions of others, we activate those same brain regions involved in performing those actions ourselves. However, the brain's ability to learn how to make movements through observation is still not well understood. Here, we use resting-state fMRI coupled with a force field learning paradigm to investigate the neural basis of motor learning by observing. On day 1, subjects grasped the handle of an InMotion2 robotic arm and performed straight reaching movements in a null field in which the robotic arm did not apply force to the hand. Next, subjects underwent a baseline resting-state fMRI scan. On day 2, subjects watched a video of an actor learning to perform straight reaching movements while the robotic arm applied a counterclockwise force field. Subjects then underwent a post-learning resting-state fMRI scan. Finally, to assess motor learning behaviourally, subjects performed straight reaching movements in a clockwise force field. Motor learning scores were calculated as the magnitude of proactive interference in terms of movement curvature. A seed-based correlation analysis was carried out to assess changes in resting-state functional connectivity (FC) from day 1 to day 2 that were related to our behavioural measure of observational motor learning. We revealed a network involving V5/MT, bilateral cerebellum, primary motor cortex and primary somatosensory cortex whose activation was significantly modulated by the amount of observational motor learning that was achieved (as assessed on day 2, after scanning). This network may be engaged to facilitate motor learning by observing.

## 1-A-7 Reduction of movement variability with practice in older adults is associated with greater motor unit modulation from 13-30 Hz

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Studies of single motor units in older adults indicate that practice-induced improvements in movement variability are associated with a decrease in discharge rate variability. However, these findings may be limited because multiple motor units are active during a muscle contraction. The purpose of the study, therefore, was to determine if the practice-induced improvement in movement variability in older adults was associated with changes in the neural activation of multiple motor units. Nine healthy older adults (72.5 ± 5.9 yrs) were instructed to accurately match a sinusoidal target for 35 s by abducting and adducting their index finger. The sinusoidal target comprised of a 0.12 Hz frequency and 12° range of motion. Each subject performed 40 practice trials, which included 8 blocks of 5 trials each with visual feedback of their movement relative to the target. We recorded multiple motor units from the first dorsal interosseus (FDI) muscle using intramuscular bipolar electrodes. Movement variability was quantified as the trajectory variability of the index finger. The neural activation of the FDI muscle was quantified by extracting the following parameters from all action potentials (spikes): 1) mean spike rate (Hz); 2) spike rate variability (%); 3) frequency modulation of the spike rate (5-13, 13-30, and 30-60 Hz). Following 40 practice trials, the trajectory variability decreased by 12% in older adults (P < 0.05) and was significantly correlated to improvements in movement accuracy (R<sup>2</sup>=0.46). Practice increased the mean spike rate by 28% (P < 0.05) and decreased the variability of discharge rate by 9% (P < 0.05). The practice-induced decrease in

movement trajectory variability was significantly associated with an increase in mean spike rate ( $R^2=0.46$ ), a decrease in motor unit discharge rate variability ( $R^2=0.52$ ), and an increase in motor unit modulation from 13-30 Hz ( $R^2=0.48$ ). Interestingly the modulation of multi motor units from 13-30 Hz was associated with the increases in mean spike rate ( $R^2=0.75$ ) and decreases in the variability of motor unit discharge ( $R^2=0.43$ ). In summary, our results support and extend findings from single motor unit studies and demonstrate that practice-induced improvements in movement trajectory variability are associated with changes in the neural activation of multiple motor units. We provide novel evidence that the practice-induced changes in the neural activation of the motor units (increases in mean spike rate and decreases in motor unit discharge rate variability) are associated with an increase in the modulation of the motor units from 13-30 Hz.

### **1-A-8 Changes in representation of trunk muscles in the motor cortex after complete thoracic spinal cord injury and rehabilitation training**

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Complete thoracic transection at T8-10 is a common model for studying Spinal Cord Injury (SCI). Contrary to adult spinalized (ATX) animals, rats spinalized as neonates (post natal day 0-6) (NTX) can generate some reflex stepping motions and a subset of these rats (~20%) is also able to achieve autonomous weight support (WS) as adults. Reorganized trunk corticospinal mechanisms are believed to play an essential role in the autonomous recovery of NTX rats, however its potential roles in ATX rats remain unclear. Motor pools for trunk muscles are broadly distributed throughout the thoracic and upper lumbar segments however how much of these multi segment muscles are under voluntary control from the cortex after complete thoracic SCI is unclear. Recently using trunk based robotic rehabilitation we showed that non-WS NTX rats recover significantly on robot whereas ATX rats do not exhibit the same level of recovery. Further robot trained NTX rats showed plastic changes in the trunk motor cortex such as an expansion of low trunk representation and an increase in cortical muscle synergies. Whether ATX rats exhibit such cortical plasticity following robot training is not clear. To investigate the reorganization of trunk motor cortex after adult SCI and rehabilitation training we divided ATX rats into three groups. The first group did not receive any training, the second group received treadmill training without perineal stimulation and the third group received robot training without perineal stimulation. 4-6 weeks after SCI we used intra cortical micro stimulation to map trunk (abdominal and back) muscles across multiple segments (mid thoracic, low thoracic and upper lumbar) in the three groups of ATX rats. We also compared trunk motor maps of ATX rats with normal rats and robot trained NTX rats. None of the three groups of ATX rats were able to recover any autonomous WS. Our preliminary results fall into three categories: First, there was a significantly larger total trunk motor area in all the ATX rats compared to normal rats and the greatest increase in area was observed for the trunk segments rostral to the injury. Second, all ATX rats had some cortical representation of trunk muscles below the injury at low thoracic level (but not for lumbar level) however this representation was smaller in area than that of normal rats. Third, robot training of ATX rats did not promote any additional plastic changes in the trunk motor cortex in these animals such as an increase in overlap of different trunk muscles involving caudal segments as we had previously observed for robot trained NTX rats. Our results thus suggest adult SCI results in cortical reorganization of trunk representation and rehabilitation training that does not induce or incorporate any autonomous WS stepping fails to promote any additional plastic changes in the trunk motor cortex.

### **1-A-9 Transfer of isometric motor learning depends on the mapping of force input to cursor movement**

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The ability to adapt to changes in body and world is a remarkable and prominent quality of our motor system. In particular, adaptation to altered arm dynamics and kinematics during reaching movements has been extensively studied. However, adaptation in isometric reaching, in which the arm remains stationary and the user controls a cursor via force input, has not received as much attention. An understanding of isometric control is important for an increasing number of applications (e.g. robot assisted surgery; control of devices for rehabilitation). In the current study, we explore adaptation to a visuomotor rotation in isometric reaching. We specifically test the transfer of learning between two arm configurations using position- and velocity- based mappings from force to cursor. Previous work from adaptation studies suggests that perturbation of arm dynamics, via a mechanical force field applied to the hand, is learned in joint (intrinsic) coordinates, whereas perturbation of arm kinematics, via rotation of a cursor representing the hand, is learned in hand (extrinsic) coordinates. We set out to determine the coordinates in which a visuomotor rotation is learned in isometric reaching. We built a planar, cable-driven manipulandum with a force sensor embedded in the handle and parallel linkages that can mechanically lock. In the isometric, joints-locked configuration, force applied on the handle in plane is mapped to the movement of a virtual cursor using either position or velocity control. Participants performed virtual center-out reaches with a spatially aligned cursor and targets displayed on a mirror above the arm. Each participant performed 'isometric reaches' to one of two training targets in the left workspace and a testing target in the right workspace; the training target was similar to the testing target in either joint or hand coordinates. Participants first performed baseline reaches in both workspaces. They were then presented with a 45° CCW rotation of the cursor in the left workspace, and trained until the original straight trajectory was restored. Finally, adaptation transfer was evaluated in the right workspace with no cursor rotation. We tested four groups of participants representing each combination of training target and control strategy. Angular error at 150ms from movement onset was used to assess adaptation. For position control, adaptation was transferred in joint space: there was an aftereffect following training to a joint-space-similar target but minimal aftereffect following training to the hand-space-similar target. For velocity control, adaptation transferred in hand space, but there were also aftereffects following training to the joint-space-similar target. This non-specific transfer was surprising, and we are exploring possible explanations, such as engagement of other motor learning mechanisms on top of the adaptation process (e.g. a bias due to model-free learning). In summary, we find that patterns of transfer depend on the mapping of force to cursor in an isometric task. The ultimate goal of this work is to understand if adaptation of isometric reaching can transfer to, and improve real world reaching movements. Training of virtual movements using force/torque input and transfer of this learning to movement would be a transformative approach to restoring motor function that can engage individuals of a wide range of abilities using simple, cost-effective devices.

## 1-A-10 The role of emotion, vision and touch in movement learning

**Jeanne Masterson**<sup>1</sup> <sup>1</sup>Dominican University of California

Motor skills involve perception as well as action, therefore with the enhancement of sensory input to the regions of the brain involved in motor processing, learning new motor skills are strengthened, creating an improved environment in the motor learning process by increasing body awareness, and a greater potential for elevated physical self confidence and positive emotional states. Visual enhancement of touch is one technique used to strengthen this sensory feedback loop. As reported by Cardelini, Longo, Driver and Haggard (2012) visual enhancement of touch facilitates processing of tactile events on one's own body by increasing activation of the somatosensory regions of the brain, which are responsible for motor recognition and action. Along with positive emotion, enhancement of touch can play an integral role in effective motor learning. The purpose of the present study is to examine whether positive emotional states and enhanced sensory input, may improve motor learning by stimulating the areas of the brain responsible for motor action. During this study three groups of participants are given pre treatment measures of self efficacy and mood. One group will be enrolled in a Pilates class that includes visual enhancement of touch and positive emotional priming, the second group will attend a regular Pilates class, the third group will have no physical task to learn. The groups participating in the Pilates class are tested on their physical skill acquisition rated on a 5 point Likert scale. All the participants are surveyed at the start and end of the study as to their physical self efficacy and mood. It is hypothesized that the group who received both the positive emotional priming and the visual enhancement of touch will have better task acquisition of the Pilates techniques and have improved mood and physical self efficacy scores. Results will be interpreted and discussed in terms of neuroplasticity and the mirror neuron system. Studies such as these are important as they may be applicable to a number of movement practices where improved motor learning is the goal. Environments such as Physical Therapy, sport specific training and general fitness for health.

## 1-A-11 A target is not necessary for visuomotor adaptation

**Ryan Morehead**<sup>1</sup>, Richard Ivry<sup>1</sup> <sup>1</sup>UC Berkeley

Visuomotor adaptation is commonly studied by having participants reach to discrete targets while a perturbation is introduced between hand position and visual feedback. Reach targets are useful because they standardize the intended final state of the effector. Motor error on a given trial is often quantified by subtracting the actual final state from this intended state. However, in many experimental contexts, the intended state is confounded with the target location. These can be separated; for example, when subjects are asked to use an aiming strategy, the motor error is defined by the aiming location and not the target location. In this context, the reach target is not relevant since adaptation is driven by the discrepancy between the predicted outcome of a motor command and the actual outcome. We conducted three experiments to explore this hypothesis. In Experiment 1, the target remained visible throughout the trial for half of the participants. For the other half, the target disappeared at reach onset, precluding a direct comparison of the reach endpoint and target location. A 22.5° rotation was gradually introduced over 240 trials for both groups. Despite the absence of explicit target error information, adaptation was not distinguishable from the control group. In Experiment 2, participants were asked to move a cursor around a workspace, with the instructions to be as random as possible. While performing this task, a visuomotor rotation was gradually applied in increments of .075° every two seconds, reaching a final value of 45° that was maintained for five minutes. Before and after the random drawing intervention, participants made 40 center-

out reaches with veridical online feedback. Participants showed a small but persistent aftereffect, indicative of visuomotor adaptation. In Experiment 3, participants made 400 center-out reaches for targets, and received pleasant auditory feedback if they hit the target. At trial 81, a 22.5° rotation was abruptly introduced. The participants were split into two groups based on the number of hits during the perturbation block. Despite this division based on performance during the perturbation block, the two groups exhibited a similar aftereffect when visual feedback was removed. This implies that the amount of adaptation between good and poor performers was the same despite the large differences in target error experienced during the perturbation block. Taken together, these experiments show target error is not necessary for visuomotor adaptation; indeed, it is unclear if target error makes any contribution to adaptation. Rather, these results add to the evidence indicating that visuomotor adaptation is driven by the discrepancy between the predicted outcome and actual outcome.

## 1-A-12 Neuronal correlates of prediction in the motor cortex of primates

**Itai Novick**<sup>1</sup>, Eilon Vaadia<sup>1</sup> <sup>1</sup>Hebrew University

Contemporary views of sensory-motor learning propose that the brain utilizes internal representations that allow predictions of the sensory consequences of actions. Yet, the neural mechanisms that underlie such predictions are poorly understood. In this study, we aimed to trace the formation of new predictions at the behavioral, physiological and theoretical levels. We constructed a computational model that estimates how cells in the motor cortex modify their activity to perform appropriate actions in a new environment. Even though sensory prediction was not calculated directly, the sensory consequences of actions were considered in the resulting behavior. To validate our model empirically, we trained monkeys to perform a behavioral task that required a new sensory prediction. Using a chronically implanted electrode array, we simultaneously recorded single cell activity in the motor cortex. The empirical neuronal activity changes, as well as the behavioral effects, were in agreement with the model's prediction. In an additional experiment, we show that human subjects exhibit similar behavioral changes. Our findings provide an alternative explanation for the generation of new predictions and demonstrate that the motor cortex is involved in the process.

## B - Control of Eye & Head Movement

### 1-B-13 Neural encoding of head-free gaze shifts in monkey superior colliculus

**John van Opstal**<sup>1</sup> <sup>1</sup>Donders Institute

We recently proposed a population-coding model that explains how cells in the midbrain superior colliculus (SC) contribute to the trajectory and kinematics of saccades (Goossens & Van Opstal, PLoS Comp Biol 2012). Briefly, the model holds that each spike from each recruited cell contributes a tiny, fixed, contribution to the saccade ("spike vector") that only depends on its location within the motor map. The saccade results from dynamic linear summation of all spike vectors. This extremely simple model predicts a linear relation between a cell's cumulative spike count, CS(t), and the straight, imaginary trajectory of the eye, S(t-) between initial and final positions ( : lead time, 20 ms). We tested this model for >20000 head-fixed saccades and 150 cells to visual targets across the oculomotor range. Interestingly, when using measured spike trains to simulate saccades, the model produced straight eye-movement trajectories with the correct velocity profiles and nonlinear main-sequence properties, although horizontal and vertical brainstem burst generators were kept linear and uncoupled. We showed that the main sequence emerges from a spatial gradient in the firing patterns along

the SC motor map. Here we test and discuss a strong prediction of the model: the linear relation between dynamic spike counts and instantaneous straight gaze-displacements should also hold for head-free gaze shifts, in which kinematics and relative eye- and head contributions vary substantially from trial to trial. We recorded from 40 single units in two monkeys trained to make large gaze shifts (up to 85 deg amplitude) to flashed targets that were elicited throughout a cell's movement field. I demonstrate that the data support the simple linear spike-count model. Acknowledgements: I am greatly indebted to Ed Freedman, Mark Walton and Stephan Quessy from the University of Rochester, NY, for constructive and lively discussions, and allowing me to collect crucial SC recordings from their monkeys.

### **1-B-14 Adaptation of micro-saccades reveals oculomotor control at the limits of precision**

**Katharina Havermann**<sup>1</sup>, Claudia Cherici<sup>2</sup>, Michele Rucci<sup>2</sup>, Markus Lappe<sup>1</sup>

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To efficiently explore a visual scene, saccades need to precisely relocate the fovea to regions of interest. When saccades consistently fail to place the target on the fovea saccadic adaptation adjusts saccade amplitude. However, saccades cover a broad range of spatial scales, the smallest (microsaccades) are just a few minutes of arc and only move the attended region across retinal locations within the fovea. It is unknown if the same adaptation mechanism that tunes larger saccades is also active in microscopic eye movements. In two experiments we show that both target-directed microsaccades and microsaccades that occur during fixation are adaptable. We first tested saccades from a fixation point to a target 20 to 30 arcmin away. The target shifted by 15 arcmin during the saccade either in or against saccade direction. We found that microsaccades decreased in amplitude in response to a 15 arcmin target back step, and increased in amplitude in response to a 15 arcmin forward step. Corrective saccades also occurred, compensating for a post-saccadic target shifts as small as a quarter of a degree. Thus, the visual system actively calibrates microsaccades at a precision smaller than the foveal region. Thereafter we apply the adaptation paradigm to involuntary microscopic saccades during fixation. Subjects were required to fixate a small dot. Whenever a microsaccade occurred the dot was shifted along the direction of the saccade by 50% of the saccade amplitude. Consistent shifts influenced the statistical distribution of microsaccade amplitudes. Shifts in saccade direction increased amplitudes and shifts against saccade direction decreased amplitude. Thus, even microsaccades that occur during fixation are actively controlled with respect to the location of the fixation point. Our findings show that the mechanisms of saccade control are plastic down to the smallest level of detail. This plasticity may serve to optimize motor performance and may be required to establish reliable representation of fine spatial detail.

### **1-B-15 Foveal and peripheral vision result in similar pointing accuracy and variability during memory-guided pointing**

**Fabian David**<sup>1</sup>, Ruth Tngonan<sup>1</sup>, Lisa Chin-Cottongim<sup>1</sup>, Daniel Corcos<sup>1</sup>

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Encoding memorized target locations and executing memory-guided reaches can be done using foveal or peripheral vision. The benefit of foveal vision in encoding and executing a memory-guided reach is that it provides the highest visual acuity. However, moving the eyes to foveate the target (once for encoding the target and again for executing the pointing movement) may result in increased extra-retinal error (afferent signal of eye position), which in turn may result in increased pointing error and variability. The benefit of using

peripheral vision to encode and execute a memory-guided reach is that extra-retinal error is minimized with no eye movements. However, visual acuity is reduced. The question that remains is which of these conditions of encoding and execution are optimal for pointing accuracy and variability. The objective of this study is to determine pointing accuracy and variability of memory-guided pointing movements in two encoding and execution conditions: foveal encoding and execution (Foveal) and peripheral encoding and execution (Peripheral). Five healthy subjects (4 female) aged 21 to 27 years (Mean  $\pm$  SD: 23.7  $\pm$  3.2) completed 2 separate testing sessions (Foveal and Peripheral) on two separate days. Subjects fixated on a central LED located at the center of a circle of radius 0.1 m. While the central LED was illuminated, the target LED was briefly illuminated at one of three locations (0° (vertical), 45° (oblique), or 90° (horizontal)) at an eccentricity of 0.1 m. The central LED then briefly flashed, which was the cue to initiate the pointing movement to the remembered target. In the Foveal condition, when the target LED appeared the subjects shifted their gaze from the central LED and foveated the target during encoding phase. During the pointing phase subjects 'looked' and pointed to the remembered target location. In the Peripheral condition, the subjects fixated at the central LED during encoding and pointing phases. The dependent variables were the magnitude of pointing error and variability. A 3 (target locations) by 2 (conditions) rmANOVA revealed that there were no differences between Foveal and Peripheral conditions with respect to magnitude of pointing error (Mean Difference: 0.01m; Confidence Interval: -0.021 to 0.041;  $p = 0.41$ ) and variability (0.003; -0.003 to 0.009;  $p = 0.24$ ). A main effect of target location was observed ( $F = 44.4$ ,  $p = 0.006$ ). Pointing error was significantly lower for the 90° target compared to the 0° (-0.019; -0.023 to -0.014;  $p < 0.001$ ) and 45° (-0.022; -0.031 to -0.013;  $p = 0.003$ ) targets. In conclusion, the benefit of increased visual acuity by foveating a target might be offset by the cost of increased extra-retinal error, thus resulting in reaching movements with similar accuracy and variability as in the peripheral encoding and reaching condition. Future studies should investigate if this relationship is maintained when multiple targets have to be encoded.

## **C - Disorders of Motor Control**

### **1-C-16 Specific brain networks relate to tremulous (3-8 Hz) and slow (0-3 Hz) oscillations in force in essential tremor**

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Essential tremor (ET) is an age-associated disorder and is the most common pathological tremor disorder in the world (Louis et al., 1998). The cardinal feature of ET is a  $> 4$  Hz kinetic tremor of the hands and arms (Louis, 2011, Louis, 2001). In addition, slow oscillations ( $< 2$  Hz) in motor output are abnormal in ET (Poon et al., 2011). This study used functional magnetic resonance imaging (fMRI) to determine if these distinct oscillations in force output have separate neural origins. We simultaneously measured force output and the blood oxygenation level-dependent (BOLD) signal during a visually guided precision grip task. Participants (14 ET, 14 controls) produced a series of 10, 2-second force pulses. Each force pulse was separated by 1 second of rest. 10 force pulses plus rest were completed to produce a 30 second force interval. Target force amplitude was assigned by the location of the target bar and varied from trial to trial. Participants were instructed to quickly reach the target, maintain force on the target while it remained green, and then quickly decrease force when the target turned red. We employed

three data filtering techniques to address tremor. First, data were filtered with a cutoff frequency of 15 Hz as per previous work from our group (Spraker et al., 2009, Spraker et al., 2010). In a separate analysis, data were filtered with a low pass filter with cutoff frequency of 3 Hz to remove the tremor component of force output. In the final analysis, we used a bandpass filter with a passband frequency of 3-8 Hz to isolate the tremor component of the force output. Standard deviation of force was calculated for each set of filtered data. Patients with ET were characterized by a higher standard deviation of force output relative to controls in all filtered force datasets. The voxelwise analysis revealed 19 regions of interest (ROIs) showing significant differences between ET patients and healthy controls. Percent signal change was extracted from each ROI and correlated with the standard deviation of force output from the low pass (0-3 Hz) and bandpass (3-8 Hz) filtered datasets. The results of this analysis reveal distinct ROIs in the cerebellum and the cortex that correlate with tremulous (3-8 Hz) and slow (0-3 Hz) oscillations in force. In particular, the results revealed a tremor network wherein brain activity scaled to tremulous (3-8 Hz) oscillations in force. Regions in the tremor network included Crus I and II of the cerebellum, supplementary motor area, inferior parietal cortex, and dorsolateral prefrontal cortex. In addition, the results revealed a sensorimotor control network wherein brain activity scaled to slow (0 - 3 Hz) oscillations in force. Regions in the sensorimotor control network included lobules IV, V, and VI of the cerebellum. The findings suggest that increased 3-8 Hz and 0-3 Hz oscillations in grip force in are correlated with distinct networks in the cerebellum and cortex.

## **1-C-17 Kinematic and EMG characteristics during reach and posture tasks in parkinsonian patients**

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Parkinsonian Patients display an involuntary tremor in the hand and arm, and an alternating burst pattern of EMGs in the flexor and extensor muscles. These pathological behaviors have been characterized in rest state of the arm and hand clinically. The ability of tremor-dominated Parkinsonian patients to maintain hand posture and to perform arm reach movement has not been investigated in task-oriented tests. We developed a new experiment apparatus to facilitate the measurement of the kinematic and EMG signals of the hand and arm of the patients in the horizontal plane during postural and reaching tasks. The forearm of the patient was supported with a fiberglass cast brace, which has a ball-bearing base embedded with five plastic balls. The plastic balls move on a plastic plate surface treated with lubricant to reduce friction. This apparatus is used in conjunction with the MotionMonitor II system to capture the motion of the arm. With this device, the subjects can perform planar arm postural and movement tasks with little damping. Testing results with normal subjects indicate that the weight of the cast and the friction of ball bearings produced insignificant effects on the oscillation frequency of the arm. The kinematic and EMG signals of planar posture and point-to-point movements were recorded in five normal subjects and three patients with Parkinson's disorder (PD). The average frequency of EMG burst and tremor was about 4.5 Hz, which agreed with that of rest tremor. In posture tasks, the amplitude of tremor was found to be dependent on hand location in the workspace. A smaller tremor was observed in the frontal area than in the lateral areas of workspace. The tremor was amplified when the shoulder and elbow joints were in more flexed positions. This is consistent with the biomechanical property of the two-joint arm. In point-to-point movement tasks, it was observed that PD patients were able to perform the reach movements specified with a much slower speed than that of normal subjects. The tremor in PD patients was suppressed before making the reaching movement, and resumed after reaching to the target posture. It appears that posture

and movement are controlled by different modules of the motor system. In PD patients, the posture module appears to be relatively intact, while the movement module is imposed with involuntary tremor signals that can be suppressed by volitional motor action.

## **1-C-18 Changes in motor module organization affect biomechanical output during post-stroke hemiparetic walking**

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Recent studies have suggested that the complex muscle activity during walking may be controlled using a neural control strategy organized around the co-excitation of multiple muscles in groups called muscle synergies or motor modules. In healthy walking, we have shown that motor produce specific task-level biomechanical functions (e.g., body support, forward propulsion, leg swing, and mediolateral balance control; Neptune et al., 2009, Allen and Neptune 2012) and synergistically work together to produce well-coordinated walking patterns. In post-stroke hemiparetic subjects, the execution of these biomechanical functions is often impaired, which adversely affects walking performance. Furthermore, post-stroke subjects often exhibit a reduced number of modules in which at least one module appears to be a merging of two or more healthy modules (Clark et al., 2010), suggesting an inability to independently activate appropriate modules. However, the relationship between merged modules and execution of task-level biomechanical functions post-stroke has not been identified. In this study, we used forward dynamics simulations to investigate whether the altered execution of task-level biomechanical functions post-stroke were due to merged modules. Specifically, we analyzed two common groups of modular organization in which two different healthy modules were merged. We generated forward dynamics simulations of a three-dimensional musculoskeletal model driven by motor modules found from collected experimental electromyography that replicated the corresponding experimental post-stroke walking kinematics and ground reaction forces. We hypothesized that the merging of motor modules would result in impaired biomechanical functions and that the specific impairments would differ between the two groups depending on which modules were merged. When the early stance extensor module (hip abductors and knee extensors) and late stance ankle plantarflexor module were merged post-stroke such that both were active throughout the entire stance phase, forward propulsion (normally generated by the plantarflexor module in late stance) and the energy delivered to the paretic leg in late stance (important for initiating leg swing and also normally generated by the plantarflexor module) were reduced. On the other hand, when the early stance extensor module was merged with the hamstrings module (active during swing into early stance), such that the muscles in both modules were active during swing and into the middle of stance, the power absorbed from the paretic leg in late swing (important for decelerating the leg prior to heel-strike and normally executed by the hamstrings module) and body support in early stance (normally generated by the early stance extensor module) were reduced. These results demonstrate that the lack of independent drive to modules reduces the ability to successfully and independently generate biomechanical functions needed during walking and that the biomechanical functions affected depend on which healthy modules are merged. Understanding these functional relationships between modular neural control strategies and biomechanical function could provide evidence-based rationale for neurorehabilitation programs that target the deficits associated with specific altered modular organizations to improve walking performance.

### **1-C-19 Non-speech movements in developmental stuttering: what do they tell us?**

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Stuttering is prevalent in about 5% of the population, with approximately 70-80% recovering, and leaving about 1% of adults with persistent developmental stuttering. It shows characteristics of both a sensory and motor disorder, with speech-motor problems being the most obvious. Studies on non-speech motor capacities in individuals who stutter are scarce, and have usually been done in adults, but the few that exist suggest that motor problems are not limited to speech, but possibly affect other motor functions such as motor adaptation, or sensorimotor integration as well, in subtle ways. The goal of our study was to investigate kinesthetic-motor integration and visuomotor adaptation in children with developmental stuttering. Four children who stutter (CWS, Stuttering Severity Index between 17-23 [mild to moderate]; mean age: 10.1 yrs) and four gender- and age-matched children who do not stutter (CWNS, mean age: 9.5 yrs) performed a center-out task, moving a joystick-controlled cursor on a monitor positioned horizontally above the joystick from a home position to peripheral targets (distance: 8.5cm); vision of the arm and the joystick was occluded. Participants performed a visual baseline condition drawing a line with the cursor from the starting position to a target at either 25°, 90°, or 155°, and a kinesthetic baseline condition, moving the joystick in the direction of either a 45° or 135° target on the screen without visual feedback of the movement path. They were then exposed to a 54° visual feedback rotation of the movement path, inducing visuomotor adaptation over 126 trials. Finally, the kinesthetic condition was re-introduced post-exposure in order to assess de-adaptation, solely based on kinesthetic feedback from the moving arm. Initial directional error (IDE), defined as directional deviation of the movement path from a vector between home and target at peak velocity, as well as root mean squared error (RMSE) as an indicator for movement straightness were used as performance measures. Results show that CWS perform similarly to CWNS during baselines and the visuo-motor adaptation. At the beginning of the post-exposure phase, the CWNS group showed slightly higher aftereffects for the 45° target; de-adaptation over 42 trials was similar for both groups. RMSE tended to be overall higher in CWS than in CMNS. Further, in the kinesthetic-motor condition post-exposure, the CWS group showed substantial overshooting of the target ipsilaterally to the moving hand. These preliminary results suggest that a) visuo-motor adaptation appears to be based on an efficient forward model, b) reaching movements predominantly based on kinesthetic-motor integration are more variable, and the compromised hand localization in 'depth' likely reflects lateralized deficits in kinesthetic-motor integration in children with developmental stuttering.

### **1-C-20 Measuring cognitive-motor integration in preclinical Alzheimer's disease: A discriminant analysis and investigation of neural correlates**

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The central hypothesis guiding our research is that different types of visuomotor compatibility are processed in separate, but overlapping, parietofrontal networks, and that these separate networks are affected differently in healthy aging versus disease. Generally when reaching for an object in the environment the visual stimulus and its required motor action are in alignment. However, the evolution of the capacity for tool-use in primates has resulted in situations where the correspondence between vision and action is not direct. A common example is the use of a computer mouse to move a cursor on a monitor, which involves a decoupling between the spatial location of

the visual target and the spatial location of the movement goal. Such learned sensory- and cognitive-motor transformations underlie much of our everyday activities (including driving), yet the basic cortical mechanisms responsible for these behaviours remain unknown. Following damage to the cerebral cortex (e.g. neurodegeneration), complex visuomotor transformations may become impaired, and, in turn, the pattern of impairment may provide insight into the underlying neural mechanisms involved in this behaviour. The objectives of our current research are 1) to characterize how the ability to integrate cognition into action is disrupted by Alzheimer's disease (AD) in its early stages and 2) to examine the neural correlates of impaired cognitive-motor integration in preclinical AD. We propose that measuring visuomotor integration under conditions that place demands on visual-spatial and cognitive-motor processing may provide an effective behavioural means for the early detection of underlying Alzheimer's-type neuropathology. To this end, we have tested participants over the age of 55, both with and without AD risk-factors (i.e. family history and/or mild cognitive impairment - MCI) on four randomly administered visuomotor transformation tasks presented on an Acer Iconia dual-touchscreen tablet: One standard task where the spatial location of the viewed target and the required movement are the same, and three nonstandard tasks where the location of the viewed target is dissociated from the required hand movement. Comparisons between at-risk and healthy control groups revealed significantly larger endpoint errors, variability and corrective path lengths in the at-risk group, as well as more direction reversal errors in MCI participants. A discriminant analysis using the five measures that showed significant differences between groups resulted in an overall classification accuracy of 90.2% (sensitivity: 77.8%, specificity: 97%). We suggest that the impairments observed in at-risk participants may reflect early neuropathology disrupting the intricate reciprocal communication between parietal and frontal brain areas required to successfully prepare and update complex reaching behaviours, and thus may serve as a functional biomarker for the underlying disease. In order to test this hypothesis, we are currently examining the underlying neural anatomy and connectivity in relation to AD risk and cognitive-motor integration performance in these participants. To date, four at-risk participants and four age-matched controls have undergone anatomical, diffusion weighted, and resting-state functional connectivity scans. Preliminary analysis of this brain imaging data will also be presented.

### **1-C-21 How is driving ability in patients with Parkinson's disease (PD) affected by subthalamic nucleus deep brain stimulation (DBS)?**

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Introduction. Patients with Parkinson's disease (PD) often drive a car after deep brain stimulation (DBS), but influence of DBS on driving ability is unknown. We investigated driving simulator performance of PD patients with DBS (PD-DBS) compared to PD patients without DBS (PD-CON) and examined the differential effect of stimulation and L-dopa in the PD-DBS patients. Patients and Methods. Driving performance of 23 PD-DBS patients was compared with 21 matched PD-CON patients in "best-on" condition. Then within the PD-DBS patients, three test-runs with 3 different conditions (cond.) were done (basic medication was maintained in each condition): cond.1: "on"-stimulation; cond.2: "off"-stimulation; cond.3: "off"-stimulation after L-dopa intake. UPDRS III (motor performance) was controlled to be comparable in cond.1 and 3. Differences in several aspects of driving times and failures between conditions were calculated by mixed models analysis. Correlation analyses were done between driving parameters and UPDRS III, gender, age, cognition, disease duration/severity and driving experience. Results. PD-DBS patients

had higher disease severity (H&Y  $3.0 \pm 0.8$  vs.  $1.9 \pm 0.5$ ) and longer disease duration ( $14.0 \pm 5.1$  vs.  $6.0 \pm 5.0$  years) than PD-CON patients. They drove by trend slower but made significantly less driving failures (rate  $2.7 \pm 1.4$  vs.  $6.5 \pm 4.7$ , total amount  $10.7 \pm 5.1$  vs.  $18.0 \pm 8.5$ , light failures  $3.8 \pm 1.7$  vs.  $11.4 \pm 5.0$ ) than PD-CON patients. In PD-DBS patients, age but not disease duration or severity showed a negative influence on driving performance with increase of failure amount and sum-score, i.e. failure quality and quantity ( $r = 0.44$  and  $0.50$ ). Experienced drivers drove faster ( $231.6$ s vs.  $299.4$ s) but comparably inaccurate. UPDRS III score in cond.1 ( $15.4 \pm 9.0$ ) and 3 ( $15.6 \pm 4.9$ ) were almost identically and lower than in cond.2 ( $24.5 \pm 6.6$ ). Comparing effects of stimulation and L-dopa on performance, total driving time as well as light failures, failure rate, amount and sum-score were lower in cond.1 than in cond.2. Values for cond.3 were in-between cond.1 and 2 without statistical differences. No significant correlation between differences in UPDRS III and driving parameters in the different conditions was seen. Discussion. Although longer and more severely diseased, PD-DBS patients drove slower but made less driving failures than PD-CON patients. In PD-DBS patients' driving performance with stimulation "on" was significantly better than with "off", indicating a superior performance with stimulation than with L-dopa that was not related to the comparable motor performance: probably it was related to a higher level driving-related non-motor effect of stimulation. Conclusion. DBS in PD patients does not have negative but maybe a favourable influence on driving performance. Stimulation effect on driving ability is comparable if not superior to L-dopa.

## 1-C-22 SCI-induced spasticity

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Two primary clinical deficits associated with Spinal Cord Injury (SCI) are spasticity and impaired voluntary control of movement. Spasticity occurs secondary to injury, can directly and indirectly change the mechanical properties of the neuromuscular system, and can lead to several forms of motor and/or sensory impairment. Many gait impairment factors are associated with lower extremity spasticity, which can negatively affect walking capacity. Recently, the LOKOMAT, a driven gait orthosis, was developed to improve locomotion. The system consists of a motorized exoskeleton, synchronized with a treadmill, to provide swing and stance assistance to a patient. Although it has been used for a number of years, its potential therapeutic effects on mitigating neuromuscular abnormalities associated with spasticity has yet to be investigated. The objective of this study was to characterize the effects of LOKOMAT training on neuromuscular abnormality associated with spasticity in incomplete SCI patients. LOKOMAT training was performed 3 days/week for 4 weeks, with up to 45 minutes of training per session. Subjects were evaluated prior to and after 1, 2, and 4 weeks of training, and the effects of training on neuromuscular properties were quantified by applying small-amplitude Pseudorandom Binary Sequence perturbations to the ankle joint at various positions over its range of motion (ROM). An advanced system identification technique was used to characterize intrinsic (muscular) and reflex stiffness at each ankle position. Abnormal modulation of intrinsic and reflex stiffness with ankle position was quantified by fitting an exponential model to the stiffness-angle curve. Three characteristic parameters were calculated: slope and intercept of the stiffness-angle curve, and maximum stiffness over the ROM. Since the training did not have a uniform impact across patients, "growth mixture" modeling and random coefficient regression were used instead of group-averaging techniques to quantify the LOKOMAT effects on neuromuscular properties. This approach identified different recovery classes for the

parameters. All classes showed a significant decrease in intrinsic and reflex stiffness (which abnormally increases after SCI) over 4 weeks of training. For intrinsic stiffness, two distinct classes were identified: Class 1 subjects had higher intrinsic stiffness parameters prior to training and showed a higher reduction rate than Class 2 subjects, which initially had lower intrinsic stiffness parameters. For the reflex stiffness parameters, three classes of recovery were identified. Consistently, Class 1 subjects started with highest reflex stiffness and decreased continuously and at a higher rate compared to other classes. Class 3 subjects started with a relatively low reflex stiffness and decreased at a lower rate, with most changes occurring over 1 week. Class 2 subjects started between the two classes and decreased at a moderate rate, mostly over the first two weeks. These results demonstrate that LOKOMAT training is effective at reducing reflex and intrinsic stiffness (which abnormally increase in SCI) and improving the abnormal modulation of neuromuscular properties associated with spasticity over the ankle ROM. The clinical implication is that patients with higher neuromuscular abnormalities prior to training can benefit more from training, and furthermore can see benefits over a longer training period. Supported by NIH-NICHD R01 and Neilsen Foundation.

## 1-C-23 Exploring the feasibility of a post-stroke neuroprosthesis: Can FES produce useful reach and hand opening during limited voluntary effort and can assistive forces be controlled using residual movements?

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Background Moderate or severe hemiparesis after stroke makes bimanual tasks difficult, if not impossible. One contributor to the impairment is involuntary co-activation in response to voluntary effort. An example is hand and elbow flexor activation during shoulder abduction effort. Functional Electrical Stimulation (FES) in a neuroprosthesis for hand opening has been attempted with limited success, in part due to involuntary finger flexion, overpowering the stimulation for hand opening, and closing the hand during voluntary reach. Helping-Hand Approach Our approach is to produce reach and hand opening through a combination of voluntary effort and FES by using limited effort as a command signal for stimulation and augmenting movement through stimulation. This could limit the expression of co-activation patterns, allowing combined effort and FES to produce the desired movement. Experimental Validation We designed two experiments to evaluate concept feasibility. The first determines if combined FES and limited voluntary effort for reach and hand opening produces useful movements poststroke. The second evaluates how well able bodied and stroke patients can control assistive forces, like those from an FES system. For the first experiment, stroke patients reached to a target and attempted to open their hand using different combinations of voluntary effort and FES. We measured the distance from the hand to the target and the amount of hand opening achieved. We found that reduced effort augmented with FES allows for greater stimulated hand opening and that FES can produce greater reach while preserving hand opening. During the second experiment, participants performed a reaching task with different types of assistance. For the assistance, a robot applied forces to the arm. The forces were controlled either by the participants' shoulder and arm electromyogram (EMG) signals or independently of effort. The EMG signals were recorded during an isometric force task and then used to train a controller that estimated voluntary force. During the task, participants reached to a target and then held the position. Outcome measures were the EMG signals generated while holding the target position and quality of the reach and hold (to measure controllability). Preliminary results for one stroke and one able bodied participant indicate that participants can

control the assistive forces well. EMG is reduced with the assistive forces, and movements to the target and during the hold are stable. **Conclusions and Implications** Reducing effort reduces the deleterious involuntary muscle co-activations. Even during partial effort for reach, FES applied to the hand produced a functional level of hand opening. This implies that some effort could be exerted as a command signal for the FES system without preventing useful movement. Preliminary results also indicate that assistive forces coupled with voluntary effort can be used to produce useful reaching movements. Considering that FES can increase force at low levels of voluntary effort, low levels of effort used as a command signal could control the supplemental forces from an FES system. Although participants had limited time to practice reaching with robot assistance, they would likely improve their control with more practice. Having a system that enables greater use of the arm and hand during activities of daily living could facilitate additional motor recovery enabling even greater use of the affected limb.

### **1-C-24 Tremor suppression by rhythmic transcranial current stimulation**

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We posit that transcranial alternating current stimulation (TACS) can suppress the amplitude of peripheral resting tremor in Parkinson's disease by phase cancelling the cortical rhythms associated with tremor expression. Tremor can dominate Parkinson's disease and yet responds less well to dopaminergic medications than other cardinal symptoms of this condition. Deep brain stimulation can provide striking tremor relief, but the introduction of stimulating electrodes deep in to the substance of the brain carries significant risks, including those of haemorrhage. Here, we pioneer an alternative approach in which we non-invasively apply TACS over the motor cortex to induce phase cancellation of the resting tremor rhythm. We first identify the timing of cortical oscillations responsible for rest tremor in the periphery by delivering tremor-frequency stimulation over motor cortex but do not couple this stimulation to the on-going tremor - instead, the rhythms simply 'drift' in and out of phase alignment with one another. Slow alternating periods of phase cancellation and reinforcement result, informing on the phase alignments that induce the greatest change in tremor amplitude. Next, we deliver stimulation at these specified phase alignments to demonstrate controlled suppression of the on-going tremor. Initial results using this technique achieved a 30-50 % average reduction in resting tremor amplitude, with some evidence that sustained stimulation may invoke adaptive mechanisms. Stimulation also induced partial entrainment and deformation of the tremor rhythm that led to a shift in frequency of around 0.5 Hz. Additionally, tremor syndromes are often associated with cortical activity at double the tremor frequency, with recent evidence suggesting that the basic and first harmonic rhythms localise to distinct cortical sources and subserve different functional roles. We therefore tested whether stimulation at the first harmonic rhythm might afford greater tremor relief. Stimulation over motor cortex at the first harmonic rhythm proved less effective (by 56 %) at modulating tremor amplitude than stimulation at the basic tremor-frequency. These results support the notion that TACS exerts a modulatory but non-dominant influence that is phase-sensitive. Furthermore, phase-cancelling cortical stimulation can attenuate resting tremor in Parkinson's disease, demonstrating the potential of TACS in the treatment of certain oscillopathies.

### **1-C-25 Absence of postural muscle synergies for balance following spinal cord transection in cats**

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Little is known about how neural mechanisms for muscle coordination are affected in motor impairment and recovery following spinal cord injury. Although cats with complete spinal cord transection can be trained to stand and step with full weight support, directionally-appropriate long-latency responses to perturbations are impaired, suggesting that these behaviors are mediated by distinct neural mechanisms. However, it remains unclear whether the long-latency responses to perturbations reflect an attenuated postural response using the appropriate muscular coordination patterns for balance observed in intact animals, or are due to fundamentally different neural mechanisms such as increased muscular co-contraction, or short-latency stretch responses. Our recent work has identified muscle synergies as fundamental building blocks of motor control, defined as spatial patterns of muscle co-activation used to achieve a task-level goal. In intact cats, muscle synergies can explain complex postural responses to multidirectional perturbations, and functionally correspond to producing forces at the ground to maintain balance. Here we investigated the changes in muscle synergies underlying reactive balance before and after complete spinal cord transection. We hypothesized that the modular organization of muscle activity for balance control is disrupted by spinal cord transection. We analyzed previously collected postural responses to multidirectional support-surface translation perturbations before and after spinal cord transection at the T6 level (Macpherson and Fung 1999). Four cats were trained to stand quietly on a force platform, and then implanted with chronic indwelling EMG electrodes. Muscle activity was recorded from 8-11 muscles of the left hindlimb in each cat during translations in 16 directions, and muscle synergies were extracted from postural muscle activity before and after spinalization using non-negative matrix factorization. In intact animals, 3 muscle synergies were required to account for >90% of the overall variability and >75% of the variability (VAF) across muscles and conditions. Muscle synergies had contributions from all muscles recorded and were directionally tuned in the response period. Muscle synergy number was reduced post-spinalization in 3 animals, and increased in 1 animal. However, muscle synergy structure was altered post-spinalization in all animals and directional tuning of muscle synergies was largely absent. Muscle synergies extracted post-spinalization could not reconstruct the muscle activity pre-spinalization, and vice versa. Furthermore, muscle synergy recruitment was correlated to subsequent force production in the intact but not spinalized condition. Our results demonstrate that the modular structure of muscle activity in sensorimotor feedback responses for balance control is severely disrupted post-spinalization, suggesting that the muscle synergies for balance control are not accessible by spinal circuits alone. Moreover, since spinal cats can stand independently, these results demonstrate that spinal mechanisms underlying weight support are distinct from brainstem mechanisms underlying directional balance control. The muscle synergy framework may be a useful measure to compare the complexity of motor patterns, which could be used to identify specific deficits in motor pattern generation to guide rehabilitation.

## 1-C-26 Tremor control using low frequency deep brain stimulation

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Deep Brain Stimulation (DBS) of the ventral intermediate (VIM) thalamic nucleus is a successful surgical therapy for the management of severe essential tremor (ET). State of the art DBS utilizes continuous high frequency stimulation of a target region for the management of drug resistant movement disorder symptoms. Closed loop DBS, where a disease biomarker is used in order to control when stimulation is delivered, may improve DBS in the future. In this study, we investigate whether it is possible to interact with and control postural tremor observed in patients with ET. To this end, we applied monopolar unilateral stimulation to the thalamus contra-lateral to the most affected limb at the postural tremor frequency and recorded tremor using a tri-axial accelerometer. We observe that VIM stimulation at the postural tremor frequency entrains and regulates tremor. In addition to temporal entrainment, when the stimulation pulse is delivered at particular phases of the tremor cycle, tremor amplitude can be suppressed or amplified. In some patients, tremor suppression and amplification could reach up to 50 % with respect to the average peripheral tremor amplitude. The degree of entrainment and regularization of tremor is directly proportional to the level of tremor suppression seen with chronic therapeutic high frequency stimulation. Our results suggest that recordings of peripheral tremor can be used to determine the optimum phase for brain stimulation, while stimulation at tremor frequency can also be used to regularise this phase through entrainment. Additionally, the degree of entrainment and regularization achieved with stimulation at tremor frequency may potentially predict DBS efficacy in postural tremor management.

## 1-C-27 Time dependent correlation between muscle synergies patterns and motor impairment in stroke survivors: a preliminary study

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The Central Nervous System (CNS) and the musculoskeletal system cooperate to generate purposeful, well coordinated behaviours. It was suggested that the CNS to improve its control of many degrees of freedom of the musculoskeletal system activates a small number of modules stored in the spinal cord (Bizzi et al. 2008, Roh. et al. 2011). Each module activates a group of muscles as a single unit known as muscle synergy. Therefore, descending motor cortical signals generate movements by combining and activating spinal modules (Cheung et al. 2009). After a brain damage, the CNS modifies its modular organization in order to preserve motor functions. How the CNS remaps this organization still remains elusive. In a previous study (Cheung et al., 2009) was reported that in stroke patients muscle synergies for both the affected and unaffected arms were similar to each other despite differences in motor performance. Cheung et al. 2012 observed that muscle synergies of the impaired arm were characterized by different patterns, including merging and fractionation. In this perspective, our goal is to investigate whether different (time-dependent) physiological processes can be observed after stroke by using muscle synergies analysis. A group of 24 stroke survivors were recruited at San Camillo Hospital (Venice, Italy) with different stroke event onset measured in post-stroke months (PSM). Patients were subdivided in two groups: acute (PSM < 6 months) and chronic (PSM > 6 months). Motor function of each patient was assessed by means of the Fugl-Meyer scale (FM). The activity of 16 upper arm and shoulder muscles were acquired during the execution of seven tasks in a

virtual reality environment. Muscle synergies were extracted from EMG signals using the Nonnegative Matrix Factorization (NMF) algorithm (Lee and Seung, 1999), which models the EMG activities as a linear combination of time-invariant muscle synergies with time-varying activation coefficients. Subsequently, we estimated the synergies merged as described in Cheung et al. 2012, where a module of affected arm could be explained as the linear combination of unaffected synergies. Spearman correlation between FM and mean number of synergies merged was performed in the acute and chronic group separately. The acute and chronic group consisted of 14(mean PSM: 3; mean age  $\pm$  std: 65 $\pm$ 13) and 10(mean PSM 16, mean age  $\pm$  std: 58 $\pm$ 12) patients respectively. We found similar relationships in both groups: the higher number of synergies merged the lower FM score, in line with findings reported by Cheung et al. 2012. However, the relationship was significant only for chronic group (chronic:  $r=-.87$ ,  $p=.001$ ; acute:  $r=-.24$ ,  $p=.414$ ). This finding indicates that the different mechanisms of cortical plasticity involved in the recovery of motor function in acute and chronic stroke (Richards et al., 2008) could be observed through the muscle synergies analysis. The degree of synergies merging seems to be unrelated to the function impairment in the acute phase. Conversely, in the chronic phase, synergies merging has a strong relationship with motor function outcome. These observations suggest that a potential and progressive collapse of the CNS control on muscle modules could be expected in stroke patients depending on two factors: the time since the brain injury and the severity of the lesion. Future analysis will be performed increasing the number of patients to prove consistency of this finding.

## 1-C-28 Responsive deep brain stimulation controlled by beta oscillations is effective for the treatment of Parkinsons disease in humans

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Adaptive neuromodulation for neurological disorders could potentially improve current treatments by increasing efficacy and reducing side effects. Here we demonstrate responsive deep brain stimulation (DBS) in human subjects with Parkinson's disease using a local field potential biomarker (LFP). Patient specific beta oscillations were filtered and monitored in real time and beta power was used to control switching of DBS. This resulted in a 58% reduction in time on stimulation compared to standard high frequency stimulation without on/off switching side effects. Clinical efficacy was assessed through blinded video ratings and compared for off, standard high frequency, closed loop & random stimulation conditions. Motor scores in the closed loop conditions were found to be most improved and were significantly lower than off stimulation (43% reduction, hemibody UPDRS subscores,  $p=0.03$ ). Stimulation was found to suppress beta power in all conditions with a significant reduction found in the closed loop condition compared to off stimulation (16.5%,  $p=0.03$ ). Closed loop deep brain stimulation using LFP biomarkers is technically achievable and efficacious in human subjects with Parkinson's disease with significant reductions in time on stimulation.

## 1-C-29 Discriminating facial expressions of emotion in Parkinson's disease

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Objective: We examined the ability of those with Parkinson's disease (PD) to discriminate facial expressions of emotions in others. We also examined the relationship between the ability to discriminate facial expressions of emotion and disease severity, facial masking, and the

ability to detect non-emotional changes in faces. Background: The ability to perceive facial expressions of emotion in others is central to the regulation of social behavior. There is some evidence that perception of emotion is impaired in Parkinson's disease (PD). The contributors of such a possible impairment remain relatively unclear. Methods: We developed psychophysical measures of (1) the ability to discriminate graded intensities of facial expressions of emotion from neutral expressions and (2) the ability to discriminate emotional expressions of graded intensity. Discrimination of commonly expressed emotions - anger, disgust, happiness, and sadness - was measured in 73 participants (38 PD, 35 age-matched controls) in Study 1 and in 49 participants (25 PD, 24 age-matched controls) in Study 2. We also explored the relationship between the ability to discriminate facial expressions of emotion and facial masking, overall disease severity, and the ability to discriminate non-emotional changes in faces, judging distinctiveness of faces. Results: Results showed first, impaired discrimination of all facial expressions of emotion in those with PD and second, a moderate positive relationship between the ability to discriminate facial expressions of emotion and measures of facial masking, overall disease severity, and the ability to discriminate non-emotional changes in distinctiveness of faces. Conclusions: The results of these studies indicate impairment in PD in the basic perceptual processes that assist more complex emotion recognition processes. These basic perceptual processes were also positively and moderately correlated with motor symptoms of PD and face perceptual processes.

## D – Fundamentals of Motor Control

### 1-D-30 Oscillatory dynamics of response competition in human sensorimotor cortex

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Neurophysiological studies in non-human primates have provided evidence for simultaneous activation of competing responses in the (pre)motor cortex. Human evidence, however, is limited because experimental approaches have often mapped competing responses to different effectors represented in different hemispheres, which restricts the analysis to between-hemisphere comparisons. In addition, for a true demonstration of competition between different active movement plans in the motor cortex, the possibility of simultaneous execution of the alternative responses has to be ruled out. Therefore, in the current MEG study we have used a unimanual Eriksen flanker paradigm with alternative responses assigned to flexion and extension of the right index finger, activating different direction-sensitive neurons within the finger representation area of the left motor cortex. Results showed that for stimuli eliciting response competition (incongruent trials) the pre-response (-275 to -75 ms) motor cortex beta-band (17-27 Hz) power decreased stronger than for stimuli that did not trigger response competition (congruent trials). Furthermore, incongruent trials elicited an additional pre-response (-275 to -175 ms) mid-frontal high-gamma band (65-85 Hz) power increase. Finally, larger effect sizes of these beta and gamma power changes correlated with greater response delay induced by response competition across participants. Our results thus provide evidence supporting co-activation of competing response plans also in the human brain, consistent with evidence from non-human primates.

### 1-D-31 Reticular nucleus of the thalamus differently gates signals coding locomotor movements of proximal and distal parts of the forelimb

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The thalamic reticular nucleus (RE) is a layer of inhibitory GABA-ergic neurons surrounding the superior-lateral surfaces of the thalamus. Anterior division of RE receives inputs from the motor cortex (MC) and the thalamic ventrolateral nucleus (VL), which is one of the major sources of afferent projections to the motor cortex. The functional properties of motor RE are still unexplained. To uncover how motion related signals are processed in this section of the RE, we recorded extracellularly from identified RE neurons in freely behaving cats during sleeping, standing, and walking on the flat surface and on rungs of a horizontal ladder. We recorded from 112 neurons in two cats. During sleep these neurons had specific firing behavior characterized by periods of silence followed by bursts of spikes, which frequency first raised and then declined. These neurons transynaptically responded to electrical stimulation of the VL and MC, but did not respond antidromically to stimulation of the cortex. Among RE neurons were units with distinct receptive fields: nineteen responded to the limb movement in the shoulder, nine responded to flexion or extension of the elbow, and eighteen were sensitive to dorso- or ventroflexion of the wrist. Neurons selectively sensitive to stimulation of different parts of the forelimb tended to be spatially separated within the RE. Neurons with receptive field on the shoulder were located primarily in the superior part of the nucleus, while neurons with receptive field in the wrist were concentrated in the inferior part. We found that neurons in the motor RE generated bursts of spikes not only during sleep. Bursts in these neurons could be seen also in alert cats during walking, primarily at the beginning of an increase in the discharge rate preceded by a long interval of silence during a step cycle. Remarkably, likelihood of bursting firing of RE neurons was related to receptive fields of these cells: the more distal was the receptive field and more inferior was cell location in the nucleus, the higher was the probability of bursts during walking. Differences in firing features of RE neurons might have an important functional consequence. An inhibitory input from regularly firing RE neurons probably only moderately modifies the activity of target VL neurons. This would allow an undisturbed passage of afferent signals from proximal parts of the limb that would contribute to shaping the cortical output controlling gross movements of the limb. In contrast, an inhibitory input from bursting RE neurons can substantially attenuate the activity of VL cells carrying on afferent signals from distal parts of the limb. This attenuation would permit non-thalamic inputs to dominate motor cortical circuits controlling fine movements of the distal parts of the limb. We suggest that the differential gating of ascending thalamo-cortical signals produced by the motor RE serves to secure balanced control of movements of the whole limb, and to facilitate voluntarily controlled accurate movements of the distal limb.

### 1-D-32 Neural signatures of reaching movement inhibition in lateral frontal areas

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Cancelling a pending movement is a hallmark of voluntary behavioural control because it allows to quickly adapt to unattended changes either in the external environment or in our minds. In humans, the ability to withhold manual motor responses seems to

rely on a right-lateralized frontal-basal ganglia-thalamic network, including the pre-supplementary motor area and the inferior frontal gyrus (IFG). These areas should drive subthalamic nuclei to implement movement inhibition via the hyperdirect pathway. The output of this network is likely to influence cortical areas underlying limb movement preparation and initiation, i.e. premotor (PMA) and primary motor (M1) cortices. Electroencephalographic (EEG) studies have shown an enhancement of the N200/P300 complex in the event-related potentials (ERPs) when a planned reaching movement is successfully stopped after the presentation of an infrequent stop-signal. PMA and M1 have been indicated as the neural sources of this ERP complex but, due to the limited spatial resolution of scalp EEG, it is not yet clear which cortical areas contribute to its generation. To uncover the role of lateral frontal cortices, we recorded epicortical ERPs from the surface of the fronto-temporal lobes of five pharmacoresistant epileptic patients performing a reaching version of the countermanding task while undergoing presurgical monitoring. We consistently found a stereotyped ERP complex on a single-trial level when a movement was successfully cancelled. These ERPs were selectively expressed in M1, PMA and Brodmann's area (BA) 9 and their onsets preceded the end of the stop process, suggesting a causal involvement in this executive function. Even the analysis of power spectra demonstrated an involvement of motor regions in suppression. However this analysis revealed also a causal involvement of BA44/45. Those areas gave greater responses in beta frequency band for successful stop than for unsuccessful-stop-trials. Importantly, the onset of these changes preceded the response recorded in the motor areas. All in all these findings support the hypothesis that motor cortices are the final target of the inhibitory command elaborated by the frontal-basal ganglia-thalamic network, to which belongs the IFG.

## 1-D-33 Sex and experience-related difference in bimanual coordination development

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Sex- and experience-related differences in bimanual coordination have been found previously in both skilled performance and in the underlying brain activity patterns (Bryden et al., 2005; Haslinger et al., 2004). Established sex-based differences in neural connectivity (Marion et al., 2003) and the elite-level athlete's extensive experience performing both practiced and novel complex visuomotor skills would seem to account for these behavioural and functional differences. To date there has been limited study of bimanual coordination development, and the interplay between sex, experience, and age in coordination development. Here, we characterize visuomotor skill performance in relation to age, sex, and athletic experience in order to indirectly gain insight into the neural processes that underlie this advanced level of eye-hand coordination. We use a novel bimanual visuomotor task composed of a modified washer-peg board. In our assessment of performance, two age and experience groups were recruited: adolescent (10 to 14 years of age, select versus house league athletes) and young adult (17 to 23 years of age, NHL/NWHL/varsity versus recreational athletes). A one-way ANOVA on bimanual task times revealed significant main effects of both athletic experience and sex ( $P < 0.001$ ). When comparing experience level within the adolescent group, there was no significant difference as a function of experience or sex. Interestingly, there were significant differences found within the young adult group. When looking at sex differences within the young adult group, elite females outperformed males and non-elite females (significantly faster performance,  $P < 0.001$ ). These results show that the effect of skill and sex is not seen until later years developmentally, however at that point there is a strong effect of sex on bimanual coordination. Thus it appears that the sex-related advantage in bimanual coordination takes place only later in development.

## 1-D-34 Agonist/antagonist tendon vibration at the elbow induces proprioceptive bias - but does not elicit noise

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Many goal-directed activities rely on our sense of limb/joint position and movement (i.e. proprioception). Muscle spindles are thought to play a critical role in allowing accurate judgments of joint position and movement, although some contribution from skin and joint receptors also exists. Evidence supporting the role of muscle spindles in proprioception has been provided by several elegant studies that found the firing rate of Ia muscle spindle afferents is increased in a one to one fashion with 80-120 HZ tendon vibration. This stimulation also alters estimates of limb position and movement. Based on these seminal findings, several more recent attempts have been made to use simultaneous vibration of agonist/antagonist muscle pairs as a proxy for eliciting proprioceptive noise about an adjacent joint's position. In the present study, the validity of this approach was assessed using multiple measures of joint position matching accuracy. Healthy young adults were blindfolded and asked to perform a memory-based elbow position matching task while experiencing no vibration or 80Hz vibration applied to the biceps and triceps tendons of the dominant arm. Target positions were established passively and varied from 20-40 deg of the starting elbow joint angle of the participant in the horizontal plane. Initial results show that, despite an increase in total error with vibration, there is no change in matching variability (i.e. variable error), as might be expected with increased proprioceptive noise. Rather, increased errors during the vibration condition were due to a change in matching bias (i.e. constant error) whereby participants consistently undershot the target elbow angle. To what extent these results differ for targets that were matched actively versus passively remains to be determined, but a follow-up test 10 min after vibration showed an equal but opposite bias in matching. This bias was such that participants overshot the target position following vibration of the biceps/triceps tendons. Taken together, these findings call into question the validity of agonist/antagonist tendon vibration paradigms as a means of increasing proprioceptive noise. Rather, it appears that increases in total error with vibration are due to changes in proprioceptive bias through a preferential effect of vibration on the lengthening muscle. The lack of noise induced by vibration may be a result of the joint tested or the nature of the vibration stimulus itself. With respect to the latter, vibration is a periodic stimulus and not stochastic in nature as is true noise. Researchers using this technique should be aware of this limitation and are advised interpret accordingly their results.

## 1-D-35 Unimanual dexterity performance in relation to measures of transcallosal inhibition

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Recent studies have shown that during unimanual motor tasks, aging adults show bilateral recruitment of primary motor cortex (M1), while younger adults show a suppression of the ipsilateral motor cortex. Additional work has indicated that increased bilateral M1 recruitment in older adults may be deleterious when performing some motor tasks. However, higher levels of physical fitness are associated with improved dexterity and fitness may mitigate the loss of both inhibitory and excitatory communication in aging adults. The goal of this study was to assess dexterity and interhemispheric motor communication in physically fit and sedentary middle-age (40-60

years) right handed participants using tests of hand dexterity and transcranial magnetic stimulation (TMS). To behaviorally assess the influence of interhemispheric communication on motor performance, participants also perform the coin rotation dexterity task while maintaining pinch force with the opposite hand (bimanual condition). We correlated these behavioral measures with the ipsilateral silent period using TMS to assess interhemispheric inhibition. Our results show that the middle-aged adults who were physically fit had better dexterity of their right hand (finger tapping and peg-board). When performing the coin rotation task the fit group had no between hand differences, but the sedentary group's left hand performance was inferior to the right hand. We found that better dexterity correlated with ipsilateral silent period duration (greater inhibition) thereby supporting the postulate that fitness improves interhemispheric motor communication.

### **1-D-36 Future movement affects the encoding of motor memory**

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Several studies have shown that contextual cues can reduce the interference observed during learning opposing force fields. Recently we demonstrated the strong contextual effect of immediate prior motion on the encoding of motor memory. Using a similar experimental procedure, here we investigate the contextual effect of future movement. Subjects performed trials in which they made centre-out movements in a randomly selected clockwise or counter-clockwise velocity-dependent curl force field. Movements during this adaptation phase were immediately followed by a contextual phase that determined which of the two fields would be experienced. The contextual phase consisted of either a movement made by the subject, or the corresponding observation of visual movement. When the future contextual phase involved subjects making a physical reaching movement, a reduction in interference during the adaptation phase was found. However, when the contextual phase involved merely observing visual cursor motion, there was no significant reduction in interference. Our results indicate that future active motion, but not visual motion, can engage different representations in motor memory. This distinction between action and observation, not found in our original study on prior motion, may suggest that motor planning plays a role in the formation of motor memories, since future planning is likely to occur with physical movement, but not with the observation of visual motion. Financial support provided by the Wellcome Trust.

### **1-D-37 Visuomotor feedback gains adapt to environmental dynamics**

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Adaption to novel dynamics requires the learning of a new pattern of feedforward motor commands in order to produce the appropriate changes in endpoint forces and limb impedance. Recently we demonstrated the up-regulation of feedback gains early in learning, some of which is maintained after complete learning. However, while steady state feedback gains in a curl field were increased, those in a constant force environment were not. These results, combined with other recent results, suggest that part of the adaption process involves tuning feedback gains to the dynamics of the environment. Here, we test this hypothesis by having subjects adapt to a variety of novel dynamics generated by a robotic manipulandum. To probe the feedback gains, we measured the magnitude of involuntary rapid visuomotor responses to rapid shifts in the visual location of the hand during reaching movements. We examined the modulation of these visuomotor responses in 3 separate experiments. In experiment 1, we examined the change in visuomotor responses to

constant loads ranging from 3 to 13 N. In experiment 2, we examined whether the magnitude of the response depends on the dynamics of the force field. Finally in experiment 3, we examined whether these responses can be tuned when the magnitude of the lateral component of the force field differs between positive and negative velocities. Throughout the experiments, visuomotor feedback responses were measured by applying perturbations of the visual location of their hand during the movement in which the hand was constrained to move in a mechanical channel. We found little change in the visuomotor feedback gains in the constant force environments (demonstrating minimal effect of background activation), but dramatic changes with the type of viscous field. Finally, in experiment 3, there was a selective tuning of the visuomotor responses depending on the lateral dynamics of the force field. Our results demonstrate that the sensorimotor control system regulates the gain of the feedback system as part of the adaptation process to novel dynamics, tuning them to the experienced forces. We argue that this demonstrates that learning results from changes in both the feedforward and feedback motor commands.

### **1-D-38 Two routes to action selection - an fMRI repetition suppression study**

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With so many ways to perform the same actions, how does the brain select which movements to make? Action selection can be guided by rules, e.g. colors of traffic lights indicate whether to stop or go. Action selection can also be guided by planning, including predictions about intended actions, e.g. posture selection for grasping a handle may depend on how comfortably the subsequent action can be solved, such as pushing a front door open (pronated) vs. pulling an oven door down (supinated). Findings from previous studies suggest that plan-based selection predominantly involves the Cerebellum (Cereb.), posterior parietal (PPC), and premotor cortices. Mechanisms involved in rule-based selection are less certain. In addition to regions involved in plan-based selection, available evidence suggests that rule-based selection specifically engages prefrontal regions, including rostrolateral PFC. The current study investigated whether these two routes to action selection involve dissociable or similar neural mechanisms by evaluating both approaches while at the same time controlling for differences in stimuli and motor responses. Participants selected a pronated or supinated hand posture to pantomime the rotation of a manipulandum to a cued orientation. Critically, how movements were selected varied per task. In the Rule task, participants followed a rule to solve the mapping between stimulus and response. In the Plan task, they selected responses allowing completion of the task comfortably, given their range of motion for forearm rotation. Thus, both tasks require identical movements while the method of selection differs. A task contrast would reveal whether similar or different brain areas are recruited for either method. As a complement to the conventional contrast approach, we used a novel fMRI Repetition Suppression (fMRI-RS) paradigm to test whether fMRI-RS effects would differ according to task. Within trials, two successive events of the same task (Rule or Plan) were presented, and stimuli and motor responses were repeated or changed. Reduced activity for repeated vs. changed conditions (fMRI-RS) was predicted for areas underlying action selection, and differential levels of fMRI-RS per task would provide evidence for dissociable neural mechanisms. Both tasks are found to engage a similar set of distributed regions relative to resting baseline, including the Cereb., PPC, Dorsal Precentral Sulcus (DPCS), and PFC. Within this network, greater activity for the Plan vs. Rule task is evident within left Cereb. and bilaterally within PPC, with greater extent of the PPC activity in the left hemisphere. Additionally, bilateral PPC, DPCS, Cingulate (SMA), and Cereb. show fMRI-RS for the Plan task exclusively. The results suggest that both methods of

action selection recruit similar brain areas, including activations within PFC, Cereb., PPC and DPCS. Differences in neural mechanisms arise with respect to unique fMRI-RS for plan-based selection within bilateral PPC, DPCS, SMA, and Cereb. Furthermore, within the common network the task contrast demonstrates that plan-based selection shows stronger recruitment of the left Cereb. and bilateral PPC. However, against expectations for simple rule-based selection, our results indicate no differential engagement of lateral PFC. Altogether, the conventional contrast and fMRI-RS approaches reveal both common and distinct neural mechanisms for rule- vs. plan-based action selection.

## 1-D-39 Motor surround inhibition in human hand

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Surround inhibition (SI) in the motor system has been proposed as a mechanism to enhance motor performance by actively inhibiting corticospinal excitability in the surround muscles which potentially could interfere with the desired movement. However its functional efficiency to suppress muscle activation in the surround muscles has not been described yet. We aimed to quantify hand motor SI in a large cohort of healthy individuals and to investigate its functional relevance to muscle activation during an isolated index finger movement. Motor SI was assessed in a cohort of 60 healthy individuals with application of transcranial magnetic stimulation (TMS) on the primary motor cortex during a motor task which involved a brief index finger flexion. Motor evoked potentials (MEPs) and electromyographic (EMG) activity were recorded from the synergist first dorsal interosseus muscle (FDI) and from the surround abductor digiti minimi muscle (ADM) at the onset of the index finger movement and compared with MEPs and EMG activity recorded at rest. The subjects were instructed to use their index finger to briefly press a small button with a self paced delay after an auditory cue. The duration of the movement was aimed to be 100ms. TMS was triggered when EMG activity in FDI muscle reached the threshold of 100microVolts (onset of movement) and in separate trials it was triggered 5000ms after the onset of the movement when the hand was resting (rest). Peak to peak MEP amplitudes were measured in both muscles. RMS amplitude of the EMG activity was also measured in both muscles during the time window when SI is known to be active (for 100ms after the onset of the movement) and at rest (5000-5100ms after the onset of the movement). SI was expressed as the ratio of MEP amplitude in ADM at the onset of the movement to MEP amplitudes at rest. SI was found to be present in 48 subjects (frequency 80%). Statistical analysis of the group data showed that there was a significant depression of the peak to peak MEP amplitudes in ADM muscle at the onset of the movement when compared to rest,  $p < 0.01$ . In contrast, EMG activity in ADM did not follow the changes in corticospinal excitability but it was modulated in the opposite direction and was found to be significantly increased at the onset of the movement,  $p < 0.01$ . EMG activity in ADM was increased at the onset of the movement compared to rest in 58 subjects (frequency 97%). MEP amplitudes and EMG activity in the FDI muscle were both increased at the onset of the movement relatively to rest. There was no correlation between the reduction of MEP amplitudes and the increase of EMG activity in ADM muscle,  $R^2 = 0.01$ . This discrepancy between the corticospinal excitability and the EMG activity in the ADM muscle indicates that down regulation of corticospinal excitability in the surround muscles during movement does not necessarily reflect suppression of EMG activity and therefore should not be used as a direct measure of finger movement individuation. Our study has significant implications for the interpretation of TMS studies in patients with movement disorders like dystonia and Parkinson's disease where SI has been described to be impaired.

## 1-D-40 Fast corrective responses to perturbations applied during reaching reflect estimated limb state: Evidence for optimal feedback control in the motor system

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The accurate estimation of limb state during movement is accomplished by integrating actual sensory information with the sensory consequences predicted by the forward model (Wolpert et al., Science 1995). According to the optimal feedback control theory of motor coordination, the estimated state of a limb should be used to generate motor commands rather than the actual state. However, there is little experimental evidence to support this notion. Thus, we examined fast corrective responses of the arm evoked by mechanical perturbation applied during two reaching tasks. Fast responses, like long-latency reflex, reflect how the brain transforms sensory feedback signals into motor commands (Pruzynski et al., Nature 2011). In this study, we created novel situations in which the predicted state was altered while the actual physical state remained unchanged, and we used this to assess whether alterations in the predicted state influence rapid responses. Nine participants performed planar reaching movements (10 cm) by moving a handle of manipulandum towards a target (KINARM End-Point Lab, BKIN Technologies, Canada). The visual target position, which was initially located at the straight-ahead position, was gradually shifted clockwise (CW) with each trial (0.5 degrees/trial); the same CW visual rotation was simultaneously applied to the cursor representing the handle position. Participants were unaware of the visual rotation. In this way, only their predicted movement was altered towards the target while their physical movement was unchanged. Fast force response (FFR) was induced to oppose a brief assistive mechanical perturbation (10 N, 50 ms), which was applied to the handle at the position of 2 cm from the starting position. Notably, the perturbation and the required limb response were identical despite rotation of the visual target. If FFR is solely determined by the actual state of the limb, then it should not be influenced by the target shift. However, we found that the FFR induced 110~140 ms after the perturbation, which was earlier than the visual response (Franklin & Wolpert, JNS 2008), changed its direction significantly in CW direction in accordance with the CW target shift. Thus, the FFR reflected the direction of the estimated movement rather than that of the actual physical movement. In the second experiment, 10 participants reached for two targets alternately located either 30 degrees CW or counterclockwise (CCW) from the straight-ahead position. Gradually increasing visual rotation was applied to the cursor in a CW or CCW direction depending on whether it was a CW or CCW target. This created a situation in which participants performed identical physical movements in the straight-ahead direction while the planned movements were towards each target (Hirashima & Nozaki, Curr Biol 2012). The FFR direction was significantly different between movements towards two visual targets, indicating two different motor responses were automatically generated by the physically identical perturbations depending on the estimated states of the limb. In conclusion, fast response to perturbation was not solely determined by the actual state of the limb. Rather, it reflected the estimated state of the limb, whereby it could be flexibly modulated according to the estimated states. Assuming that the estimated state was used to generate feedback motor commands, these results are consistent with the optimal feedback control theory.

## **1-D-41 A novel robotized TMS system enabling the stimulation of multiple adjacent points of the human brain**

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Transcranial magnetic stimulation (TMS) has been widely used as a noninvasive method to stimulate the brain. The placement of 2 TMS coils at distinct positions, such as at the premotor and motor cortices (Mochizuki et al., J Physiol 2004) or bilateral motor cortices (Ferber et al., J Physiol 1992), enables us to investigate how two regions of cortices interact with each other. However, because of the relatively large size and peculiar shape of the coil, the configurations in which 2 coils can be placed together are limited, thereby resulting in an inability of the conventional TMS technique to stimulate 2 very adjacent points. Here, we introduce a novel method to overcome this problem. With this method, a TMS coil is moved quickly from one place to another with an industrial robot arm. A similar system with an industrial robot arm is already commercially available (SmartMove; Advanced Neuro Technology, Netherlands), but this system mainly aims to automatically and reliably place the coil at a certain point by adjusting the coil position relative to a participant's head with a feedback control. A figure-of-eight coil was attached to the endpoint of an industrial robot arm (RV-2SD; Mitsubishi Electric Corporation, Japan). The robot arm was controlled by LabView RT software that was operated on a PXIe-1071 platform (National Instruments Corporation, USA). First, we evaluated the movement time and movement accuracy by moving the coil from the vertex to another position in 5 directions (forward, left-forward, leftward, left-backward, and backward; movement distance = 10, 20, 30, 40, and 50 mm) with the maximal speed over a mannequin head. The surface of the coil was set to contact the mannequin head with an appropriate orientation at the two points. The movement of the coil was recorded with a high-speed camera with a sampling frequency of 1 kHz and a spatial resolution of 0.25 mm (VW-9000, Keyence Corporation, Japan). The average time necessary to move the coil each movement distance was  $129.6 \pm 12.3$ ,  $180.1 \pm 10.5$ ,  $256.0 \pm 14.6$ ,  $307.3 \pm 15.9$ , and  $384.0 \pm 13.0$  ms for 10, 20, 30, 40, and 50 mm, respectively. Variations in the position within each movement condition were less than 1 mm for all movements. Thus, this system enable us to accurately stimulate 2 points that are separated by 2 cm with an interstimulus interval of up to 200 ms. We used this system to investigate how the preceding TMS at one point affected the motor-evoked potential (MEP) evoked at another adjacent point. We searched the hotspots of the first dorsal interosseous muscle (FDI) and the biceps brachii muscle (BB) with a stimulator (Magstim 200; The Magstim Company Limited, UK). Typically, these two hotspots were separated by less than 20 mm. With 2 Magstim stimulators, we applied 2 pulses to the TMS coil with interstimulus intervals of 300, 500, and 1,000 ms. Stimulus intensity was set to 120% of the resting motor threshold of each muscle. We observed the suppression of the MEP of the FDI when the preceding TMS was applied to the BB hotspot 300 ms before. However, an interstimulus interval longer than 300 ms did not inhibit the MEP of the FDI. These preliminary results likely indicated the presence of lateral inhibition within the motor cortex. Our novel robotized TMS system is a promising tool for exploring the interactions of adjacent brain regions and how their connections change when performing various motor tasks.

## **1-D-42 Bihemispheric tDCS over motor cortex does not influence free choice**

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An interesting question in neuromotor behavior is how much control humans exercise over their actions. Previous research has shown that differences in the pattern of activation in each visual hemisphere prior to the presentation of free choice determined which side was picked for responding (Bengson et al., 2012). Similarly, neural accumulator and efficiency models suggest that in order for a response to be initiated, a certain activation threshold for a response needs to be achieved. As such, it may be suggested that the motor cortex hemisphere with a higher level of activation would be chosen since that threshold would be reached fastest and easiest. Of interest in the current study was whether modulating motor cortex excitability would affect the response side chosen during a free choice reaction time (RT) task. One technique that has been shown to modulate motor activation levels is transcranial direct current stimulation (tDCS), a form of neural stimulation that can increase (anodal) or decrease (cathodal) the excitability of underlying neural tissue. It was hypothesized that by up-regulating the excitability of one motor cortex while concurrently down-regulating the other motor cortex participants would be more likely to "choose" the response side corresponding to that of the up-regulated hemisphere. Participants performed a choice RT task in which they were instructed to make either a 10° right or left wrist flexion movement to target upon presentation of visual imperative stimuli: the illumination of a box on the right side of a computer screen corresponded to a right response and a box on the left corresponded to a left response. This forced choice paradigm was presented in 80% of trials whereas in 20% of trials illumination of the central fixation circle corresponded to a free choice (i.e., participants were instructed to pick either right or left, but not always the same). Participants performed a pre-tDCS test phase of 100 trials, followed by a post-tDCS phase of 100 trials. Between phases, bihemispheric tDCS was applied over both the right and left motor representations for wrist flexors (from Cz: 4.7 cm lateral and 1.1 cm anterior). Constant current stimulation (1mA/min) was delivered bilaterally via 8.1 cm<sup>2</sup> electrodes for 10 mins, followed by an 8 minute rest period. Two double blind sessions (anode right, anode left) separated by at least 48 hours were completed by each participant. Post-tDCS results showed no change in the proportion of right or left hand responses on free choice trials for either tDCS polarity compared to pre-test (all  $p$ 's > .05). Interestingly, tDCS led to faster reaction times for both right and left responses ( $p$ 's < .05) irrespective of tDCS polarity (in the forced choice condition). Together, these results suggest that the tDCS montage used was unsuccessful in increasing the activation in one hemisphere and decreasing activation in the other. In accordance with recent evidence from finite element modelling (Datta et al., 2012), our results suggest that the electrode montage resulted in diffuse current flow with the peak electric field occurring midway between the two electrodes rather than under each electrode. Consequently, this resultant current may have led to increased activation of more central structures such as thalamus or SMA, resulting in faster RTs but no change in the proportion of lateralized free choice responses.

## 1-D-43 The identification of a rapidly-decaying, high-precision proprioceptive sensory memory & its effects on motor adaptation

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Although working memory is generally recognized as the short term store that dominates cognitive information processing, an even more transient form of memory has been identified in both the visual and auditory systems. These vivid “sensory memories” are modality specific, can have a resolution that far exceeds that of working memory, and are extremely short-lived: visual sensory memory has a duration of only a few hundred milliseconds while auditory sensory memory has generally been reported to last a few seconds (Sperling 1960, Cowan 1998). Here, we demonstrate the existence of a high-precision, rapidly decaying proprioceptive sensory memory. We find that this memory can double the endpoint precision when reaching to a remembered location, its presence is associated with altered visuomotor adaptation, and it decays with a time constant of just 1-2 seconds. To investigate short-term proprioceptive memory, we designed a task to measure the reliability of proprioceptive information after various delays ranging from 0 to 25 seconds. We found that when subjects returned without visual feedback to a remembered location, there was a 46% reduction in endpoint variability when returning after 2s in contrast to a reduction of only 3% after 6s. This striking increase in the precision of the proprioceptive sense at very short time delays is very similar to short term performance increases associated with visual and auditory sensory memories. This finding points to a rapidly-decaying proprioceptive sensory memory that can be used to improve the reliability of movements to recently visited locations by nearly a factor of two. We investigated how this high precision but transient memory might be used in visuomotor learning. We found that after performing movements to a target with a 30 degree rotational perturbation applied, no-feedback movement sequences approaching the same target from other directions had endpoints biased away from the target toward the proprioceptive memory of the target (30 degrees from the displayed target). Interestingly, this bias toward a proprioceptive memory was much stronger when the remapped location was visited very recently. In fact, this increase was most pronounced at latencies of just 2-4 seconds, suggesting that the improved reliability of proprioceptive information at short latencies effected adaptive changes in motor planning. The parallel increase in proprioceptive precision and endpoint bias toward a remembered hand location may give new insight into the mechanism for Bayesian integration in the motor system. Although a host of recent studies have demonstrated Bayesian-like integration in motor control whereby decreases in the reliability of the prior or increases in sensory likelihood reliability lead to greater sensory weighting, these studies have generally relied on designs in which participants have ample opportunity to observe the relevant changes in reliability. In contrast, the changes in reliability that we demonstrate could not be readily observed since movement endpoints were never shown. Therefore, these results suggest that the motor system has direct access to both the content and reliability of proprioceptive memories. This could only be the case if the reliability of the proprioceptive memory were intrinsically encoded alongside its content as suggested in several intriguing theoretical models of neural encoding (Ma et al. 2006) for which direct experimental evidence is scant.

## 1-D-44 Non-linear filtered electromyograph (EMG) from hand muscle can produce recognizable vowels in real-time

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Children with severe tetraplegic CP have very limited ability to interact with their environment. With only slow and depersonalized touchscreens or typing devices for tetraplegic children to communicate, their rate of communication could significantly improve if meaningful speech could be somehow restored. Toward this end, one critical question is whether speech production relies necessarily on vocal musculature and vocal neural innervations. In particular, since the conduction delay of vocal nerves from central nervous system (cranial IX and X) is much shorter than that of skeletal muscles, the use of myocontrol from limb muscles for speech restoration may not be possible. Here we tested whether non-linear filtered electromyograph (EMG) from healthy hand muscle could achieve a challenging initial goal - producing recognizable vowels in real-time. We had previously developed a non-linear stochastic filtering algorithm to produce clean, low-latency signals of surface EMG. In this experiment the EMG was collected from dominant flexor pollicis brevis of healthy adult to drive a speech synthesizer to create vowel sounds comprising specific formants. Since the perception of a vowel is mostly affected by the lowest two formants (F1 and F2), we used the EMG to directly move F1 and F2 around the 2D frequency space such that all vowels of standard English could be produced. Five vowels (/i/, /a/, /u/, /e/ and /au/) were chosen as candidate targets, which in sequence formed a 2D trajectory in the frequency space. We parameterized the vowel trajectory such that a single normalized EMG signal could traverse all 5 vowels. The quality of the synthesized vowels was examined in two ways. First the sound spectrograms were quantitatively compared with those calculated from real human speech. Second we recorded synthesized vowels in pseudorandom order, and played them back to two naïve adult listeners who were asked to identify each vowel. The fraction identified correctly will be presented. Our results suggest that despite the morphological and neurological difference from vocal muscles, skeletal muscles are potentially capable of producing meaningful speech. The results provide an encouraging first step towards our goal of testing myocontrolled speech synthesis for children and adults with motor disorders.

## 1-D-45 Two distinct patterns of brain activation during motor action selection in older adults

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Older adults often show changes in neural activation during the performance of motor execution tasks compared to younger adults. Dorsal premotor cortex (PMd) has been shown to be an important neural resource during motor action selection (AS) in young adults. However, the role of PMd for AS in older adults has not been reported. Additionally, it is not known how variability in AS performance between individuals relates to PMd activation in older adults. The current study hypothesized that PMd would be an important resource for AS in older adults as shown by a significant correlation between PMd activation and AS performance. In a single data collection session, 16 older, nondisabled adults (65.0±9.0 years; 10F/6M) performed a right or left joystick movement with the dominant, right hand under 2 conditions. In the action selection (AS) condition, participants moved right or left based on a visual cue. The execution only (EO) condition involved simple movement repetition in the same direction on every cue. After a practice period (3 blocks of 36 trials), the two conditions (AS, EO) were performed during

functional MRI (fMRI) in a 3T scanner with MRI compatible joystick. For each run, periods of movement alternated with periods of view only in a block design (2 runs per condition). Response accuracy in the AS condition was 88.05±9.0% across participants during fMRI. Reaction time (RT) for the AS condition ( $0.752 \pm 0.102$  ms) was significantly longer than for the EO condition ( $1.202 \pm 0.143$  ms) ( $p < 0.0001$ ); movement time did differ between conditions. Task performance across both conditions activated a motor network that included left primary motor, PMd, supplementary motor area, and parietal cortices, and right cerebellum. Regression analysis during AS revealed two significant clusters that had a significant positive correlation with RT cost (AS RT-EO RT): left PMd and left dorsal lateral prefrontal cortex (DLPFC) ( $p < 0.001$ ), i.e., individuals with longer RT had greater activation in PMd and DLPFC during AS. Psychophysiological interaction analyses were performed to determine if the connectivity between PMd, DLPFC, and M1 (slope extracted between regions for each condition) varied with task performance (RT cost). The change in connectivity between regions did not significantly correlate with RT cost. However, two subgroups were identified for left PMd-M1 connectivity: one group had an increase in connectivity from the EO to AS condition ( $n = 9$ ) while the other group had a decrease in connectivity ( $n = 7$ ). The group with increased connectivity had significantly greater connectivity during the AS condition ( $p < 0.002$ ), performed the AS task with significantly less RT cost ( $p < 0.05$ ), and were younger ( $p < 0.03$ ) compared to the decreased connectivity group. Overall, these findings suggest two distinct strategies for performance of the AS task in this cohort of older adults. The more successful strategy entailed increasing connectivity between PMd and M1. The less successful strategy did not involve increased connectivity between regions; instead, individuals increased the magnitude of activation of PMd and engaged DLPFC. This difference in strategy may reflect varied levels of task difficulty between individuals or changes related to aging. Future work will investigate whether neural recruitment during AS predicts motor learning in AS-intensive conditions.

### 1-D-46 Seeing what you want to see: a Bayesian account

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**Introduction:** People tend to perceive their own abilities as superior to others. These illusions of superiority are not only common in many aspects of life, but are also linked to good mental health. Other misperceptions, such as visual illusions have been successfully explained by Bayesian models (Kersten et al., 2004). According to these models, the brain generates a percept by combining imperfect sensory information about the external world with expectations of possible sensory events, called priors. Here we ask whether self-performing a task affects the priors people use when perceiving the outcome, using Bayesian models to explain the overestimation of performance. **Methods:** We developed a visuomotor task to examine how subjects integrate priors with sensory information, either when performing goal-directed actions themselves or when observing these actions. Ten right-handed subjects (five female) aged 19-27 (mean:  $24 \pm 2$ ) performed the task, in which a ball traversed the screen horizontally (rightward or leftward motion). Subjects were asked to press a button to stop the ball when it was vertically aligned with a target. Following the button press, the ball vanished, and subjects used a cursor to indicate where the ball was when it had disappeared. In another condition, subjects observed the computer performing the task. Motor demands were equated by performing a reaction time task on when the ball vanished. Eye gaze position was monitored in both conditions to ensure there were no differences in fixation. We fitted Bayesian models to infer the distribution of priors for self-generated and observed actions, and compared them to the actual performance distribution. **Results:** Priors for self-generated

actions were consistently narrower (i.e. smaller SD) relative to both the actual performance distribution ( $t_9 = -6.844$ ,  $p < 0.001$ ) and the priors for observed actions ( $t_9 = -3.356$ ,  $p = 0.008$ ). In contrast, priors for observed actions were similar to performance distribution ( $t_9 = -1.078$ , ns). If the priors for one's own actions underestimate the perception of errors, would subjects with narrow priors show increased performance variability? We found no consistent relation between priors and performance SDs for the 10 subjects that were tested ( $r = 0.38$ ,  $p = 0.28$ ). **Conclusions:** Our results suggest that when performing goal-directed actions, the brain uses priors that represent exaggerated expectations of goal success. Although priors are also used when observing actions, these more closely represent the actual performance (Körding and Wolpert, 2004). Consequently, people underestimate their own errors while more accurately perceiving the errors of observed actions. Our data suggest the self priors do not reduce motor performance, consistent with the notion that high-level perceptual processes can be independent of sensorimotor prediction processes (Flanagan and Beltzner, 2004). Nevertheless, this Bayesian account suggests that goal priors for our own actions may underlie common illusions of superiority, so that when acting we tend to see what we want to see. **References** Kersten D, Mamassian P, Yuille A (2004) Object perception as Bayesian inference. *Annual Review of Psychology* 55:271-304. Körding KP, Wolpert DM (2004) Bayesian integration in sensorimotor learning. *Nature* 427:244-247. Flanagan JR, Beltzner MA (2000) Independence of perceptual and sensorimotor predictions in the size-weight illusion. *Nature Neuroscience* 3:737-41.

### 1-D-47 Ventral premotor area and anterior intraparietal sulcus contributions for updating hand preshaping during perturbations of object shape

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It is known from primate physiology studies that the region in the anterior portion of the intraparietal sulcus (area AIP) and the ventral premotor cortex (area F5) contain neurons whose firing rates are tuned to the features of object shape and to the hand shape used to grasp an object. This work lends to the idea that these regions may contribute to the planning and/or updating of ongoing reach-to-grasp actions. Indeed, human imaging studies have revealed that the human homologs of these regions (parietal area aIPS, and inferior precentral gyrus / Brodmann area 44, which we will refer collectively as PMv, respectively) are recruited during reach-to-grasp actions. Further support, at least in the case of aIPS, has been garnered from transcranial magnetic stimulation (TMS) studies in which TMS-based disruption of neural activity in parietal cortex led to kinematic decrements in performance. However, this work only used a one-dimensional perturbation to study grasp updating (aperture size or aperture orientation) and have neglected to probe the role of PMv. Because aIPS and PMv both encode 3D features of objects and grasp shape, we set out to test the extent to which each region contributes to updating of the entire hand shape, rather than updating a single grasp meter (which presumably can be achieved simply by a scaling solution). To test this, 8 healthy right-handed young adults observed a rectangular target object for 200ms before vision was blocked with liquid crystal glasses. The object was initially oriented such that the bottom edge was either parallel to the table or at a 45-degree angle (square and rhombus orientation, respectively). Following the initial view period, subjects were cued to reach-grasp the object such that the four fingers were either adducted and flexed together (square object) or abducted and less flexed (rhomboid object). At the start of movement, vision was restored again for another 200ms revealing to the subjects that the object orientation either remained unchanged or was perturbed to the other orientation (rhombus-to-square or square-to-rhombus), requiring them to either maintain the planned hand shape, or to update it. Double pulse TMS (50ms apart) was used to

disrupt processing in aIPS and PMv either in the second viewing interval or immediately afterward, to tease apart processes related to updating versus execution. Subjects also performed the task with Sham TMS to the vertex as a control block. Kinematic analyses revealed that scaling of peak excursion of finger abduction and flexion was significantly affected and delayed when TMS was applied to PMv and aIPS at the updating interval, but not at the execution interval. Eleven joint angles submitted to linear discriminant analysis for classifying the hand shape identified a key difference between aIPS and PMv disruption on the evolution of hand shaping. aIPS-TMS led to a delay of hand shaping that eventually recovered to the level of the Sham-TMS condition, without increasing movement time. Conversely, PMv-TMS led to a delay and an entirely different hand shaping pattern that was also associated with ~15% longer movement times. Our findings suggest that PMv and aIPS form unique but complementary nodes required for updating in the cortical reach-to-grasp network. Based on our findings, we speculate that aIPS may be integrating sensory information while PMv may be supplying a model of the grasp shape, which if disrupted must be rebuilt de novo.

## E - Integrative Control of Movement

### 1-E-48 Inter-manual, but not intra-manual reaching tasks induce visual encoding of purely kinesthetic sensory information

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We recently proposed a new sensori-integration model that assumes when controlling reaching movements, the brain concurrently compares the target and hand position in visual and kinesthetic modalities. We further hypothesized that the brain avoids comparisons that require sensory transformations whenever at least one direct comparison is possible. Although this hypothesis was supported by our experimental findings, it is apparently incompatible with the results of other studies in which evidence has been found for a reconstruction of visual representations of movement in tasks where both target and hand positions were sensed kinesthetically and hence where a direct target-hand comparison could have been performed. This apparent contradiction, however, could be ascribed to the fact that, in contrast to our experiments, participants in these previous studies sensed the target with one limb and performed the movement with the other. Our hypothesis is that the reconstruction of visual representation of the tasks observed in these studies was indeed induced by the impossibility of performing a direct kinesthetic target-hand comparison, because the necessity of transferring sensory information from one limb to the other requires sensory transformations, meaning that the kinesthetic comparison is not ?direct?. We set out to test this hypothesis by asking subjects to reproduce with their unseen hand the orientation of kinaesthetically sensed targets in two different conditions. In one condition subjects felt the target orientation with one hand and reproduced it with the other. In the other condition, subjects sensed the target and then reproduced the orientation with the same hand. The importance given by the brain to the visual representation of the considered, purely kinesthetic, task could be quantified thanks to our novel virtual reality experimental setup. The results clearly support our hypothesis. In the intra-manual condition, where a direct comparison between target and hand was possible, subjects did not use a visual representation of the task, whilst in the inter-manual condition, where an inter-limb transformation was necessary, subjects clearly reconstructed a visual representation of this purely kinesthetic task. We show that the observed difference between the two experimental conditions cannot be predicted if the necessity of inter-limb transformation is not taken into account. Moreover, we demonstrated that the complete lack of visual representation of the task in the intra-

manual condition is indeed to be theoretically expected, if the correlation between the direct kinesthetic comparison and the reconstructed visual comparison is considered. In particular, our sensory-integration model shows that there is no advantage to reconstructing a visual target-hand comparison when a kinesthetic direct comparison is possible, because the reconstructed comparison does not increase the information content about the movement. On the other hand, when a direct target-hand comparison is not possible, using a visual representation of the task becomes advantageous, because the correlation between concurrent comparisons is smaller. In conclusion, this work appears to reconcile our sensori-motor integration model with previous studies, by providing both experimental and theoretical proofs.

### 1-E-49 Direct projections from dorsal premotor cortex (F2) to the superior colliculus in macaques

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There is growing evidence that neurons in the deep layers of the superior colliculus (SC) are involved in the initiation and execution of arm movements in monkey and man. It is well known that for controlling gaze the frontal cortex, in particular the frontal eye field (FEF) is functionally connected with the SC. In order to demonstrate similar cortico-subcortical projections also for initiating and executing arm movements we injected the anterograde tracer biotin-dextrane into the representation of the arm in the dorsal premotor area (PMd). More specifically, before tracer injections in one animal we physiologically mapped the region in PMd which projects to the SC by antidromically electrically stimulating regions in the superior colliculus where neurons are active during reach movements. Anterograde labelling of fibers and terminals was discerned in the intermediate and, much stronger, in the deep layers of the lateral SC over the entire anterior-posterior extent of the SC. In addition, fibers and terminals were labelled in the underlying reticular formation, and the pontine nuclei. These results were confirmed by two more injections into PMd without antidromic electrical stimulation. By contrast, a more anterior injection involving the frontal eye field and sparing PMd revealed anterograde transport mainly in the intermediate layers of the medial part of the anterior and middle portion of the SC as well as of the whole medio-lateral extent in the posterior SC. These data add the functional anatomical verification for reach specific information being sent from PMd to the superior colliculus and supports the role of the SC in reaching. Importantly the differential distribution of terminals from PMd and FEF projections suggests parallel information processing for gaze and reach in line with our published physiological results.

### 1-E-50 A common urgency/vigor signal governs speed-accuracy trade-offs in both decision-making and movement execution

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If we consider that decisions and movements are ultimately aimed at yielding rewards, the total elapsed time between stimulus onset and final movement completion can be seen as a temporal cost that discounts the reward rate. In this study, we test the hypothesis that a unified mechanism for reward rate maximization determines the speed-accuracy trade-off during both decision-making and movement execution. In the “tokens” task, the monkey initiates a trial by placing a cursor in a central circle in which 15 small tokens are randomly arranged. The tokens begin to jump, one-by-one every 200ms (pre-decision interval), from the center to one of two peripheral targets. The animal’s task is to move the cursor, as soon as he feels sufficiently confident, to the target which he believes will ultimately receive the majority of tokens. After movement

completion, the remaining tokens move more quickly (post-decision interval) to their final targets. Thus, the monkeys faced a trade-off: either wait to get more information, or make an early guess and save time. To induce an adjustment of this trade-off, two post-decision intervals, either 50ms or 150ms, were tested in separate “fast” and “slow” blocks of trials. In both fast and slow blocks, the monkeys’ accuracy decreased as a function of time, suggesting that decisions were based on the product of the information provided by the tokens and an “urgency” signal that grew over time. In fast blocks, decisions were made earlier and less accurately than in slow blocks, suggesting that the urgency level was higher. Among neurons recorded from the dorsal premotor and motor cortex many reflected the time course of the information provided by token movements and reached a consistent peak at the estimated moment of decision. Consistent with the urgency-gating model, the activity of these cells was amplified in fast blocks compared to slow blocks. We found that our model also predicts the duration of the reaching movements following the choice. Both monkeys executed shorter movements after longer decisions and movements were shorter in fast blocks compared to slow blocks. Together, these speed/accuracy trade-off adjustments, in both decision and movement time, allowed animals to significantly increase their reward rate in the fast blocks. This led us to propose that a common urgency signal modulates both the decision policy as well as action motivation (or movement “vigor”) according to motivational factors such as reward rate. Consistent with this, neurons that show a burst of activity between the time of decision and movement onset, known to be correlated with movement speed, were also correlated with decision duration in the way predicted by the urgency signal, which follows a different time course in the two blocks. Moreover, preliminary analysis of monkeys’ eye movements revealed that the velocity of saccades executed before decision time tends to increase over the time course of a trial, and is higher in fast blocks compared to slow blocks, as predicted by the urgency signals estimated based on monkeys’ decision policy. This suggests that despite the fact that eye movements are not relevant for reward rate maximisation in the tokens task, both the eye and arm system receive the same urgency signal that serves as a global source of vigor for decisions as well as movement execution. Support: CIHR (MOP-102662), CFI, FRSQ, and EJLB Foundation, FYSEN and GRSNC fellowships to DT, and GRSNC fellowship to JT.

### 1-E-51 Postural responses to electrical stimulation of individual ampullary nerves in human subjects

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**Purpose:** We have developed a prosthesis that stimulates individual ampullary nerves of the vestibular labyrinth to treat intractable Meniere’s disease in human patients. This allows us to evaluate individual semicircular canal contribution to the control of balance and posture in human subjects. **Methods:** 4 patients with intractable Meniere’s disease were implanted unilaterally with a vestibular prosthesis, based on a Nucleus Freedom cochlear implant, employing three arrays of stimulating electrode sites inserted in the perilymphatic space adjacent to the ampulla of each semicircular canal. 17-116 weeks following implantation, we tested the effects of electrical stimulation of individual canals on posture, as measured by computerized dynamic posturography. 2 second 300 pulse/sec trains of biphasic pulses of constant current were delivered during two postural contexts: stable support surface with eyes open and with eyes closed. In addition, in separate experiments on the same day, we recorded binocular eye movements and verbal descriptions of the perceptual experience of the subjects under the same stimulation conditions while seated in the dark. **Results:** Electrical stimulation produced brief postural perturbation followed by a return to upright stance. With eyes open and eyes closed, stimulation of the posterior canal produced an initial forward sway, while stimulation of the

anterior canal produced an initial backward sway. The amplitude of the initial sway increased with stimulation current. Sway responses were elicited by electrical stimulation at currents below threshold for electrically induced eye movements. The subject’s self-reported description of their perceptual experiences during seated stimulation was typically consistent with both eye movement direction and the overall direction of sway. **Conclusions:** Electrical stimulation of individual canals in human subjects produces consistent postural responses. The direction of the postural response to stimulation in a specific canal and the scaling of that response with current are consistent with the direction of the oculomotor response and self-reported perceptual experience in seated subjects to the same electrical stimulation meters.

### 1-E-52 Effect of motor imagery on pupil dilation

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“The two gunfighters stepped into the street. Their eyes narrowed to slits....” There was, of course, no need to be told that their eyes narrowed to slits, because gunfighters’ eyes always narrow to slits. It’s one of Hollywood’s most enduring clichés. But have you ever wondered why? Here, we suggest a simple answer: anticipating a specific motor activity - in this case, drawing a gun - causes pupil dilation, which in turn blurs vision, which is corrected for by squinting. Clearly, other factors, in particular arousal, would also contribute to pupil dilation, but as we show in the present paper, not only motor activity, but imagined motor activity is alone sufficient to provoke significant pupil dilation. Prior to the execution of any motor activity, time is necessary for its preparation. For instance, before performing a tennis serve - or a gunshot -, environment parameters, racket dynamics together with knowledge of how our limbs move in space are integrated by the central nervous system. This computational step is performed by internal models. The task that 20 participants were asked to perform was specifically designed to be a low-arousal, non-cognitive one. In a first “real movement” session, participants used a computer mouse to keep a randomly moving cursor on the computer screen within a circle in the center of the screen. The step size of the cursor’s random walk was either large (“difficult” condition) or small (“easy” condition). Each tracking trial was continuously performed during 25 seconds. Participants executed ten trials in each condition that were randomly intermixed. The random character of the task was such that it was not possible to develop cognitive strategies to improve performance. To quantify whether these unconscious motor processes are demanding on internal resources, we continuously measured pupil dilation. Some 500ms after the cursor appeared, pupil dilated very rapidly as demonstrated by increases in pupil diameters in both conditions. In the “difficult” condition, pupil diameters reached values 15% larger than in the “easy” condition ( $p < .001$ ). In motor imagery, body movements are internally simulated without actually being executed. Some computational steps are therefore also necessary even when no movement is actually performed. In a separate “mental imagery” session, participants saw the same random walk of the cursor as in the “real movement” session. However, in this condition they placed their hand on the computer mouse and were instructed not to move the mouse, but, rather, to imagine that they were using the mouse to confine the cursor within the circle. As in the “real movement” session, pupil diameters reached 5% larger values in the “difficult” condition ( $p < .001$ ). This shows that motor imagery by itself is sufficient to induce differences in pupillometry. The present study is unique in its attempt to eliminate factors related to cognitive workload and arousal and to focus on the effects of motor activity on pupil dilation. This finding has important methodological implication as it provides a reliable indirect real time measurement of resources consumed by motor imagery and has a much better time resolution than mental chronometry.

## F – Posture & Gait

### 1-F-53 The use of partial body weight support system on static and dynamic surfaces for children with cerebral palsy

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Cerebral palsy (CP) describes some disorders of movement development and function. Gait plays a key issue in children with CP as walking attainment is considered an important functional goal for these children. Partial body weight support (PBWS) is a strategy commonly used for rehabilitation of individuals with gait impairment. However, PBWS is often used as individuals walk on motorized treadmills. In terms of task-specific gait training, we could ask if the type of surface children with CP walk with PBWS influences the intervention. In this way, this study investigated some gait characteristics of children walking with different percentages of PBWS and the effects of gait training using PBWS system on static (ground level) and dynamic (treadmill) surfaces. Four children with diplegic CP (mean age, 8 years old) were videotaped as they walked freely and with PBWS at three different percentages of body unloading (0, 15 and 30%). All children were able to walk using PBWS system, and overall, they presented slower and shorter strides and lower cadence when they walked with PBWS compared to free walking. No changes were observed on support and swing periods among the different conditions. Two of these children were trained three times per week during six weeks with PBWS on moveable and fixed surfaces, respectively. They were videotaped walking before and after intervention, and two other tests were employed as well: 10 m walking test and gross motor function measure (GMFM). Overall, both children improved gait pattern and walking speed after intervention. This was a first attempt of using PBWS system as children with CP walk on static and dynamic surfaces during gait intervention. These strategies of gait training seem promising and more investigations have been conducted with other children in order to verify the benefits of gait training with PBWS on two different walking surfaces.

### 1-F-54 Walking on uneven terrain elicits increased electrocortical network activity compared to flat terrain

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Control of human walking on smooth surfaces involves many neural substrates in both the spinal cord and cortex (e.g. prefrontal, sensorimotor, post parietal and anterior cingulate) [1]. Uneven terrain requires more step-to-step adjustments, and thus, likely greater cognitive attention. We hypothesized that high-density EEG would reveal greater electrocortical activity in subjects walking on uneven terrain than on flat terrain, specifically in the: post parietal cortex, which translates between sensory and motor reference frames [2]; sensorimotor cortices, which show increased activity in complex walking tasks [3]; and anterior cingulate cortex, which is involved in error identification and correction [4]. We recorded limb kinematics and EEG data while 13 healthy young subjects walked for 25-minute trials on both uneven and flat terrain on a treadmill at 1.0 m/s. Uneven terrain consisted of a normal treadmill with surface height adjusted at regular intervals by wooden blocks. We adopted methods similar to our recent research [1]. We high-pass filtered (1 Hz) and merged all EEG data before analysis. We also removed noisy channels based on magnitude, kurtosis, correlation, and standard deviation, and noisy frames based on interquartile range, before performing independent component analysis. We selected

electrocortical sources based on power spectrum, dipole location, and scalp mapping from those explaining >85% of scalp map variance. We used k-means in EEGLAB to cluster electrocortical sources across subjects using vectors encoding dipole locations and power spectra. The data were time-locked to right heel-strike, left toe-off, left heel-strike, and right toe-off. We calculated event-related spectral perturbations (ERSP's) for each cluster and connectivity between clusters with the weighted phase-lag index (WPLI) [5]. Results indicated electrocortical clusters representing right and left sensorimotor, post parietal, and anterior cingulate cortices. ERSP analysis revealed high power at alpha (8-12 Hz) and beta (12-30 Hz) frequencies around double support in each cluster in uneven terrain walking. We also found high power at these frequencies around double support during flat walking, but with smaller magnitudes. We found greater power at faster frequencies in sensorimotor cortices prior to heel-strike, which was more pronounced for uneven terrain. WPLI results revealed high connectivity values in the uneven terrain condition between most clusters at 5-14 Hz frequencies during double support. Cluster connectivity was low for all frequencies over flat terrain. Our findings suggest cortical network activity involving post parietal, sensorimotor and anterior cingulate cortices increases with terrain unevenness during human walking. These findings appear related to direct cortical recordings in cats showing increased neuronal firing in post parietal and motor cortices when negotiating obstacles [2], but that research has not explored cortical network connectivity. Our connectivity results suggest strong cortical involvement in human walking in the real world. 1. Gwin, JT, et al. (2011). *Neuroimage*. 54(2):1289-1296. 2. McVea, DA and Pearson, KG (2009). *Progress in Motor Control: A Multidisciplinary Perspective*. 629:293-315. 3. Kurz, MJ, et al. (2012). *Neuroimage*. 59(2):1602-1607. 4. O'Connell, RG, et al. (2007). *Eur. J. Neurosci*. 25(8):2571-2579. 5. Vinck, M, et al. (2011). *Neuroimage*, 2011. 55(4):1548-1565.

### 1-F-55 Effects of manipulation of visual stimulus characteristics on postural control in dyslexic children

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Several studies have shown that dyslexic readers suffer from visual deficits that might also affect postural control performance, but a causal relationship has yet to be established. One step toward establishing such a relationship would be to demonstrate that postural control performance can be altered by manipulating some of the visual stimulus characteristics. Therefore, the goal of this study was to investigate the effects of visual stimulus characteristics manipulation on postural control in dyslexic children. Thirty-six children aged between 9 and 13 year-old, 18 dyslexic and 18 non-dyslexic children, stood upright inside of a moving room, as still as possible. Thirteen trials, each lasting 60 s, were performed. The first one was performed with eyes closed. In the following trials, children were asked to look at a target at different conditions of distance between participant and target (25 e 150 cm) and vision (with and without goggles occluding peripheral vision). Four trials were performed in which the room remained static and eight trials with the room moving (frequency of 0.2 Hz, peak velocity of 0.38 cm/s and amplitude of 0,3 cm). Two infrared OPTOTRAK emitters were used to record participant's body sway and, when occurred, movement of the room. Mean sway amplitude, coherence, stimulus frequency sway amplitude, gain, phase, position and velocity variability were calculated. The results revealed that dyslexic children swayed with greater magnitude in all conditions (without vision, stationary and moving room) than non-dyslexic children. When the room remained stationary, all participants showed greater magnitude of body sway in the 150 cm distance compared to 25 cm distance. In addition, dyslexic children swayed with larger magnitude of body sway in the condition with goggles compared to the no goggles condition. Visual

manipulation induced body sway in all children, however, dyslexic children showed lower values of coherence than non-dyslexic children. Although dyslexic children showed greater body sway magnitude with the goggles in the conditions of static room, such result was not observed when the room was oscillated. These results suggest that in the presence of a structured stimulus, that is, frequency, position and velocity well defined, dyslexic children show behavior that is similar to non-dyslexic children. On the other hand, in the absence of such stimulus, it seems that dyslexic children are more dependent on information coming from peripheral region of the visual field compared to non-dyslexic children.

### **1-F-56 Strychnine alters ankle flexor-extensor muscle activity pattern in chick embryos**

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During late-stage embryogenesis in chicks, repetitive leg movements are produced by alternating flexor-extensor leg muscle patterns at frequencies comparable to locomotion in hatchlings. Current models for control of locomotion suggest that the pattern and rhythm of leg muscle activity for stepping are separately controlled. One aim of our investigations is to determine if leg muscle patterns and rhythms in late-stage chick embryos are separately controlled. In fictive spinal preparations for study of locomotion, the inhibitory neurotransmitter, glycine appears to selectively control alternating flexion-extension of leg muscles. In mammals, strychnine, a glycine receptor antagonist, disrupts the alternation in motoneurons and produces synchronous bursting. The objective of this study is to determine if glycine produces flexor-extensor alternation during spontaneous stepping in late-stage chick embryos. Embryonic day 20, the ankle flexor (tibialis anterior, TA) and extensor (lateral gastrocnemius, LG) muscles were implanted bilaterally with silver bipolar electrodes for electromyographic recording (EMG). Employing a within-subject design, spontaneous muscle activity was first recorded for 2 hours. Strychnine was then given by intraperitoneal injection and recording continued for an additional 2-3 hours. Effects of strychnine were tested by comparing locomotor-related burst parameters before and after strychnine (7 embryos): burst duration, cycle duration, burst frequency and relative phase of LG burst onset. TA was selected as the reference for relative phase analyses because it is the most reliably rhythmic muscle during spontaneous stepping. The LG relative phase range of 0.3-0.7 was defined as symmetric flexor-extensor alternation. Strychnine disrupted flexor-extensor alternation in all embryos. Relative phase analyses indicated that the distribution of LG burst onsets shifted after strychnine application. The majority of LG bursts symmetrically alternated with TA before strychnine application ( $67 \pm 20\%$ ), and decreased after ( $42 \pm 23\%$ ). The decrease characterized 5 of 7 experiments. This shift was largely due to an increase in the proportion of LG bursts having a relative phase of 0.0-0.3 (before:  $31 \pm 21\%$ ; after:  $52 \pm 25\%$ ). In addition, TA and/or LG burst frequency increased after strychnine in all embryos from a range of 4-7 Hz (before) to 6-10 Hz (after). Also, both burst duration and integrated area increased in TA and LG in the majority of embryos. Interestingly, strychnine administration also disrupted left-right alternation of ankle muscle bursting in 5 of 5 experiments. The shift in LG burst onsets suggests that in late stage chick embryos, glycinergic inhibition contributes to the burst pattern of flexor-extensor alternation in ankle muscles during stepping. The increases in burst frequency, duration and integrated area also appear to be consistent with glycinergic modulation of burst pattern. Rhythmic activity persisted after strychnine, possibly indicating that rhythm generation is not dependent upon glycinergic inhibition. Thus, our results appear to be consistent with models that distinguish control of pattern versus rhythm. Although beyond the scope of this study, disruption of left-right alternation after strychnine raises the possibility that glycinergic inhibition modulates both flexor-extensor

and left-right leg patterns for stepping in chick embryos. Work supported by NIH grant HD053367.

### **1-F-57 Methods for large-scale wireless recordings in unrestrained monkeys**

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In recent years, large-scale brain recordings in nonhuman primates have been a driving force for both fundamental neuroscience and the field of brain-machine interfaces (BMIs), where neuronal ensemble patterns reveal principles of distributed neural processing and serve as a communication link between the brain and external devices. Here we report a combination of methods for sampling activity from multiple cortical areas in unrestrained monkeys; a wireless recording system and optical tracking of animal behavior. The processing of streams of neural signals in real time and extraction of behavioral parameters are key for BMI operations and basic neuroscience. The key factors that distinguish our system are superior quality of single-unit recordings and a higher number of neural channels, durability of signal and flexibility. These systems facilitate studying primate behavioral neuroscience, as demonstrated in preliminary data of unrestrained behaviors and research into primate locomotor modalities.

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

### **1-G-58 Motor personalities and motor moods in the retention of visuomotor adaptation**

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Although individual differences in motor learning ability are widely acknowledged, the mechanisms responsible for these differences are not well understood. Here we carefully study inter-individual differences in the short-term memory for visuomotor rotation (VMR) learning by repeatedly testing and retesting the retention of VMR learning at variable delays during multiple 2-hour sessions for different subjects. This design allows us to compare the magnitude of differences in retention between individuals - which we refer to as "motor personalities" - and between different sessions for a given individual - which we refer to as "motor moods" - with trial-to-trial differences within each session. We tested 16 subjects, each on 3-4 sessions over the course of a few different days. After a baseline period, subjects trained on a 30° VMR (clockwise or counter-clockwise, alternating between consecutive sessions). During this 200-trial training period they consistently reached asymptote, at about 95% of the 30° VMR. In the subsequent testing period, subjects were exposed to a pseudorandomly selected time delay ( $t$ ), tested for retention with a no-visual-feedback probe trial, and then repeatedly retrained and retested. The testing loop (delay - probe - retrain) was repeated 8 times for each testing block: once for each  $t$  spanning {0, 3, 6, 10, 20, 30, 60, 120} sec. The testing period for each session contained 8-12 such blocks and was succeeded by a 200-trial washout. We found that memory for VMR adaptation decayed rapidly with time, but the amount of decay was limited, suggesting that a portion of the adaptation was temporally stable. The subject-averaged decay curve was remarkably well fit ( $R^2=99.4\%$ ) by a single exponential function with a time constant of  $16.5 \pm 2.3s$  (mean  $\pm$  SEM) and a decay of only  $4.9 \pm 0.9^\circ$  (from an initial level of  $28.6 \pm 0.2^\circ$ ). The session averaged data displayed considerable variability: some sessions showed little to no decay whereas others displayed more than 50% decay. Moreover, some subjects displayed

consistently different amounts of decay than others, with 10-fold differences in some cases. Correspondingly, most of the session-to-session variability (56%) was due to differences between individuals ( $p < 0.001$ ). In contrast, only 3% of the same variability was due to session order ( $p > 0.4$ ). We next examined the extent to which the differences in decay between blocks could be explained by consistent between-session differences within individuals. We found that, even within the same subject, some sessions displayed consistently different amounts of decay than others: 41/60 sessions displayed significantly different ( $p < 0.05$ ) decay than the other sessions from the same subject. A nested ANOVA revealed that whereas person-to-person differences account for 40% of the variability in single-block decay levels, a remarkable additional 31% is explained by session-to-session differences within individuals (both  $p < 10^{-12}$ ). This result indicates that the block-to-block variability in decay is not large enough to explain the considerable person-to-person (motor personality) and session-to-session (motor mood) differences in our data. In our sample, person-to-person differences are not substantially explained by sex ( $< 3\%$  variance explained (VE)), age ( $< 1\%$  VE), height ( $< 4\%$  VE) or weight ( $< 4\%$  VE). Thus, further work will be needed to understand the cause of the motor mood and motor personality differences that we demonstrate here.

## 1-G-59 Is there a reaching speed that minimizes metabolic cost?

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Human movement is remarkably similar across individuals. For example, why do healthy young adults reach using similar speeds? Models that minimize terms such as error, jerk, and effort can simulate observed movement behavior. However, there is little experimental evidence for how the brain represents effort, or even what the actual metabolic (energy) requirements are for the task. Further, these models predict that minimizing energy alone cannot result in a non-zero optimal reaching speed (i.e. the optimal speed is to not move at all). Here we sought to measure the actual metabolic demands of a reaching task, and determine whether there is a metabolic minimum when reaching at different speeds. We hypothesized that metabolic rate (J/s) would increase with reaching speed but that metabolic energy expended per movement (cost per movement, J/mvt) would have a U-shaped relationship with reaching speed. Cost per movement essentially accounts for different movement durations. So while slower speeds may have lower metabolic rates, they require more time and thus may cost more overall. Seated subjects ( $n = 8$ ) reached horizontally towards a target 20 cm away using a robotic arm at different speeds, including their preferred speed. We used expired gas analysis to measure their O<sub>2</sub> and CO<sub>2</sub> rates and calculate metabolic power. We then subtracted out the baseline sitting metabolic power to get net metabolic power. We calculated net cost per movement by multiplying net metabolic power by movement duration ( $J/s \times s = J/mvt$ ). There were two other groups of 8 subjects who completed the experiment at target distances of 10 cm and 30 cm. Metabolic power increased with faster reaching speeds. For the 20 cm reach, the metabolic power for each subsequent faster speed was significantly higher ( $p$ 's  $< 0.05$ , 1-tailed paired t-test). For the 10 cm and 30 cm reaches, the metabolic power for the three and two slowest speeds, respectively, were not significantly different. Surprisingly, these curves exhibit a constant offset of  $\sim 0.23$  J/kg-s, independent of reach distance. This offset is not included in traditional effort-based cost functions and indicates that there is a constant metabolic cost associated with the reaching task, above the cost of sitting, which penalizes slow movements. Cost per movement had a U-shaped relationship with average velocity for all 3 distances. The minimum cost per movement was significantly less than the cost per movement for the neighboring speeds ( $p$ 's  $< 0.05$ ). The preferred speeds were slightly slower than

the metabolically optimal speeds ( $p = 0.42$  and  $p = 0.24$ , respectively) for the 10 and 20 cm reaches. The preferred speed for the 30 cm reach was significantly slower than the metabolically optimal speed ( $p < 0.046$ ). We found that metabolic power (J/s) increases with faster reaching speeds and there is a metabolic minimum in terms of cost per movement (J/mvt). This metabolic minimum results from a previously unobserved constant metabolic cost that penalizes slow movements. Although the source of this metabolic offset is not clear, future modeling efforts should consider including it in their cost functions. The preferred reaching speeds (or movement durations) were near the optimal speeds (or movement durations) that minimized cost per movement. Overall, these findings suggest that people may reach with a given speed in part to minimize metabolic cost.

## 1-G-60 The impact of motion stimulus variability on the temporal dynamics of a target selection task

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Random-dot kinetogram stimuli with different degrees of coherent motion in one of two opposite directions (Britten et al 1996) have been widely used in behavioral and neural studies of sensorimotor decision-making about action choices. Data suggest a process that accumulates evidence across time about the log likelihood ratio for alternate choices. From a neural perspective, this reduces to a process whereby a hypothetical "neuron/anti-neuron" pair each accumulate a signal about the net difference in evidence for and against their preferred choice and race to a decision bound (Gold & Shadlen 2001, 2007). However, the random-dot stimuli used in most studies contain coherent motion in only one of the two directions against a random-motion background and therefore cannot test how the putative neuron/anti-neuron pair might respond to different degrees of simultaneous evidence for the two opposing choices. The closest test to date used stimuli with different amounts of simultaneous coherent motion in 3 directions 120° apart (Niwa & Ditterich 2008; Bollimunta & Ditterich 2012). We tested the neuron/anti-neuron model by pairing different amounts of coherent motion signals in two opposite directions against a background of dots moving in Brownian motion. In each frame of the stimulus, dots were divided into three subgroups. Two subgroups conveyed the coherent motion signals in opposite directions. The third subgroup moved in Brownian motion. Any one dot was randomly chosen to be in one of the 3 subgroups over successive frames. This approach conveyed motion signals without the perception of overlaid dot patterns sliding transparently across one another. We used two different types of stimuli for the coherent dot motion populations. In the "narrow-coherence" (NC) set, the vector component in the coherent direction replaced the background Brownian motion of these dots for that frame. In the "Brownian-drift" (BD) set, the coherent vector component was added to their Brownian motion, rather than replacing it. As a result, the NC set confined the coherent motions to the two opposing directions, whereas the BD set distributed the signal over a much broader range of dot motions. For each set, different amounts of unidirectional coherent motion (0 - 32%) were superimposed on different amounts of base coherence signal (0 - 32%) moving simultaneously in both directions, resulting in combinations of coherences ranging from (0%/0%) to (64%/32%) for a total of 52 stimuli. Consistent with Ditterich et al (2008, 2012), reaction times and success rates in the BD and NC set were primarily driven by the net coherent motion evidence, but the RTs for low net coherent-motion stimuli (0 - 8%) also tended to decrease as the base coherence (i.e., total motion energy) increased. Ditterich et al speculated that this latter effect could be due to signal-dependent noise in the evidence accumulation process but did not specify to what degree this variability was peripheral (stimulus) or central (neural) in origin. Analysis of the motion stimuli in this study and

diffusion model simulations suggest that this latter effect could be explained at least in part by the instantaneous signal-dependent variability of the dot stimuli presented, and thus has a peripheral origin.

### **1-G-61 Prospective error to determine motor learning: A step toward a unified model of motor learning**

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When we try to perform new sports moves or manipulate new tools, we learn how to generate appropriate motor commands. Recent studies have shown that the learning process can be approximated by a simple linear state-space model. In this framework, an appropriate set of motor primitives (elements of motor control and learning) is activated according to the desired movement, and a weighted linear sum of the activities of the primitives determines the motor command. When the motor command results in movement error, the weighting meters are modified to decrease the error. However, the manner by which the activity of motor primitives is determined is still controversial. One naïve idea is that the desired movement determines the activity; a recent study by Gonzalez-Castro et al. (PLoS Comp Biol 2011) showed the possible involvement of the executed movement in determining the activity. Here, we propose an alternative model, in which the predicted error of an upcoming movement, called the prospective error (PE), determines the recruitment pattern of the primitives. This assumption is based on recent findings that showed some motor-related neurons encode PEs rather than the desired or executed movements (Popa et al, JNS 2012). Specifically, we constructed a novel computational model by assuming that motor primitives are activated according to the PE that is predicted from the error that observed in the just-preceding trial. Importantly, this model can account for several different and seemingly unrelated phenomena in motor learning such as savings after short and long washout trials (Zarahn et al., JNP 2008), anterograde interference (Sing & Smith, PLoS Comp Biol 2010), spontaneous recovery (Smith et al., PLoS Biol 2006), modulation of the learning rate because of uncertainty of error feedback (Burge et al., J Vis 2008), the relevance of error (Wei & Kording, JNP 2009), and structural learning (Braun et al., Curr Biol 2009). Although these phenomena have been conventionally explained by different models, our model can explain them in a single framework. In addition, this model predicts the following novel phenomenon that other conventional models were unable to predict. Motor adaptation to a constant visual perturbation (e.g., 30° rotation) is faster after experiencing the randomly changing errors (e.g., from -45° to 45° rotation) in every 2 trials than after experiencing the errors in a purely random manner. This is because, in the latter of the consecutive trials, the primitives that are activated based on the preceding error gradually acquire the knowledge to compensate for the same movement error (e.g., primitives for 30° PE learn the 30° rotation). To examine this prediction, subjects moved a manipulandum that controlled a cursor on a horizontal screen toward a straight, forward target. While the hand was forced to move only straight, forward by the manipulandum, the cursor's movement direction was randomly changed from trial to trial (Group 1) or in every 2 trials (Group 2), in which PEs and visually observed errors were manipulated. After the participants experienced these conditions, they were exposed to a constant visuomotor rotation (30°) in test trials. As predicted by our model, participants in Group 2 adapted to this rotation faster than by those in Group 1. These results suggested that motor primitives are recruited according to the PE, and that the PE is the key to a unifying theory for motor learning.

### **1-G-62 Effects of motor optimization and social interaction on an interpersonal force matching task**

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In goal-directed joint actions where two persons integrate their motor performances to achieve a single goal, an infinite number of combinations of individual contributions can reach the goal. Two important factors should be considered to define the contributions. First, motor optimizations between the persons could define the interpersonal organization in a similar way to intrapersonal motor coordination such as bimanual coordination. Second, social interactions between the persons, which are sometimes irrational from the viewpoint of motor optimization, might be involved in the interpersonal organization as well. It is, however, unknown how and to what degree these two aspects contribute. In order to investigate effects of motor optimization and social interaction on motor coordination, thirty pairs performed an interpersonal force matching task by using their index fingers. The goal of the task was to match the average of their exerted forces to a target force for 16 s. immediately before, they matched their individual forces to the same target force for 4 s. In the later 16 s only the averaged force was presented to the pairs; the force distributions between persons and their contributions to the error correction were redundant. Results demonstrated that not only individual motor performances such as maximum force of the index finger, but also a social aspect significantly affected the force distribution. Participants with autistic tendencies as indicated by higher scores on the Autism-spectrum Quotient test, exerted stronger force than their partners. They also showed higher gains for the error correction. Interestingly, these social effects were not observed when the task was performed individually. Results suggest that social interaction as well as motor optimization play a critical role in the interpersonal organization of goal-directed actions.

### **1-G-63 Sensorimotor performance in robot-assisted surgery**

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In teleoperated robot-assisted surgery (RAS), a surgeon manipulates a pair of robotic master manipulators in order to send commands to a patient-side robot. This approach provides many advantages over open surgery and laparoscopic surgery in terms of access, accuracy, dexterity, and visualization. However, it is not currently known how to best (1) train surgeons to operate such teleoperation systems, and (2) design the robot to optimize human sensorimotor task performance. We hypothesize that employing models of the human operator (the surgeon) can improve robot design, control, and surgical skill assessment and training. In addition, because RAS facilitates efficient collection of data about the trajectories of the surgeon's hands and instruments, it provides an opportunity to develop and test novel hypotheses about the control of movement and about acquisition of skill in complex, real-life tasks. The current study is the first attempt to understand the effect of teleoperation in RAS on movements of novices and experienced surgeons when compared to their freehand movements. We focused on the well-studied reach and reversal movements, and explored two aspects of motor coordination: movement kinematics, and exploitation of mechanical redundancy in the control of hand-held tools (i.e. the minimal intervention principle). We instrumented a clinical RAS system (da Vinci Si, Intuitive Surgical, Inc.) with a sensorized lightweight grip fixture, and we placed magnetic pose trackers on the arm of each participant. Participants sat at the master console, and were asked to make consecutive center-out horizontal movements as quickly and accurately as possible, without being restricted to a plane. They performed the experiment freehand, by holding the fixture detached from the

master manipulator, and via teleoperation, with the fixture attached to the master manipulator. To ensure consistent visual feedback, a monitor placed on the surgical table presented to the user, via the endoscopic camera, the experimental screen and a cursor that represented the planar position of the master manipulator. Kinematic analysis of participants' movements revealed statistically significant effects of teleoperation and level of expertise in several aspects of motion, including target acquisition error, movement speed, and movement smoothness. Moreover, there were directional patterns in these effects, suggesting that they might be related to the dynamics of the manipulator and to the adaptation of experienced surgeons to these dynamics. To analyze mechanical redundancy exploitation, we used the Uncontrolled Manifold framework, and calculated the ratio between joint angle variability that does and does not result in hand trajectory change. Consistent with previous studies, we show that participants exploited redundancy to stabilize their horizontal (task-relevant) but not vertical (task-irrelevant) movements. Interestingly, this stabilization is stronger for experts than for novices, and weaker in teleoperated movements than in freehand. We will discuss extending this framework to study clinically relevant tasks, such as suturing or knot tying, where there exist trajectory and mechanical redundancy. In addition, these tasks involve interaction with tissue and suture, and therefore, perception of mechanical properties of environment and its interplay with action become important aspects of successful performance.

## 1-G-64 The influence of threat on movement control under risk

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Nearly every aspect of our behavior is framed by risk, and people can respond to risk very differently. While some individuals readily confront high-risk situations in order to obtain high rewards (risk-seeking behavior), others may prefer low-risk situations even if it means obtaining low rewards (risk-averse behavior). Such risk-sensitivity has been studied in economic decision-making tasks, and recent work indicates that emotional states (such as sadness, anger, and threat) play a critical role in decision-making processes. However, the role that risk plays in movement decisions is not understood. Here we address the question of whether risk-sensitivity transfers across dissimilar movements and whether it is influenced by threat. Healthy young adult subjects made rapid arm-reaching movements (ARM task) and whole-body leaning movements (WB task) to move a cursor to the edge of a virtual cliff under various risky environments. They received an explicit point score for each movement, earning higher point rewards as they moved closer to the cliff edge but incurring a point penalty for moving beyond the cliff edge. We quantified risk-sensitivity by comparing subjects' actual movement endpoints to endpoints predicted by a subject-specific, risk-neutral model of movement planning. We found subjects were risk-seeking in both tasks, but they were significantly more risk-seeking in whole-body movements than in arm-reaching. Subjects moved closer to the cliff edge than predicted by the risk-neutral model, moving 9.0% farther than the model in the WB task and 1.5% farther than the model in the ARM task. To determine possible mechanisms underlying this observed risk-sensitivity, we adjusted our model to fit subject-specific parameters associated with cumulative prospect theory (CPT). Consistent with risk-seeking behavior, most subjects overvalued the point rewards (ARM:  $\beta_{945} = 1.13 \pm 0.17$ ; WB:  $\beta_{945} = 1.42 \pm 0.27$ ) and undervalued penalties (ARM:  $\beta_{946} = 0.76 \pm 0.31$ ; WB:  $\beta_{946} = 0.33 \pm 0.37$ ), with significantly larger distortions in the whole-body task ( $p < 0.005$ ). In both movements, subjects also overestimated their movement accuracy (ARM:  $\beta_{947} = 1.13 \pm 0.22$ ; WB:  $\beta_{947} = 1.22 \pm 0.17$ ). We are now investigating the effect of emotion, specifically threat, on risk-sensitivity during economic and movement decisions. Subjects

will perform seated arm-reaching movements, standing whole-body movements, and an equivalent seated and standing economic decision-making task. In each motor and non-motor task, subjects will choose between risky lotteries, playing some lotteries for monetary compensation. They will perform each task at low and at high elevation. Risk-sensitivity will be quantified by fitting subject responses to a model of choice based on CPT. We expect that increasing postural threat will lead to proportionally similar changes in risk-sensitivity for both motor tasks as well as for the non-motor task. Findings will transform our analysis of the influence of emotional state on movement decisions under risk. Our results will help determine whether there are generalizable principles such that movement decision-making in various emotional states can be predicted and trained using equivalent, motor or non-motor economic decision-making tasks.

## 1-G-65 A model to estimate the channel capacity in pointing movement using assistive communication devices in children with cerebral palsy

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There are approximately 500,000 children in the United States with speech or writing impairments that require assistive technology to communicate and participate in social activities. Most of these children may require computer-based augmentative communication devices such as adapted keyboards or programmable touch screens. However, communication with these devices is significantly slower than verbal communication. In addition, children with cerebral palsy (CP) may also be impaired in their ability to use such devices. Indeed, they showed an increased signal dependent noise that leads to higher variability and slowness in the movements. The communication rate is the primary outcome to determine the success in assisted communication, and it can be interpreted as the speed of information transmitted by an assistive device in bits/s. Therefore, optimal user interface of these devices become essential to increase the information rate for these children. We hypothesized that due to poorer motor control, children with CP are characterized by a reduction of channel capacity while interacting with assistive communication devices. The goal of this study was to develop a mathematical model to estimate the channel capacity in children with CP and control subjects. The model was fitted based on the number and size of buttons on the screen underlying the Fitts' and Hick's Laws. Since the Fitts' Law relationship is also influenced by both the perceived cost to miss the target and prior information related to the correct target location, these factors were included in the model. Custom software on the iPad® was used in a discrete pointing movement varying number (n), size (w), and space between targets (s), and included a highlighted condition that provides information about target location on the screen prior to movement (HL). The total time, the sum of reaction and movement time, was used as the outcome to construct the model for estimating the information rate and computing the maximum channel capacity of all possible values of n, w, s and HL for each subject. Interestingly the results showed that the model predicts the difference in information rate between groups by estimating lower channel capacity in children with CP with respect to control subjects. The results will be further used to optimize subject-specific user interface of assisted devices to maximize communication rate in children with motor and speech impairments.

## **1-G-66 A stimulator/amplifier using hundreds of electrodes for neural motor control**

**Scott Hiatt<sup>1</sup>**, Christopher Smith<sup>1</sup>, Daniel McDonnell<sup>1</sup>, Shane Guillory<sup>1</sup>

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Many emerging fields of investigation into neural motor systems require an integrated recording and stimulation platform with hundreds of independently controlled channels. Current stimulation solutions limit these experiments due to the lack of simultaneous recording and stimulation from the same implanted microelectrodes, the small number of independent stimulation channels, and the high cost per independent channel. We describe the design of a stimulating amplifier system capable of addressing 512 channels for use in neural interfaces research. Creating an integrated stimulation and recording platform offers many advantages over independent systems. Microelectrodes can be implanted and used continuously for stimulation without the need to disconnect the recording device, which currently requires physically disconnecting from the amplifiers or using a switch appliance. A single integrated headstage for stimulation and recording also facilitates very rapid recovery from stimulus artifact allowing observation of the neural systems response. Also, the closed-loop response to incoming recorded spikes can be translated to stimulation in other locations with latencies impossible for a separated stimulator and amplifier configuration. We have surveyed commonly used stimulation protocols and amplifiers and chosen a set of design specifications. For microelectrode stimulation we have chosen currents of at least 1mA, a current resolution of no greater than 10 $\mu$ A, and a time resolution of 1 $\mu$ s. Stimulation channels should be completely independent, instead of a few multiplexed stimulation channels, allowing for arbitrarily complex stimulation protocols. The stimulators should allow for arbitrary waveform shape and voltage bias. The amplifiers should be very high impedance, very low noise, have an integrated fast settle to remove stimulation artifact. The full system should be physically small to allow immediate proximity to the electrode site to reduce noise contamination and facilitate digitization as close to the electrode site as possible. Based on these criteria we have fabricated a 32-channel stimulation/recording headstage that fits on a circuit board approximately 2" x 1.3" and weighs 5.2g; this we integrated with our medically isolated data acquisition system. The link from the data acquisition to the headstage is fully digital with a wire less than 1/8" thick to carry data and power for 128-channels, sampled at 30ksp/s each. The complete system allows for up to 512 channels of neural data recording and stimulation. Supported by NIH R44 EY017247.

## **H – Poster Cluster (Churchland)**

### **1-H-67 A large untuned signal in motor cortex predicts movement onset**

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Cognition may be essential for intelligent behavior, but natural selection cares only about our actions. The most critical moments in our lives thus occur in the instant when an internal plan is triggered to become an overt movement. But what is that trigger? The answer is largely known for eye movements, but remains unknown for limb movements. Our prior work suggests that movement generation depends upon the sudden onset of strong dynamics with a large oscillatory component. That work addressed how pre-torsory activity is translated into movement activity, but did not address a more basic

question: what recruits the sudden onset of dynamics in the first place? This conundrum is similarly evident when viewing the responses of single neurons: one moment neurons are exhibiting relatively stable pre-torsory activity, and the next moment firing begins changing in complex ways. Presumably there must be some neural signal that arrives in motor cortex and produces this sudden change in dynamics. Our working hypotheses make two predictions regarding the properties a putative 'trigger' signal might have. First, we have reported that neural dynamics are similar regardless of reach condition (e.g., up versus down). The presence of condition-independent dynamics predicts a condition-independent (untuned) trigger signal: the trigger should determine when movement is made, not which movement is made. Second, we predict the trigger signal should be large, as it must produce a large change in dynamics. We tested these predictions by analyzing neural recordings from two monkeys performing a delayed reach task. Neural responses were recorded using a pair of 96-electrode arrays implanted in motor and premotor cortex. We first analyzed trial-averaged rates, and asked whether there exists a component of the population response that is both large and condition-independent. One expects any incoming trigger signal to be mixed, at the single-neuron level, with tuned signals that relate to the specific movement being generated. We therefore used a recently developed dimensionality reduction technique (dPCA; Machens, 2010) to analyze the population response. We find that the largest signal present in the population response is condition-independent and changes sharply just before movement onset. At the individual-neuron level, this signal corresponds to a large increase or decrease (depending on the neuron) in firing rate, independent of the particular movement being made. This untuned component has been noted previously, and was suggested to perhaps relate to reach speed (which for many tasks is nearly identical across reach directions). However, we further found that the untuned component was nearly identical for reaches with different speed profiles and with different durations. Thus, the signal depended only on when movement was made, and not on which movement was made. The condition-independent signal has a timecourse suggesting a relationship to movement triggering: it rises sharply ~200 ms before movement onset, just before the tuned component of the response begins to change. Furthermore, of the signals found by dPCA, the condition-independent signal was the best predictor of reaction time on a trial-by-trial basis. In summary, the population response in motor and premotor cortex shows a large, untuned signal that predicts when the monkey will move, but not which movement he will make.

### **1-H-68 Quantifying representational and dynamical structure in visual and motor cortex responses**

**Jeffrey Seely<sup>1</sup>**, Matthew Kaufman<sup>2</sup>, Adam Kohn<sup>3</sup>, Matthew Smith<sup>4</sup>, J Movshon<sup>5</sup>, Nicholas Priebe<sup>6</sup>, Stephen Lisberger<sup>7</sup>, Stephen Ryu<sup>8</sup>, David Sussillo<sup>8</sup>, Krishna Shenoy<sup>8</sup>, Larry Abbott<sup>1</sup>, John Cunningham<sup>9</sup>, Mark Churchland<sup>1</sup>

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Systems neuroscience often employs models that explain neural responses in terms of represented stimulus features or movement parameters. The response of a motor cortex neuron might be explained in terms of the control signals being carried, much as the response of a visual cortex neuron might be explained in terms of the sensory features being represented. Yet it has recently been suggested that motor cortex responses might be dominated not by the control signals that constitute the final output, but by the intrinsic dynamics of pattern generation necessary to produce that final output. Here we examine whether it is possible, in a model-free manner, to determine when responses are dominated by represented

meters and when responses are dominated by intrinsic dynamics that relate only indirectly to those meters. We analyzed population recordings from visual areas V1 and MT (recorded during the presentation of visual stimuli) and from primary motor and premotor cortex (recorded during a delayed reach task). We intentionally avoided fitting specific tuning or dynamical models. We instead asked whether basic features of the data tend to obey or violate expectations of representational and dynamical systems. Datasets consisted of a set of firing rate values: one for each neuron, condition (stimulus or movement type), and time bin. Our analysis involved a higher-order generalization of SVD (a tensor decomposition) to expose two kinds of structure potentially present in the data. First, when responses reflect tuning for stimulus parameters, structure should be best captured by variations in that tuning across neurons. Second, when the responses reflect the evolution of fixed dynamics from a set of initial states, one per condition, structure should be best captured across conditions. Simulations confirmed these expectations: it was possible to determine the model class without ever having to fit an instance of that class. We then applied this method to six neural datasets. For population recordings from visual areas V1 and MT, the dominant structure was across neurons, consistent with a representational framework. For population recordings from motor and premotor cortex, the dominant structure was across conditions, consistent with a dynamical framework. This result is relevant to the ongoing debate regarding which parameters are represented or controlled by motor cortex. Specifically, our method shows that a given number of dynamical modes can always capture more variance in the motor datasets than an equal number of represented parameters, regardless of what the parameters are. This suggests that a minority of the observed response properties can be explained directly in relation to the represented output parameters. Many of the other response properties will relate to the dynamics necessary to produce that final output. The fact that the sensory datasets did obey the representational expectation indicates that our method is not systematically biased, and agrees with the expectation that the computational strategies employed by motor cortex are fundamentally different from those employed by sensory cortex.

## **1-H-69 A recurrent neural network that produces EMG from rhythmic dynamics**

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It remains an open question how the firing rates of neurons in motor cortex (M1) lead to the EMG activity that ultimately drives movement. Recently, (Churchland et al., 2012)[1] reported that neural responses

in monkey M1 exhibit a prominent quasi-rhythmic pattern during reaching, even though the reaches themselves are not rhythmic. They argued that M1 could be understood as “an engine of movement that uses lawful dynamics”, i.e., that M1 could be viewed as a dynamical system. A major question posed by their work is finding a concise set of equations for a dynamical system that uses rhythmic patterns to drive EMG. We approached this problem by training a nonlinear recurrent neural network (RNN) (Sussillo and Abbott, 2009) to generate the recorded EMG during the same reach tasks used in [1]. We trained the RNN to simultaneously generate the EMG activity recorded from three muscles for 27 ‘conditions’ (reach types). The network was provided with condition-specific static inputs as an initial condition, derived from the actual pre-tory activity of recorded neurons. The RNN architecture consisted of a simulated M1 circuit, which provided input to three separate spinal cord circuits, one for each muscle. The model makes two main points. First, it is possible to produce realistic EMG activity using a network of this structure with the inputs provided. In particular, the input received during planning (derived from real neural data) provided a sufficiently detailed set of initial states to allow successful production of EMG for all 27 conditions. Second, the network naturally employs a solution that seems not unlike that used by the brain. This is true both on the surface level -- simulated neurons appear very realistic, and on a mechanistic level, a large untuned component carries the neural state into a region of dynamics that produces strong oscillations. These condition dependent oscillatory dynamics, in turn, drove the spinal circuits to generate the EMG. After training the RNN, it generated EMG with normalized RMS of 0.04. We investigated the nature of the sM1 population dynamics by applying a recently-developed technique for identifying dimensions containing dynamical structure, jPCA1. The dynamics in the 1st jPC plane were strongly oscillatory and explained 23% of the variance of the network activity. These rotations were produced by dynamics in the RNN whose linear approximation - around a local fixed point - contained strongly oscillatory structure reflected by eigenvalues with a large imaginary component. In addition to the rotational dynamics, we found a strong component of the neural trajectory, roughly orthogonal to the jPC plane (80 degrees), which carried the trajectories into the rotation. This component was similar across all conditions, and is thus captured by the ‘cross-condition mean’. We emphasize that neither the similarities of the RNN units to M1 neurons, nor the oscillatory patterns were built into the system. 1. Churchland, M. M. et al. Nature (2012), 2. Sussillo, D. & Abbott, L. F. Neuron 63 (2009).

## Session 2 Posters are listed by theme.

### A - Adaptation & Plasticity in Motor Control

#### 2-A-1 Functional reorganization of spinal cord circuitry after locomotor training in human spinal cord injury

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Activity-dependent plasticity as a result of reorganization of neural circuits is a fundamental characteristic of the central nervous system that occurs simultaneously in multiple sites. Improvements in walking ability have been achieved with locomotor training in people with spinal cord injury (SCI), and changes have been reported in walking speed, step length and step symmetry. However, the neuronal mechanisms underlying recovery of walking ability with locomotor training have not been determined. In this study, we used the soleus H-reflex as a window to determine the reorganization of spinal neuronal networks with locomotor training. We established the phase-dependent modulation pattern of the soleus H-reflex before and after body weight supported robotic gait training (BWSRGT) in 14 people with a SCI. In 9 out of 14 SCI subjects, the soleus H-reflex modulation pattern during assisted stepping before and after training was recorded in both legs. In addition, recovery of walking ability and posture were evaluated clinically. Eleven subjects had sensorimotor incomplete SCI (AIS C-D) and two subjects had complete SCI (AIS A-B). They received an average of 45 BWSRGT sessions, 1 h/day, 5 days/week. During stepping, the soleus H-reflex was elicited on the ascending limb of the recruitment curve and the M-wave ranged from 2 to 10% of the maximal M-wave. H-reflexes were evoked randomly at different phases of the step cycle based on the signal from the foot switch which was divided in 16 equal bins. To counteract changes in muscle geometry a supra-maximal stimulus was delivered to the posterior tibial nerve 80 ms after the test H-reflex. The BWS, treadmill speed and guidance force by the robotic exoskeleton changed from 46 %, 0.51 m/s, and 90 % before training to 18 %, 0.79 m/s and 39 % after training. The main effect of locomotor training was the re-establishment of soleus H-reflex depression during the swing phase of gait. However, when the soleus H-reflex modulation pattern was compared between the right and left legs before and after training, we found that reorganization of spinal neuronal networks followed two specific patterns. The first pattern corresponded to an heterologous reorganization pattern, i.e. when the right soleus H-reflex was facilitated, the left soleus H-reflex was depressed at the same phase of the step cycle post-training. The second pattern corresponded to a homologous reorganization pattern, i.e. the soleus H-reflex was modulated in the same direction in both right and left legs for a given phase of the step cycle post-training. The re-establishment of the soleus H-reflex phase-dependent modulation and depression during the swing phase of gait is likely due to reorganization of reciprocal Ia inhibition and ongoing modulation of Ia afferent transmission driven by plastic changes in spinal and supraspinal neuronal pathways. These results constitute the first neurophysiologic evidence that locomotor training reorganizes neuronal networks that generate patterned motor activity, modifying spinal reflex function, in the chronic lesioned human spinal cord. Supported by the New York State Department of Health and The Craig H. Neilsen Foundation.

#### 2-A-2 Increased hip torque rather than step width is used to maintain medial-lateral locomotor stability during unpredictable challenges to balance control

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To maintain medial-lateral (ML) balance control during locomotion the CNS can choose to adapt the locomotor pattern by increasing step-width or frontal plane hip torque. In cases of disease or aging, and anticipated instability among unimpaired adults, step-width rather than hip torque is commonly increased to maintain ML balance control. This suggests that under conditions of locomotor balance challenge, the CNS may preferentially control ML stability by increasing step-width rather than frontal plane hip torque. However, it remains unknown whether increasing step-width is a compensation for anticipated instability, aging and impairment, or truly the preferred strategy of the CNS to control ML gait stability. We hypothesized that an increase in step-width not hip torque would be preferred by the CNS to manage ML gait stability. As such, unimpaired adults would be expected to increase step-width, not hip torque to control ML gait stability in response to an unexpected and sustained locomotor balance challenge. This hypothesis was tested by examining frontal plane kinematics and kinetics among 16 unimpaired adults prior to and during adaptation to a novel locomotor task which challenges ML gait stability, asymmetric split-belt treadmill walking. Participants initially walked in a tied-belt configuration to assess baseline performance, after which they were unexpectedly introduced to a split-belt configuration for 720 strides. Initial and final balance strategies were assessed by comparing the first 20 and last 20 strides of adaptation to baseline performance. Surprisingly, participants initially adopted a narrower rather than a wider base-of-support as evidenced by a decrease in lateral foot placement relative to the CoM and step-width. This coincided with an increase in ML hip torque, indicating a preference for increasing hip torque rather than step width to maintain ML gait stability. The success of this strategy in maintaining ML stability was evident by a reduction in peak ML CoM velocity and excursion during the initial response. By the end of adaptation, ML CoM velocity had returned to baseline levels, while ML CoM excursion, lateral foot placement relative to the CoM and step-width all remained below baseline values. Although it decreased over the course of adaptation, ML hip torque remained elevated compared to baseline. These results demonstrate that among unimpaired adults, a high torque, narrow-based gait, not an increase in step-width, is the preferred adaptation of the CNS to maintain ML gait stability during unanticipated challenges to ML balance control. The adoption of a wide-based gait in cases of disease and aging may be due to an inability to generate the necessary rate or magnitude of hip torque, an area of potential research for locomotor balance training and rehabilitation technology. The selection of a high-torque, narrow-based gait rather than an increase in step-width commonly observed in studies of anticipated gait instability suggests that the CNS may select different balance strategies based upon the presence or absence of prior knowledge regarding conditions. Additionally, the CNS may prefer a high-torque, narrow-based gait to minimize the increase in metabolic cost required to maintain ML balance, and to preserve maneuverability in the plane of progression to achieve additional locomotor goals.

#### 2-A-3 Cerebellar neuronal network model during adaptive robot control

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The climbing fiber (cf) activity originating from the inferior olivary nucleus drives the plasticity at synapses of parallel fibers (pf) with Purkinje neurons (Pk) in the cerebellum. It has been proposed that with this plasticity the cerebellum is able to generate adequate motor

commands for complex coordinated movements such as playing fast arpeggios on the piano, or fast and precise compensatory eye movements such as the vestibuloocular reflex (VOR). However, it is still unclear what kind of information is encoded by the cf activity. Theoretical and neurophysiological studies hypothesized that it may encode sensory error (SE), motor error (ME) or a composition of both. In the present study, we tested these hypotheses in real world by employing a cerebellar neuronal network model configured for adaptive robot control. The cerebellar model was constructed to run in real-time and connected to an unstable robot, namely a two-wheeled balancing robot. The number of neurons that composes the model along with the interconnection architecture are configured following physiological and anatomical evidence of the vestibulo-cerebellum involved in the VOR motor learning. Namely, it includes 7 mossy fibers, 755 granular neurons, 5 Golgi neurons, 15 basket/stellate neurons, and one Pk that provides the sole output of the cerebellar model. These numbers are the maximum that allowed the real-time execution of the model on a laptop computer. A conventional artificial neuron model was employed for each neuron and the covariance rule was used for driving plasticity at pf-Pk synapses (long term potentiation and long term depression were considered). In addition, we have included a classic proportional and derivative (PD) feedback controller to serve as the non-cerebellar pathway in the VOR circuitry. The PD controller receives sensory error signals and generates a motor error signal that is inhibited by the Pk output to generate the motor command to the robot. In the real world experiment, when ME (PD controller output) was employed as cf activity, the cerebellar model in tandem with the PD controller adaptively improved balancing control of the robot, and also successfully managed abrupt perturbations (increase of robot weight) that the PD controller alone cannot handle. In contrast when SE (motion error) was the cf activity, the model response was lagged against desired trajectory, and the robot became unbalanced toward either forward or backward motion. When the external perturbation was added the controller with SE was not able to continue the control (the robot fell down). When a composition of SE and ME signals was employed, the overall performance was better than when ME was used. These results suggest that cerebellar motor learning using ME is more robust than that using SE, and the combination of ME and SE produce best adaptive performance.

## 2-A-4 Altered long-latency responses reveal parallel adaptation of feedforward and feedback control

**Tyler Cluff<sup>1</sup>**, Stephen Scott<sup>1</sup>

<sup>1</sup>Queen's University

An important concept in motor neuroscience is that adaptation modifies feedforward control processes, altering motor commands to compensate for changes in the physics of our limb and environment. In addition, recent studies have highlighted feedback responses that express knowledge of voluntary behaviour, leading to the inevitable hypothesis that feedback responses should adapt when we learn new motor skills. Although previous work has shown that learning affects feedback processing, the caveat is that force field adaptation increases muscle activity during reaching. This additional muscle activity amplifies muscle stretch responses, making it difficult to separate the effects of motor learning from automatic spinal processes. Here we provide direct evidence for simultaneous adaptation of feedback control and voluntary behaviour. We examined the adaptation of feedback responses using a combination of joint-based loads and strategic target placement. Subjects reached to three targets configured in joint-based coordinates using a robotic exoskeleton device (KINARM, BKIN Technologies, Kingston, Canada). Target 1 required combined shoulder and elbow motion, target 2 required only elbow motion, and target 3 required only shoulder

motion. After a block of unloaded reaching trials, we applied a viscous elbow load to investigate the adaptation of feedback responses and voluntary behaviour. At targets 1 and 2, we found substantial hand-path errors when the elbow load was initially applied, followed by mirror after-effect deviations when the load was removed after training. Adaptation increased elbow extensor activity to reach target 1 (baseline vs. late adaptation:  $t(18)=3.55$ ,  $p<0.01$ ) and elbow flexor activity to reach target 2 ( $t(18)=7.03$ ,  $p<0.001$ ). Reach-related muscle activity was unaltered at the probe target ( $t(18)=0.961$ ,  $p>0.05$ ). We examined feedback responses by perturbing the elbow ( $\pm 2$  Nm perturbations) at the onset of reaching movements to the probe target. Adaptation produced a clear reduction in perturbation-evoked hand motion ( $t(18)=3.23$ ,  $p<0.01$ ), which returned to near baseline levels when the viscous load was removed after training. While there was no adaptation in pre-perturbation activity (-50-0 ms post-perturbation) or the short-latency spinal response (20-45 ms), long-latency (45-105 ms;  $t(18)=3.16$ ,  $p<0.05$ ) and early voluntary muscle responses (105-200 ms;  $t(18)=2.64$ ,  $p<0.05$ ) depended on the viscosity of the elbow load (2 Nm.s  $> 1$  Nm.s load). Importantly, we found that reaching errors correlated negatively with changes in the long-latency response ( $r=-0.82$ ,  $p<0.01$ ), showing subjects that adapted more to the elbow load displayed greater modulation of muscle stretch responses. In conclusion, we have provided clear evidence that changes in voluntary behaviour are correlated with altered feedback responses. Thus, a key part of motor learning is to adjust rapid feedback corrections to consider the requirements of novel motor skills.

## 2-A-5 Reliability in the location of hindlimb motor representations in Fischer-344 Rats

**Shawn Frost<sup>1</sup>**, Maria Iliakova<sup>1</sup>, Caleb Dunham<sup>1</sup>, Scott Barbay<sup>1</sup>, Paul Arnold<sup>1</sup>, Randolph Nudo<sup>1</sup>

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The purpose of the present study was to determine the feasibility of using a common laboratory rat strain for locating cortical motor representations of the hindlimb reliably. Methods: Intracortical Microstimulation (ICMS) techniques were used to derive detailed maps of the hindlimb motor representations in six adult Fischer-344 rats. Results: The organization of the hindlimb movement representation, while variable across individuals in topographic detail, displayed several commonalities. The hindlimb representation was positioned posterior to the forelimb motor representation and postero-lateral to the motor trunk representation. The areal extent of the hindlimb representation across the cortical surface averaged 2.00  $\pm$  0.50 mm<sup>2</sup>. Superimposing individual maps revealed an overlapping area measuring 0.35 mm<sup>2</sup>, indicating that the location of the hindlimb representation can be predicted reliably based on stereotactic coordinates. Across the sample of rats, the hindlimb representation was found 1.25-3.75 mm posterior to Bregma, with an average center location  $\sim$  2.6 mm posterior to Bregma. Likewise, the hindlimb representation was found 1-3.25 mm lateral to the midline, with an average center location  $\sim$  2 mm lateral to midline. Conclusions: The location of the cortical hindlimb motor representation in Fischer-344 rats can be reliably located based on its stereotactic position posterior to Bregma and lateral to the longitudinal skull suture at midline. The ability to accurately predict the cortical localization of functional hindlimb territories in a rodent model is important, as such animal models are being used increasingly in the development of brain-computer interfaces for restoration of function after spinal cord injury.

## **2-A-6 Evidence for independent control of the visuomotor mapping for the planning rapid online correction of reaching movements**

**Valeriya Gritsenko<sup>1</sup>, John F. Kalaska<sup>1</sup>**

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During visually-guided reaching movements, the motor system presumably uses visuomotor mappings between target locations and arm movements to plan and initiate a proper response toward the target. It also has feedback circuits that inform the motor system of the state of the limb and the environment. If any unexpected changes in the environment occur after the onset of the reaching movement, the motor system can recruit these circuits, such as the “rapid online correction mechanism” (rOCM) (Pelisson et al; 1986), to correct the unfolding movement and compensate for the perturbation. To date, it is still not clear to what degree the circuit(s) that solves the visuomotor mapping for the planning/initiation of reaches and for the rOCM is shared or independent. One study, in which subjects learned a complete visuomotor inversion over several thousand trials and experienced a target displacement in every trial, suggested that the same circuit is shared by both systems (Abdelghani & Tweed; 2010). In contrast, a study in which subjects learned a mirror transformation but never experienced target displacement during the learning phase suggested that the circuits were separate (Gritsenko & Kalaska; 2010). However, the latter study involved far fewer learning trials and reaching movements to only 3 targets in fixed locations from one starting position, whereas the subjects in the former study performed a continuous sequence of reaches to targets at random locations. We therefore performed a study in which participants made reaching movements in a visuomotor transformation (either a mirror transformation or a complete inversion in different subjects) for 1800 trials over 5 daily sessions. Visual feedback of the transformed cursor position was available at all times. We presented rare “probe” trials, in which the target jumped 10 degrees clockwise or counterclockwise, to assess the state of adaptation of the rOCM compared to that of the initial voluntary reaching response. This new task was more immersive than Gritsenko & Kalaska (2010) because we included 18 targets to cover the full range of directions from a central starting position. Our results suggest that after long-term practice of a visuomotor transformation, the subjects readily adapted their planning of the initial reach direction, but failed to adapt their rOCM. Instead, subjects seemed to suppress (mirror group) or diminish (inversion group) the gain of their rOCM in the direction of the target displacement, while applying a late appropriate mirror or inversion correction. Our findings are consistent with the hypothesis of independent circuits for each visuomotor mapping mechanism.

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## **2-A-7 Learning to draw with the non-dominant hand**

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Distal movements of the hand and fingers are largely under the control of the contralateral cerebral hemisphere. As a result of cerebral asymmetries, the two hands show substantial differences in performance (i.e., hand dominance) with the dominant right hand (DH) displaying higher levels of precision performance. Whether this asymmetry is immutable, or can be offset through extensive training with the non-dominant left hand (NDH) remains unknown. Here, we trained the NDH of right-handed healthy adults (age  $33 \pm 14$ , 6 female). Participants used a digitizing tablet to complete a precision drawing task (PDT), by drawing continuous lines (45-180 mm) within provided boundaries (3 mm or 5 mm tolerance). Stimuli consisted of 45 distinct closed figures, presented in pseudo-random order. Participants were instructed to move as quickly as possible while staying within the boundaries. This task tests the participants' skill at

making precise continuous movements, which occur in normal life primarily via writing and drawing. Unlike writing, the PDT allows straightforward quantitative measurement of behavioral speed and accuracy. Nine participants practiced the PDT using their NDH for up to 10 days, with 90 trials (15-25 minutes) of training each day. We defined criterion performance as NDH drawing speed reaching 80% of baseline DH drawing speed. 6/9 participants reached criterion performance within 10 days of training ( $6.5 \pm 2.4$  days). Of the participants who reached criterion, 5/6 remained at or above criterion 1 week post-training, and 3/6 remained at or above criterion 4 weeks post-training. Our data demonstrate that experience can indeed alter hand asymmetries in precision control. Short frequent training sessions with pseudo-random stimuli can lead most participants to substantially improved precision drawing with the NDH, and can lead to long-term performance changes in some participants.

## **2-A-8 A brief period of reinforcement-based perceptual training causes long lasting changes in motor learning**

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Motor learning is typically modeled by examining how individuals compensate for disturbances that drive a movement away from a sensory target. When the motion path of a reaching movement is perturbed or the sound of the voice is altered adjustments in motor commands lead to compensation for the disturbance. These error-based models of motor learning assume by default that the sensory targets of behavior are well defined, but when an infant first reaches for a toy or speaks her first word the targets of movement are poorly defined if known at all. How are the sensory goals that shape error-based motor learning acquired in the first place? Here we use speech production to study the effects of reinforcement-driven perceptual training on error-based motor learning. We hypothesized that a simple reinforcement paradigm could be used to alter the perceptual targets of speech. Reinforced alterations in speech perception would be revealed by predictable changes in the amount of error-based adaptation in a speech-learning task. To manipulate perception, speech perceptual tests were administered to subjects over headphones, some of which included reinforcement designed to alter the perceptual distinction between the words “head” and “had”. An acoustical effects processor was then used to implement a speech motor learning task. During production of the word “head”, the effects processor changed the sound of the vowel in real-time so that subjects heard a word from the headphones that sounded more like “had”. The amount of compensation for this perturbation was examined to test the idea that alterations in speech perception shape speech motor learning. We found that minutes of reinforcement-driven perceptual training can change the sensory targets of speech. These rapid changes in speech perception subsequently cause alterations in error-based speech motor learning that last for days. The experiments show that the perceptual targets used as benchmarks for the maintenance of accurate speech are easily and rapidly altered. More generally, the work suggests that reinforcement learning plays a central role in defining the sensory targets that drive error-based motor learning.

## **2-A-9 Which Gaussian noise bandwidth best improves sensorimotor performance and is most pleasant?**

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Modern attempts to improve human performance focus on the stochastic resonance (SR) phenomenon. Recently, we reported that for Gaussian noise (0-15 Hz), an optimum level of noise, applied to the human index finger during stationary isometric force compensation induces an improvement in the motor performance via the SR phenomenon (Mendez-Balbuena et al., 2012). Here, we compare in 10 subjects the SR effects on the performance (mean absolute deviation) as well as on the subjective pleasantness, applying three different Gaussian noises chosen on the basis of the sensitivity of the fingertip receptors (0-15 Hz, 250-300 Hz, 0-300 Hz). We document that during the transitory phase only the 0-300 Hz noise induced SR effect on the performance ( $p=0.012$ ). In contrast, during the stationary phase SR improved the motor performance for all three noise frequency bandwidths ( $p=0.005$ ). However, this improvement was stronger for 0-300 Hz ( $p=0.007$ ) and 250-300 Hz ( $p=0.005$ ) than for 0-15 Hz noise. No significant difference was found between the 250-300 Hz and 0-300 Hz noise. Further, we document the higher subjective pleasantness of the 0-300 Hz ( $p=0.022$ ) and 250-300 Hz ( $p=0.004$ ) noise than of the 0-15 Hz noise. No significant difference in pleasantness was found between 0-300 Hz and 250-300 Hz noise. Thus, we show that the most appropriate noise that could be used in haptic gloves for tremor patients and surgeons is 0-300 Hz, as it has a beneficial effect during both transitory and stationary phases and also is the most pleasant one.

## 2-A-10 Reoptimization of motor behaviors

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Each task requires a specific motor behavior that is tuned to task demands. For instance, writing requires a lot of accuracy while clapping does not. It is known that the brain adjusts the motor behavior to different task demands as predicted by optimal control theory. In this study, the mechanism of this reoptimization process is investigated by varying the accuracy demands of a reaching task either on a trial-to-trial basis (random schedule) or in blocks (blocked schedule). Twenty human subjects were asked to reach to a target by moving the manipulandum of a robotic arm (Kinarm, Bkin technologies, Kingston, Canada). The dimension of the target parallel to the movement was kept constant (5mm) while its orthogonal dimension (5 or 80 mm) varied either randomly from trial to trial (random schedule) or every 100 trials (blocked schedule). During one fifth of the trials, the hand was deviated away from its trajectory by a stiff virtual wall (perturbation trials). Importantly, visual feedback about the lateral position of the hand was withheld during the movements. Clearly, the influence of task demands on the motor behavior differed across schedules. For instance, the rejection of the perturbation largely varied with task demands in the blocked schedule but not in the random schedule. The force applied by the subjects to resist the perturbation was larger for the smaller target ( $p<0.00001$ ). Interestingly, this effect was more important in the blocked schedule than in the random schedule (interaction:  $p=0.0008$ ). That is, subjects exhibited different motor behavior in the different schedules despite identical accuracy demands. Therefore, while reoptimization has been considered immediate and automatic, this difference across schedules suggests that the reoptimization of the motor behavior is neither happening on a trial-by-trial basis nor obligatory. In the optimal control framework, bradykinesia of Parkinson's disease patients (slowness of movements) is explained by a loss of sensitivity in the reward term of the cost function. Therefore, I tested the hypothesis that Parkinson's disease patients are not able to modulate their motor behavior with task demands. Overall, the results suggest that motor behaviours are not reoptimized on a trial-by-trial basis and that there might be a cost that prevents reoptimization when task demands change frequently.

## 2-A-11 Trial-by-trial error correction strategy during mirror-reversal transformation learning

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Humans are capable of adapting to an environment in which the leftward-rightward relationship between motor commands and visual errors is reversed (i.e. mirror-reversal; MR), such as when wearing reversing prism goggles (Sugita, 1996). Previous study investigated the underlying mechanism of MR adaptation by using reaching tasks with multiple targets and their sudden jumps, focusing on the sign reversal of the direction of initial aiming and online correction response (Gritsenko & Kalaska, 2010). However, it is still unclear how trial-by-trial error correction is influenced during MR adaptation. In a normal visuomotor environment, movement is implicitly corrected in the opposite direction of the movement error observed in the previous trial. In the MR condition, however, such movement correction could further aggravate the movement error and make the motor control system unstable as even very small errors could be amplified with trials. This error amplification mechanism could make performing even a simple reaching task to a single target quite hard. However, the success in the adaptation to the MR condition (Sugita, 1996) strongly suggests possible alterations in this error correction rule. In the current study, we investigated the change in trial-by-trial error correction and its relationship with the direction of initial aiming or online correction response during training of reaching toward a single straight ahead target under MR condition. Furthermore, to clarify what drives the changes in error correction, we explored the effect of visual feedback during reaching. Twelve participants were asked to make horizontal reaching movements to a straight ahead target on an opaque screen above the hand, with a cursor indicating the hand position. Participants were divided into 2 groups; one group was provided with online visual feedback of their movement and encouraged to make online movement correction, and the other was provided with visual feedback only at the end of movements. They performed 1,800 training trials under MR condition in total over 2 days. Transformation was introduced without notice. Initial aiming direction of reaching movements to 4 peripheral targets and the online correction response to sudden target jumps upon movement onset were tested before, during, and after MR adaptation. Visual feedback was not provided during peripheral target and target jump tests. Surprisingly, angular errors at peak velocity were augmented initially, even though there was only the single target. Errors decreased during training and there was no significant difference between groups. The probability that an error on a particular trial was augmented on the subsequent trial was significantly reduced in the final phase of training compared to the initial phase. On the other hand, the probability that participants moved to the opposite side of the target to the previous trial, which may require cognitive effort, was significantly increased in the final phase. The initial aiming direction to peripheral targets and the online correction response to target jumps was not changed from baseline in both groups. Our findings suggest that the cognitive strategy to reverse the sign of trial-by-trial error correction may be crucial to overcome the error amplification caused by MR. Such reversal is driven by prediction errors observed at the end of movements and independent to changes in the initial aiming and online movement correction.

## 2-A-12 Effect of transcranial direct current stimulation on motor learning and retention in young and elderly adults

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Motor learning allows the acquisition and long-term retention of new motor skills by eliciting brain plasticity. Normal aging is typically

associated with reduced plasticity in the central nervous, which in turn may lead to a decreased capacity to learn in the elderly population. The aim of the present study was twofold - to assess motor learning in young and elderly subjects by a visuomotor rotation task, and to test whether anodal Transcranial Direct Current Stimulation (TDCS) over the primary motor cortex (M1) affected learning and retention in these subjects. We predicted that without stimulation, both motor learning and retention would be stronger in young adults than in the elderly. We also expected TDCS to have a stronger effect on learning in the elderly participants than in the young adults. Twenty young adults (age:  $22.4 \pm 3.3$  years old) and twenty elderly participants (age:  $60.2 \pm 8.9$  years old) were recruited. Each subject was asked to follow a target that jumped from the centre of a computer screen to one of 8 locations situated concentrically about the screen, using a cursor. The cursor was controlled by moving a joystick with their right hand. After an initial baseline phase where the relationship between the joystick and cursor was veridical, the cursor movements were rotated counter-clockwise by  $60^\circ$  relative to the joystick movements. Large initial errors quickly reduced over time. Following the learning phase, subjects rested for 50 minutes before being asked to repeat the task with the same cursor rotation to assess short-term retention. The session ended with a washout phase, in which the movements of the cursor and the joystick were restored to normal. Ten young adults and ten elderly received anodal stimulation over M1 during the learning phase and for 10 minutes immediately following, while the remaining participants received sham stimulation for the same period. Initial results follow our predictions. In the absence of stimulation, young adults display a significant greater capacity to learn compared to the elderly. Moreover, anodal TDCS over M1 led to better retention in the elderly relative to sham, and a greater improvement in learning relative to young adults.

## B - Control of Eye & Head Movement

### 2-B-13 The effects of unilateral vs. bilateral subthalamic nucleus deep brain stimulation on visually-guided saccades and anti-saccades

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**Objectives:** There is evidence to suggest that compared to unilateral subthalamic nucleus deep brain stimulation (STN DBS), bilateral STN DBS produces deleterious effects on cognitive-motor tasks. We investigated the effects of unilateral and bilateral STN DBS on visually-guided saccades (VGS) and anti-saccades (AS). Due to the cognitive demands of the AS task (saccadic inhibition), we hypothesized that bilateral STN DBS would have a deleterious effect on anti-saccade task performance compared to unilateral stimulation. **Methods:** Four patients with advanced PD and bilateral STN DBS completed 4 separate testing sessions over 4 consecutive days. Each day, patients were tested off their anti-parkinsonian medication under 1 of 4 stimulation conditions: no stimulation (OFF-STIM), left stimulation (LT-STIM), right stimulation (RT-STIM), and bilateral stimulation (BIL-STIM). Each testing session began 3 hours after the appropriate stimulators were turned off for the condition of that day. The order of conditions and saccade tasks (VGS vs. AS) was randomized. Saccadic latency, gain, and peak velocity were measured for both tasks. Additionally, we measured the rate of erroneous prosaccades for the AS task. **Results:** The data are preliminary, descriptive findings. For the VGS task we found that: 1) saccadic latency was lowest for BIL-STIM (Mean  $\pm$ SD:  $186 \pm 60$  ms)

compared to all other conditions (OFF-STIM,  $208 \pm 95$  ms; LT-STIM,  $200 \pm 41$  ms; RT-STIM,  $227 \pm 122$  ms); 2) primary saccade gain was similar across all conditions (OFF-STIM,  $0.88 \pm 0.07$ ; LT-STIM,  $0.82 \pm 0.17$ , RT-STIM,  $0.86 \pm 0.06$ ; BIL-STIM,  $0.87 \pm 0.07$ ); and 3) peak saccadic velocity was lowest for BIL-STIM ( $2.29 \pm 0.33$  m/s) relative to all other conditions (OFF-STIM,  $2.40 \pm 0.40$  m/s; LT-STIM,  $2.34 \pm 0.26$  m/s; RT-STIM,  $2.34 \pm 0.21$  m/s). For the AS task we found that: 1) BIL-STIM ( $414 \pm 207$  ms) increased saccadic latency relative to all other conditions (OFF-STIM,  $360 \pm 160$  ms; LT-STIM,  $346 \pm 169$  ms; RT-STIM,  $362 \pm 192$  ms), 2) relative to OFF-STIM ( $0.79 \pm 0.24$ ), primary saccade gain was similar for BIL-STIM ( $0.81 \pm 0.27$ ); however, unilateral stimulation improved primary saccade gain (LT-STIM,  $1.01 \pm 0.33$ ; RT-STIM,  $0.91 \pm 0.28$ ), 3) all stimulation conditions (LT-STIM,  $1.92 \pm 0.29$  m/s; RT-STIM,  $1.86 \pm 0.45$  m/s; BIL-STIM,  $1.86 \pm 0.46$  m/s) increased peak saccadic velocity compared to OFF-STIM ( $1.70 \pm 0.24$  m/s); and 4) the percentage of erroneous prosaccades increased under all stimulation conditions (LT-STIM, 33%; RT-STIM, 28%; BIL-STIM, 44%) compared to the OFF-STIM condition (23%). **Conclusions:** Stimulation appears to have a minimal effect on VGS performance. In contrast, bilateral STN DBS appears to have a negative effect on AS performance. During bilateral stimulation, patients had increased saccadic latency and an increased percentage of erroneous prosaccades. A likely explanation for these results is that bilateral STN DBS may interfere with cognitive processes involved with saccadic inhibition.

### 2-B-14 Cerebellar and vestibular contributions to optimal gaze shifts

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There are infinitely many ways of combining eye and head movements during large gaze shifts to a new target. Selecting a unique set of movements suggests an underlying optimization principle. Recently, we showed that minimizing the consequences of noise on gaze variability during the post-movement period can account for all stereotyped kinematic parameters of gaze shifts, such as relative eye and head contributions, durations, velocity profiles, and the counter-rotation of the eyes when gaze has reached the target and the head still moves towards it (Saglam et al. 2011). The minimum-variance principle not only accounts for natural eye and head movements but also explains the changes in the kinematic meters of gaze shifts after the head moment of inertia is experimentally increased. In the present work, we investigate the role of vestibular input and the cerebellum in the re-optimization process of gaze shifts with altered head dynamics. We compared 10 healthy subjects with 9 patients with idiopathic general cerebellar atrophy and 5 patients with complete chronic bilateral vestibular loss. Subjects and patients performed large horizontal gaze shifts towards flashed targets in darkness (75- and 80-degree target steps, 43 steps per experiment) with and without increased head moment of inertia. The head moment of inertia was increased using a helmet with eccentrically placed masses. Increasing the head moment of inertia led to characteristic head oscillations at the end of the head movement. They were larger in both patient groups than in healthy subjects. Head oscillations increased gaze variability in all groups, significantly more in vestibular patients than in cerebellar patients or healthy subjects. Over the course of several gaze shifts, head oscillations and gaze variability decreased. At the end of the experiment, oscillations were minimal in healthy subjects, but higher in cerebellar and vestibular patients. Gaze variability was minimal in healthy subjects and cerebellar patients but significantly higher in vestibular patients. Cerebellar and vestibular patients had larger positional error from the target than healthy subjects. These results indicate that 1) Head oscillations cause increased gaze variability even in healthy subjects and cerebellar patients where the eyes counter-

rotate to compensate for head movements. This explains why it is beneficial to control the head movement during gaze shifts in a way to decrease head oscillations. 2) On-line head control to decrease oscillations requires vestibular and cerebellar processing. This is why oscillations are larger in both patient groups than in healthy subjects during the first gaze shifts. 3) Cerebellar patients - just as healthy subjects - use eye movements to compensate for head oscillations to decrease gaze variability. We suggest that cerebellar patients cannot perform on-line head control because they fail to update their internal head model to the experimentally altered head properties. They can, however, make use of eye-counter-rotation to decrease gaze variability because eye properties are unaltered. 4) Cerebellar processing is necessary for gaze shift accuracy (small positional error). 5) Vestibular input is crucial to maintain accurate and precise (non-variable) gaze shifts. Acknowledgments: Supported by BMBF (Project IFB 01EO901) References: Saglam M, Lehnen N, Glasauer S (2011) J Neurosci 31:16185-93.

## 2-B-15 The development of the saccade-pursuit interaction: evidence for immaturity of cerebellar functions in children

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It has been shown in earlier studies that there is a synergy between saccades and smooth pursuit in visual tracking (Orban de Xivry & Lefèvre, 2007). However, it remained to be investigated how this synergy develops in children as well as the impact of specific pathologies as prematurity or cerebral palsy (CP), which is a disorder of movement and posture due to a lesion of the fetus or infant brain. To investigate this question subjects were asked to pursue a target projected on a screen. Horizontal eye movements were recorded in 58 control, 50 cerebral palsied and 17 premature children aged 5 to 16 years using an infrared eye tracker. Results were compared to those of 16 adults. The oculomotor task consisted of a double step-ramp paradigm (De Brouwer, Missal, Barnes, & Lefèvre, 2002). Each trial began with a fixation followed by a step-ramp (Rashbass) of the target that started moving horizontally at a constant velocity of 15 deg/s in a predictable direction determined by the initial fixation position. After a random duration ranging from 0.6 to 0.8 s, this target stepped in position to the left or to the right (position step) and continued moving at a different velocity (velocity step) ranging from 30 deg/s in one direction to 60 deg/s in the other direction. We found children have lower pursuit performance. They show increased delays for pursuit initiation, lower initial acceleration of the eye and reduced pursuit gain. Close results were found in patients with degenerative cerebellar lesions (Moschner et al., 1999). The early mature saccadic system does not fully compensate for the lower pursuit performance in childhood. This reduced error correction suggests that children have a lower sensitivity to visual errors compared to adults. Decreasing processing delays with age and the maturation of brain areas such as the cerebellum can explain these results. Compared to control children, premature and CP children exhibit larger pursuit latency for pursuit initiation. In addition, position error during pursuit is also significantly larger and more variable for CP children. These differences are softened in response to a change in target velocity or position during ongoing pursuit. With the exception of these small differences, cerebral palsied children have an oculomotor performance surprisingly close to control despite their motor disabilities. The oculomotor performance of premature children is intermediate between control and CP children's behaviour.

## 2-B-16 Eye movements resulting from canal specific electrical stimulation in human subjects

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Introduction: There has been rapid development of vestibular prosthesis technology in recent years, with the hope of restoring vestibular function to patients with vestibular loss. Most of this development has taken place in animal models. We hypothesize that the rhesus monkey model is a useful analog to implantation of such a device in human subjects. To test this hypothesis, 4 human subjects were implanted with a vestibular prosthesis using identical surgical techniques performed by the same neurotologic surgeon as for previous studies in rhesus monkeys. Methods: The devices were identical in monkey and human subjects, consisting of a Cochlear Freedom receiver stimulator modified with 3 electrode sites on each of three leads implanted into the perilymphatic space adjacent to the ampullae of each semicircular canal. The device was capable of generating biphasic pulse stimuli with independently controlled current amplitude (iÜ 400 ÷ 1A), pulse rate (20-600 pps), pulse width (50-400 ÷ 1s/ phase) and interphase gap. In the laboratory, the devices were controlled by identical NIC-2 research interfaces, which allowed us to deliver preprogrammed biphasic pulse trains. We varied current amplitude and pulse frequency to map the response of the subjects by recording eye movements using IR video-oculography in humans and scleral coils in monkeys. Subjects were seated in a rotary chair in the dark, and were required to intermittently acquire point targets with eye movements. Results: Both monkey and human subjects tolerated the electrical stimulation without displaying any signs of distress. We observed that electrical stimulation typically produced eye movements largely in the plane of the implanted canal in monkeys, but less consistently so in humans. Current thresholds for eliciting a response were higher in human subjects than in monkeys. The responses of the human subjects had lower slow phase velocities at higher currents than those of monkeys. There was considerable variability in the velocity versus current or pulse frequency relationship between subjects in both groups. In human subjects, there was often a decrease in slow phase eye velocity such that the highest velocities were elicited immediately following onset of stimulation. In humans, the slow phase velocities recorded initially after implantation were higher than the velocities recorded months or years later in the same subjects to the same stimuli. In monkeys, the responses often remained unchanged for long periods of time. Changes in slow phase velocity versus current were often lled by changes in the amplitude of compound action potentials elicited by electrical stimulation, despite consistent electrode impedances. Both groups displayed clear relationships between current amplitude and slow phase eye velocity, however the pulse frequency versus slow phase eye velocity relationships were less robust for the human subjects than for the monkeys. Conclusions: Both human and monkey subjects show qualitatively similar responses to electrical stimulation with identical vestibular prosthesis implants. Human subjects and monkeys differ in terms of the current thresholds, the direction and magnitude of the slow phase velocities achieved, and the longitudinal changes in the efficacy of stimulation.

## C - Disorders of Motor Control

### 2-C-17 Reach-to-grasp kinematics in hemidystonic cerebral palsy

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In hemidystonic cerebral palsy (CP), movement is often uncoordinated. In this study, we developed a novel method to quantify abnormalities of reach-to-grasp kinematics to better understand how the timing of movement is specifically affected by wrist dystonia due to CP. Participants included 11 patients (DYS, age 17.4y +/- 5y, 3 female) and nine healthy volunteers (HV, age 16.9y +/- 5y, 8 female). An optical motion capture system computed joint angles of the shoulder (three axes), elbow, and wrist (three axes). Seated participants reached forward with one hand to grasp and lift a rod (1-inch diameter) placed within reach at midline on a table. Five trials were attempted for each hand. Principal component analysis was applied at each 1% of movement time (MT) to the seven joint angles in the dominant arm of the HV group (HVD). The first three components (84.5% +/- 0.03% of total variance) were used to describe normal movement patterns. Joint angles of all subjects were normalized and filtered through the three-dimensional time-varying component space of HVD and projected back into the seven-dimensional joint space for comparison. Error between the projected estimates and actual joint angles was computed. Significant timing abnormalities were defined as the points in time when the error in HVD (non-dominant), DYSd, or DYSnd exceeded three standard deviations of error in HVD. In DYSnd, abnormal wrist angles (forearm rotation, wrist deviation) were seen early (30%, 45% MT) in most patients, and may be due to involuntary movements. Abnormal shoulder rotation was commonly observed at the end of the movement, which may be compensatory for impaired wrist orientation due to dystonia. There were distributed shoulder adduction/abduction abnormalities in half the DYSnd group, and may also reflect compensation for extraneous or limited movements at other joints. Shoulder (30% MT) and elbow (60% MT) flexion/extension were abnormal in patients, more commonly in DYSnd than DYSd. The presence of DYSd abnormalities highlights the distributed effect of unilateral brain injury. The ranking of the quantity and magnitude of joint deviations (DYSnd > DYSd > HVD) was preserved in other measures of task performance, including MT, and hand trajectory smoothness. This study provides a method to analyze arm kinematics based on normal time-varying joint synergies, rather than considering each joint separately or averaged across the entire movement. Knowledge of timing abnormalities can provide insight into the mechanisms underlying abnormal movements in dystonia.

## 2-C-18 Galvanic evoked vestibulospinal reflexes in the lower limbs of chronic hemiparetic stroke subjects

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Spasticity is a prevalent and often disabling condition following hemispheric stroke. It can often impede movement and interfere with activities of daily living. Although common, the neural mechanisms that underlie post-stroke spasticity are not fully characterized. One of the many possibilities is increased motoneuron excitability for which there are a number of probable sources. The objective of this study is to examine whether excessive excitatory synaptic input from disinhibited lateral vestibulospinal pathways, may contribute to spasticity by driving spinal motoneurons abnormally close to their activation threshold. In order to address our objective, the focus of this study was to determine if vestibular mediated reflexes differ between the spastic and contralateral lower limb musculature of hemiparetic stroke subjects. Galvanic vestibular stimulation was used to non-invasively evaluate the influence of descending lateral vestibulospinal pathways on motoneuron output. We tested the hypothesis that synaptic drive from the contralesional or spastic vestibular nucleus (VN) is increased causing augmented lower limb motoneuron excitability on the spastic side as compared to

contralateral side. Motoneuron excitability was quantified by measuring vestibulospinal reflex amplitudes. Vestibulospinal reflexes were evoked using bipolar, binaural galvanic vestibular stimulation (20 ms, 4 mA square wave pulses, 150 pulses, ISI 500 ms) delivered via surface electrodes affixed over the mastoid processes. Four chronic stroke subjects stood unsupported on a flat surface with their head rotated 90 degrees and their eyes closed. Short latency (SL) vestibulospinal reflexes were measured from the spastic and contralateral medial gastrocnemius muscles. We calculated an asymmetry ratio (AR) in SL reflex amplitude, defined as  $100 \times ((\text{Spastic SL} - \text{Contralateral SL}) / (\text{Spastic SL} + \text{Contralateral SL}))$ , to evaluate side-to-side differences between the spastic and contralateral limbs. In two subjects, we observed increased SL responses when expressed as a percentage of prestimulus EMG activity (spastic:  $26.7 \pm 18.4\%$ , contralateral:  $20.9 \pm 11.1\%$ , AR:  $0.10 \pm 0.09$ ). However in two other subjects, we observed opposite responses (spastic:  $11.1 \pm 3.0\%$ , contralateral:  $16.1 \pm 0.2\%$ , AR:  $-0.19 \pm 0.14$ ). Subjects with larger responses in the spastic limb had more excitable deep tendon reflexes, measured in the biceps brachii, when compared to those with larger contralateral limb responses. These pilot data suggest that descending vestibulospinal signals to the spastic motoneurons may be enhanced in some, but not all, stroke subjects. An enhancement of vestibulospinal signals to spastic motoneurons may arise from disinhibition of key supraspinal nuclei following stroke and could potentially explain the lateralized manifestation of spasticity post-stroke.

## 2-C-19 The effects of deafferentation on reach, grasp and object manipulation

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Deafferentation leads to clear degradation of voluntary control and the loss of sensation is particularly noticeable in complex multiple joint arm movements and in multiple digit hand grasping and manipulation. There have been few studies of how patients with deafferentation adapt their grasp and manipulative behaviour to accommodate their sensory loss, and yet this might be highly informative for developing artificial hands, or robots, that are required to grasp objects with minimal haptic sensation. We are therefore testing the hand actions of chronically deafferented patients reaching, grasping and lifting everyday objects. In advance, we have tested the grasp action of healthy participants before and after acute sensory degradation caused by ischaemic pressure block. Six right handed participants were recruited under local ethical approval, and a liberty motion tracker was attached to the distal phalanx of each finger; additional markers were attached to the back of the hand and to each object being grasped. Calibration of the digit markers allowed estimation of the finger-tip of each finger. Each participant was required to reach, grasp, lift and return to the table top 20 everyday objects, lifting each one 10 times. On a second session they then had a pressure cuff applied above the elbow, and when sensation of the index finger was lost (as assessed by von Frey filaments), they repeated 5 more lifts of 7 of these objects. We used Procrustes analysis to analyse the grasp hand postures independent of hand position, and the reliability of each posture before and after sensory loss. We also monitored grasp times, and object slips. As expected, sensory loss degraded grasp action, and data are presented suggesting that particular grasp types are most severely affected. These preliminary results provide a platform on which the data from deafferented patients can be compared to neurologically intact grasp actions. Supported by the Wellcome Trust and Royal Society.

## 2-C-20 The neural representation of the pelvic region and its implications for localizing the source of chronic pelvic pain

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Urologic Chronic Pelvic Pain Syndrome (UCPPS) has an enormous impact and burden to patients and society. UCPPS manifests in men as Chronic Prostatitis/Chronic Pelvic Pain Syndrome (CP/CPPS) and causes considerable morbidity - in the form of spontaneous pain, and urinary and sexual dysfunction - resulting in significant decrease in quality of life for the patients and their families. The prevalence of CP/CPPS-like symptoms could be as high as 16% of men in the United States. Previous electromyographic studies of CP/CPPS patients have clearly identified impairments in the neuromuscular control of the pelvic floor. In addition, recent neuroimaging investigations have characterized brain function during spontaneous pain in CP/CPPS patients - functional activation in the anterior insula was positively correlated with self-reported spontaneous pain intensity. However, it remains unclear whether the anterior insula is independently contributing to the pain perception or representing impaired neuromuscular control at a different locus. Here, we sought to determine if anterior insula activation could be driven by manipulations to pelvic muscles not specifically related to the experience of spontaneous pain. We collected functional magnetic resonance imaging (fMRI) data using a 3 Tesla Siemens Trio from ten men (mean age of 35 years) in the age range typical of CP/CPPS onset. 6 participants had reported a history of CP/CPPS symptoms while 4 participants had no history of CP/CPPS. To identify brain regions involved in pelvic muscle contraction, participants voluntarily contracted pelvic muscles to the sound of a metronome during a first set of fMRI data acquisition runs. To identify brain regions associated with pelvic nociception, the participant continuously rated their discomfort as a physical therapist applied pressure to induce pain in specific pelvic muscles during a second set of fMRI data acquisition runs. Analysis of fMRI data was performed in FSL 4.1.9, seeking voxels that were significantly correlated to pelvic contraction and/or reported pain intensity. Statistical inferences were drawn at the voxel level with  $p < 0.05$  corrected for multiple comparisons. In the standard space of the Montreal Neurological Institute brain template, previous brain imaging studies found peak activation associated with spontaneous CP/CPPS pain at 44, 14, -4 (x,y,z in mm), which is a location clearly within the anterior insula. We observed robust activation at this location during pelvic muscle contraction ( $Z=2.76$ ) as part of a larger cluster of anterior insula activation (peak  $Z=3.96$  at x,y,z=54,10,10 mm with 3089 voxels). In addition, we observed robust anterior insula activation during pressure-induced pain (peak  $Z=5.43$  at x,y,z=48,16,2 mm with 3745 voxels). We conclude that the anterior insula plays an important role in the sensorimotor representation of the pelvic muscles, and that anterior insula activation associated with CP/CPPS pain may reflect impaired neuromuscular control, even possibly occurring outside of the brain. Future studies may require simultaneous measures of brain and muscle activation to localize the site(s) of impaired neuromuscular control in UCPPS patients.

## 2-C-21 Eye movements and postural stability in traumatic brain injury

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The aim is to identify physiological variables for eye movements, postural stability and gait that characterize the effects of a mild or moderate traumatic brain injury (TBI) on the vestibular and ocular motor systems. The motivation is to help identify the pathological

basis for problems with balance and spatial orientation in TBI. This could help to develop appropriate treatments and strategies for physical therapy. Eye movements were recorded with the I-Portal system (Neuro Kinetics). Horizontal and vertical saccades and pursuit were examined and the vestibulo-ocular reflex (VOR) and visual suppression of the VOR were tested with sinusoidal rotation over the frequency range, 0.01 to 2.56 Hz. Postural stability was analyzed with the NeuroCom Equitest protocol. The results included the following: (a) abnormal use of visual and vestibular inputs for controlling postural stability; (b) a normal or increased gain of the vestibulo-ocular reflex (VOR); (c) reduced visual suppression of the VOR at both low and high frequencies, (d) abnormal vertical pursuit and frequently a difference for up versus down. Multivariate analyses identified patterns of abnormal eye movements. Future studies will address motor behavior in subjects with a history of TBI but no clinical systems and longitudinal studies to track the progression of symptoms and the underlying pathophysiology over time and with age.

## 2-C-22 Evoked potentials from deep brain stimulation in childhood dystonia

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Childhood dystonia is a debilitating movement disorder characterized by involuntary muscle contractions that lead to repetitive movements and/or abnormal postures. Deep brain stimulation (DBS) of the globus pallidus internus (GPi) is becoming a more common treatment for childhood dystonia despite an incomplete understanding of the exact role of GPi in the sensorimotor system. To this end, we hypothesized that stimulation of GPi leads to activation of cortical sensorimotor areas. Specifically, we predicted that cortical regions ipsilateral to DBS would show a greater response than regions contralateral to stimulation, and that the size of the response would be related to magnitude and duration of the stimulation waveform. To investigate the effects of GPi stimulation on cortical activity, we recorded scalp electroencephalogram (EEG) during DBS in children (ages 10-21 years old) with dystonia. We analyzed evoked potentials (EPs) in the EEG, which followed a large electrical artifact. Similar to observations in adults, we found that the largest evoked potentials (EPs) were located over the ipsilateral hemisphere and had latencies consistent with neural projections originating in the GPi that synapse in the thalamus. Both the electrical artifact and the evoked potential magnitude increased as the amplitude and pulse width of the stimulating waveform increased. This is important because it provides evidence that evoked cortical activity is positively correlated to both the strength and the duration of the electrical stimulus, and thus, seems to depend on both the resistive and capacitive properties of neural tissue. Additionally, our results suggest that EP amplitude may be related to improvements in motor function. These results support the idea that during dystonia, there is abnormally high motor cortex activity (leading to unwanted postures and movement), which can be modified through high frequency stimulation of the neural pathway involving GPi, thalamus, and cortex. In addition, we have developed a simple electrical circuit model to explain how EP amplitudes relate to DBS waveform properties. Using this model, we can estimate an "effective impedance" for each set of contact polarities in a given subject, which is proportional to the neural conduction in GPi-thalamus-cortex connections (where high impedance may be an indicator of abnormalities--e.g. lesions--within the circuit).

## 2-C-23 Assessing mu rhythm in spinal cord injury patients

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Event related desynchronization (ERD) of mu waves, or mu suppression, has been observed in response to a number of perception of motion studies including movement of the self and other, imagined movement, and point-light display. Mu suppression can be especially pronounced when the movement has social relevance and is being generated by a biological entity indicating successful social adaptation. Painful stimuli elicit a mu rhythm suppression, especially when the subject is perceived to be similar to the observer. The suppression is a neural response that is considered to be an EEG marker for empathy. A person feels one pain when they can imagine themselves experiencing the same effect. We have adapted this paradigm to examine mu suppression during perception of painful and control conditions in participants with spinal cord injury. Spinal cord injured and control participants were presented with pictures of upper extremities and lower extremities either experiencing an injection with a syringe or rubbed with a soft stimulus. Similar to previous studies, the participants were instructed to imagine the feeling of the person experiencing these effects and the corresponding emotional state. EEG recordings were made using 60 electrodes across the head. Mu suppression responses that correspond to specific stimulus locations (hand/arm vs. foot/leg) and type (painful vs. soft) are analyzed with respect to injury location (C1-C8, T1-T12) and completeness. The mu suppression result pattern provides a window into understanding the extent to which current body state influences perception of pain and the corresponding empathetic response.

## 2-C-24 Deep brain stimulation of the subthalamic nucleus improves haptic perception in Parkinson's disease

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Deep brain stimulation (DBS) of the subthalamic nucleus (STN) is an established treatment for ameliorating motor symptoms of Parkinson's disease (PD), a neurodegenerative disorder affecting the dopamine producing neurons within the basal ganglia-thalamocortical pathways. Mounting evidence suggests that PD is also associated with perceptual deficits such as decreased kinaesthetic and haptic sensitivity (Zia et al., 2000; Konczak et al., 2007; Li et al., 2010), yet the effect of STN-DBS on sensory processing is largely unknown. Thus, this study investigated whether STN-DBS affects somatosensory processing, specifically the processing of tactile and proprioceptive cues, by systematically examining the precision of haptic perception of object size. Thirteen mild to severely affected PD patients with implanted STN-DBS and thirteen healthy, age-matched controls judged, without vision, the heights of two blocks they haptically explored using a precision grip. First, a reference block was presented (6 cm in height) followed by a comparison block (5.2-6.8cm). Participants verbally indicated which block was taller (verbal judgment). Then, while still grasping the comparison block, they opened the other hand to match the perceived height (motor judgment). Patients were tested, without medication, during DBS ON and OFF, probing with both their more and less affected hand. Based on verbal responses, percentages of correct responses were calculated and sensitivity functions were fitted for each group and discrimination thresholds (DT) were derived. DT was defined at the 75% response level (correctly perceived as taller). Based on motion capture data, grip aperture

during the motor judgment was obtained and the deviation between aperture and physical objects size (aperture error) were calculated. The main results were: 1) PD patients showed a significant deficit in haptic acuity. Specifically, when PD patients used their more affected hand to probe during the DBS-OFF state their DT was elevated by 192% compared to controls (DT, CONTROL: 6.13cm; DT, PD: 6.38cm) and aperture error increased by 105% (mean  $\pm$  SE, control: 0.75cm  $\pm$  0.03; PD: 1.53cm  $\pm$  0.06). 2) DBS improved haptic acuity in PD patients. When using the more affected hand to probe, DBS improved verbal judgments by 26% and decreased aperture error by 20%. 3) Probing with the motorically more affected hand resulted in decreased haptic precision compared to probing with the less affected hand in both the verbal and motor judgments. This study confirms haptic precision decline in PD and offers first evidence that STN-DBS improves somatosensory function by documenting improvements in haptic precision. Further, when the less affected hand probed, haptic acuity improved compared to when probing with the more affected hand. This held true for the verbal as well as for the motor judgments, which was unexpected given that the motor judgment was actually made by the motorically more affected hand. Taken together, the results indicate that STN-DBS not only improves motor, but also haptic function and that DBS-related improvements in movement accuracy are not explained by improvements in motor function alone, but rather by improved somatosensory processing.

## 2-C-25 Finger independency and multi-finger force control in children with DCD

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Children with developmental coordination disorder (DCD) have been reported to have deficits in manipulative skills, which affect their performance in daily and school activities. Previous research suggests that their deficits are not related to a lack of strength, but may be due to difficulties in managing tasks that have many kinetic possibilities. In this study, finger independency and visual force control were investigated in children with and without DCD. Nine children, 9 to 10 years of age, diagnosed with DCD, and nine age-matched typically developing children were asked to perform two isometric tasks, maximum voluntary force production (MVF) and visual force control (VFC), in seven different finger conditions [Index (I), Middle (M), Ring (R), Little (L) IM, IMR, and IMRL]. For the VFC tasks, the participants were asked to continuously control their finger forces at 20% of the MVF. To examine finger force independency, maximum voluntary force (MVF), force enslaving (FE) and force sharing (FS) values were computed. To analyze the ability of children with DCD to visually control their finger forces, the following performance measures were calculated: rate of force change, initial overshoot, coefficient of variation (CV), root mean square error (RMSE), and inter-trial variability. The results from the MVF task showed that children with DCD as compared with TD children (a) produced similar levels of maximum finger force; (b) demonstrated less finger independency; (c) had similar finger-force sharing patterns. In addition, from the VFC task we found (d) larger performance errors in children with DCD; (e) and lower inter-trial consistency as compared to their TD peers. Our findings suggest that the impairments in manipulative skills often observed in children with DCD may be related to deficits in finger independency, as well as their inability to integrate well the use of feedback and feedforward strategies. In addition, the results showed that children with DCD do not have difficulties in reducing the number of joint/muscle-level degrees of freedom in order to achieve a common motor task.

## 2-C-26 Poor motor performance and motor learning in childhood dystonia: speed-accuracy and movement variability in complex daily-life activities

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For most children, repeated practice of a task leads to an improved performance. However, the theory of Failure of Motor learning predicts that both poor sensory feedback and increased motor variability contribute to slow, abnormal or absent learning of a skill. For this reason our hypothesis is that, in childhood dystonia, longstanding deficits of sensory and motor functions interfere with normal improvement in skill with practice. Thus, there is a strong need to understand the link between motor and sensory deficits in childhood dystonia and the failure of subsequent skill learning. It has been shown that in children with dystonia, motor speed is significantly reduced in order to account for increased variability, and the nature of the relationship between speed and accuracy is altered during simple point-to-point movements. Most speed-accuracy tasks are characterized with Fitts' Law, which is a model to account for the time it takes to point at something, based on the size and distance of the target object. Although this is a useful approach, it has mostly been applied in terms of the end-state goal. However it is unknown whether this performance quantification applies to more complex tasks involved in daily life, where subjects are required to manipulate dynamically complex objects and modulate continuous safety margins that are coupled to the object kinematics. In this framework, we have defined a task mimicking eating with a spoon, where the performance is constrained along the entire movement trajectory because a safety margin is required in order to avoid spilling food. Children with dystonia and age-matched control subjects were sat at a table and they were asked to transport a marble in a spoon back and forth between two targets in the sagittal plane, without letting the marble fall from the spoon. The task was performed in 5 blocks on a single day: the first and last blocks were testing; the second, third and fourth blocks were training. During the testing blocks, subjects were asked to move between the two targets as fast as they could, pausing on each target for 2 seconds. For this task, in order to test if motor behavior follows Fitts' Law, movements were performed at 5 different Indexes of Difficulty (ID) by constraining the target widths, without varying the target-to-target distance. During the training blocks the target width was set to the middle ID. The 3 training blocks were separated by enough time to reduce the effect of fatigue. For all blocks, the kinematics of the spoon were recorded by means of a motion capture system. Thus far we found that individuals did indeed follow a Fitts's Law relationship for this dynamically complex task. Further analyses focus on differences in the speed-accuracy relationship, movement variability, trajectory optimization and learning rate quantification between children with and without dystonia. Future related work will investigate if the poor motor skill acquisition in children with dystonia can be improved through enhanced sensory feedback (using a EMG-based vibro-tactile biofeedback device) and reduced perceived movement variability.

## D - Fundamentals of Motor Control

### 2-D-27 Temporal sequencing of instruction cues changes movement related activity in primate primary motor and ventral premotor cortex

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Providing information about an upcoming motor action with time to prepare decreases reaction time, compared to making that same action without a preparatory period. Neural activity during instructed delays plays a preparatory role, organizing the transformation of cues into specific action plans so that motor circuits can be engaged more rapidly at the time of motor execution. For the same intended action (such as a reach and grasp), previous studies would predict that motor areas would issue the same motor command for the same intended action when the action is produced, whether or not it is formulated with the benefit of preparatory activity. In this study, we examined differences in movement related neural activity when cues about the object to be grasped, the grasp type and the go cue were presented one at a time (sequential task) or all at once (simultaneous task). That is, does preparation change subsequent movement related activity in premotor and motor cortex (PMv and MI)? Neural activity was recorded in two macaque monkeys (Macaca Mulatta) using chronically implanted microelectrode arrays in MI (48 channels) and PMv (96 channels). In the sequential task one of two objects was presented followed 2 sec later by a colored light that instructed the monkey to prepare either a power grip, a precision or a key grip (depending on the object). After an additional 2 sec delay, a go cue signaled the monkey to reach to, grasp and lift the object. In the simultaneous task, object, grip-type and go cue were presented at the same time. Both tasks required reaching to the same location and performing the same set of grasps (lifting with the same grip from the same location), only the timing of the object and grip type cues differed between tasks. Differences in firing rates for single units (SNR > 1.2) between the sequential and simultaneous tasks and grip responses were evaluated around start of movement (-0.5 to 0.5s window). Approximately 38% of PMv neurons (ave. = 61 in Monkey R and 145 in Monkey S) and 48% of MI neurons (R=60; S= 77) were "selective" for task; that is, for the same grip type they displayed significant differences in spike counts between sequential and simultaneous conditions ( $p < 0.01$  Kruskal-Wallis test). Neurons were classified as grip selective if they showed a difference in firing for one of the four grip/object conjunctions. A subset of cells showed different grip selectivity in the two tasks, with more cells showing grip selectivity change in PMv (62% in PMv vs. 31% in MI). These data suggest that temporal changes in cue presentation alter movement related activity in PMv and MI, with larger effects in PMv. Taken together, our results support the idea that when identical movements are called for by differently timed cue presentations, PMv generates a novel firing pattern with each context, while MI comes closer to recapitulating the same patterns, thus establishing a more direct link with the kinematics common to both tasks. These results further suggest that ensemble activity in premotor and motor cortex is sensitive to the prior context in which the same ultimate behavior is intended.

### 2-D-28 Differences between the single cell activity of the rostral and caudal subregions of PMd during decoupled/complex visuomotor control

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The planning and execution of visually-guided reach movements has become more complex as we have evolved to use tools. Tool-use typically requires a spatial decoupling between gaze direction and

hand orientation in order to successfully interact with the object of interest. Here we examine the role of the premotor cortex in this behaviour. The goal of this study was to characterize the neural activity within the caudal and rostral subdivisions of the dorsal premotor cortex (PMdr and PMdc) when going from the most basic reaching movement to one that involves a simple dissociation between the action of the eye and hand. We were specifically interested in exploring possible changes in neuronal firing in PMdr and PMdc when the eyes and hand were decoupled by moving along different spatial planes, and whether these differences were topographical. We recorded the local field potential (LFP) and single unit activity within PMdr and PMdc from two rhesus macaques during the planning phase of two types of visually-guided reaching movements. Monkeys (macaca mulatta) were trained to move their eyes and displace a cursor reflecting finger position from a central to a cued peripheral target under standard (direct interaction) and non-standard (eye-hand decoupled) conditions. Similar to our previously reported LFP results, we observed distinct task-related differences as well as topographical differences between the single cell activity of PMdr and PMdc. Specifically during early non-standard reach planning, a significant increase in the discharge rate of single neurons within PMdr were observed when compared to standard reaches. In contrast, PMdc shows this task related increase only during late reach planning. By movement onset, these topographical and task-related differences were less prominent. A significant increase in firing rate during standard reach, when compared to non-standard reach, can be seen within PMdc, while no task related differences were seen within PMdr. Our results suggest functional differences between PMdr and PMdc during visually-guided reaching. PMdr showed enhanced activity during the early planning of a decoupled reach, when the integration of the rule-based aspects were occurring. PMdc is more active during the late planning and early movement phase of a decoupled reach when the reliance on proprioceptive feedback and online control would be important. More broadly, our results highlight the necessity of accounting for the non-standard nature of a motor task when interpreting movement control research data.

## **2-D-29 Startle neural activity is additive with normal cortical initiation-related activation**

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Investigations concerning advance motor preparation in humans during various reaction time tasks have revealed that motor pre tory state can be explored using a loud (124 dB) startling acoustic stimulus (SAS). Startle research has shown that if the requisite motor action is prepared by the individual in advance of the imperative go-signal, the unexpected presentation of a SAS can involuntarily trigger the early release of the prepared action, revealing pre tory-related activation levels in the motor system. To date these studies have predominantly focused on motor activation occurring between the "Get ready" signal and the imperative stimulus (IS) or "go-signal." The purpose of the present experiment was to investigate the time course of activation related to initiation processes occurring after the IS (but before response output) by presenting a SAS at specific time points following the IS. It was hypothesized that the RT facilitation due to SAS would decrease with increasing time after the IS. Participants performed five blocks of 30 trials involving a targeted 20 degree wrist extension movement. In 20% of these trials, a white noise SAS (120dB) was randomly presented 0, 25, 50, 75, 100, or 125 ms following the imperative "go" stimulus. Kinematic and EMG data were collected. Results showed that contrary to expectations, RT facilitation due to SAS did not decrease in conjunction with increased IS-SAS delay. Specifically, premotor RT for control trials was 118 ms, and premotor RTs for SAS trials were 88, 91, 99, 105,

111, and 122 ms for the 0 to 125 ms SAS delays respectively. These findings suggest that additional initiation-related activation resulting from the SAS has an additive effect with the normal initiation activation rate. Based on a neural accumulator model, we propose that once the normal cortical initiation process is underway, additional activation provided does not override the process, but adds to the rate at which activation is accumulated. Supported by NSERC.

## **2-D-30 Feedback effects in a spinal wipe reflex**

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Spinal bullfrogs can execute targeted hindlimb reflexes from multiple starting points in the workspace. These movements can be constructed using a simplified set of controls comprised of a linear combination of muscle synergies (primitive based model). The role of continuous and discontinuous feedback in such a reflex system has been debated over many years. Feedback is essential in creating awareness of self and surrounding. In a spinal prep, biomechanical feedback comes from mainly two sources: cutaneous and proprioceptive segmental inputs. A wipe reflex is known to incorporate cutaneous input both to trigger and to correct. This was reported in correction studies wherein the frog limb responds to a physical obstacle by circumventing it. Proprioceptive information is also used in organization of the wipe reflex. This was seen in experiments where the starting position was altered and the resulting wipe reflex had modulated EMG activity adjusting trajectories to varying initial joint configurations. We have conducted various live animal and simulation studies to examine the effects of various feedback modalities during a wipe. In one study where we applied a robotic elastic field to the ankle, the frog responded by rearranging the motor pattern while still preserving the basic modular architecture of the muscle activations. We found strong evidence for environment stiffness based modulations of the motor primitive amplitudes. We also found associated spinal interneurons that correlated strongly with these modulated responses. Finally we used the Opensim platform to run 3d dynamic simulations on a 5-link, 7-degrees of freedom (dof), 21-muscle actuated model o the frog hind limb. We have previously published the importance of joint space estimation in fine tuning the directionality of a wipe reflex. Our first aim was to validate the efficacy of initial joint space estimation in conjunction with continuous spindle feedback. Certain studies have suggested that the intrinsic musculoskeletal properties of the biomechanical system are capable of handling force perturbations imposed during a wipe reflex. We have found evidence in live-frog experiments that perturbations of the muscle spindle system lead to phase modulation of some motor primitives. In our second aim, we studied the effects of multi-level force perturbations in conjunction with spindle feedback during wipe simulations. We use target error (minimum distance to the target) to quantify the success of the wipe reflex. Our results strongly suggest that initial corrections based on joint angles, significantly improve targeting accuracy, leading to a robust reflex performance with minimal online correction. When continuous spindle feedback was applied in simulation with and without initial position adjustment correction, the paths tend to converge on a central trajectory. In all cases, addition of feedback improves targeting error. However feedback effects on reducing target error also become significant when applied in the context of force perturbations. Therefore a continuous feedback control model would be effective in reducing target errors by enhancing the online correction capabilities of the system, especially earlier in trajectories, away from the workspace center. We are now testing if such adjustments occur in the real system, or real feedback better resembles an intermittent control. Supported by NIH NS072651, NIH NS040412, NSF CRCNS IIS 0827684 .

## 2-D-31 Symbolic encoding of complex actions by movement primitives

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A fundamental problem in neuroscience is to understand how the brain translates a symbolic sequence of action descriptors into the appropriate muscle commands. This is of particular interest in the context of brain-machine interfaces and neuroprosthetics. Our hands are essential for interaction and manipulation of the environment and hence the most complex limbs of our body. Therefore, loss of their function is a severe handicap. Yet, prosthetic replacements - even if mechanically equally sophisticated as real hands - can only replace the most basic functions as the robotic control and coordination of so many degrees of freedom is beyond the capabilities of current computers and algorithms. We take the view that the brain achieves this feat by mapping the necessary computation onto a finite and low-dimensional subset of control building blocks of movement, characterised by high correlation between a subset of the hand's joints - motion primitives. To investigate this possibility, we collected annotated hand movement data of subjects wearing a lightweight and unobtrusive data glove and performing various tasks from their everyday life such as eating, drinking, manipulating keys, etc. (Belic & Faisal, 2010). This data was subsequently analysed by our method which studies the local correlation structures of the data and compares them to pick out all unique components of movement (Thomik & Faisal, 2012). This yields some interesting results: (1) the number of such structures is limited to around 25 per subject and (2) the structures are not unique to a single subject but are found across several subjects simultaneously. This suggests that there may be a universal set of movement primitives which can be augmented and refined to comply with individual needs. Furthermore, this technique allows computing the reverse problem by asking at any point in time which primitive was most likely to have produced the data observed. In this way, we can generate a symbolic sequence ("behavioural barcode") of movement, compressing a very complex movement into a sequence of actions which may potentially reflect the underlying brain activity. Apart from potentially informing on underlying neuronal computations, this compression has also the potential of empowering more sophisticated prosthetic control by matching codes instead of trying to decode exact muscle activation.

## 2-D-32 Patterns of muscle activation in the high frequency bellydance shimmy

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The bellydance hip shimmy is a high frequency rotation of the pelvis in the frontal plane produced by alternately flexing and extending the legs and alternating right/left lateral lumbar spine flexion. This movement requires extensive training to master. The question was to identify muscle activation patterns across subjects as an indication of control strategies. Method: Muscle activation patterns were recorded using electromyography (EMG) from 3 subjects with no training in performing this movement, 5 subjects with less than 7 months of training and an expert who has performed for 30 years. The EMG of ankle, knee, hip and trunk muscles was rectified, filtered at 12 Hz and cross correlated to calculate lags between burst peaks to determine the activation sequence. Results: A clearly identifiable rhythmic pattern of muscle activation, ranging from 3 to 6.5 Hz (across subjects), was identified in knee, hip and trunk muscles in all subjects. Some subjects could only sustain the rhythmic activity for very short periods (~ 2 s). Muscles which typically showed strong clear phasic patterns included vastus medialis (VM), external and internal obliques (EO, IO), longissimus thoracis (LT) at vertebral levels T10, L1, L3 and L4, iliocostalis lumborum (IL) at L2, and multifidus

(MU) at L4. For 8 subjects the general order of activation was the same: VM preceded activity in the erector spinae (ES). Hip and abdominal muscle activity either coincided with or preceded activity in the ES below L2. In 6 subjects, VM activity occurred earlier than at L1 by 26% to 76% of the mean cycle. Activity in the ES at different vertebral levels was asynchronous in 6 subjects occurring in a rostral to caudal order with activation at L4 lagging that at L1 by 14% to 26% of the mean cycle and was greatest for the most experienced subjects. In the three subjects with no training and one with limited training ES activity across L1 to L4 was synchronous (2% to 10% of the mean cycle). The more highly trained subjects appeared to have tighter timing in onset of muscle activation. A coordination ratio is proposed to distinguish between skill levels. The lag between ES L1 and L4 is divided by the total spread in muscle activation onsets. A higher ratio indicates separation in onset timing above and below L3 independently of a greater timing spread. A low number indicates almost synchronous activation across all muscles. Conclusions: Pattern analysis of muscle activity during the shimmy shows a generally distal to proximal order of activation (knees, hips, spine) but with activation in the ES above L3 preceding that below: 1.) VM + HAM (knee/hip extension) 2.) LT L10 + LT L1 + IL L2 3.) LT L4 + MU L4. It appears that with training, timing of activation onsets becomes more focused (active over a narrower range of the cycle) while the ability to independently control activity at lumbar levels becomes more well-developed.

## 2-D-33 Synaptic distribution patterns of rubromotoneuronal cells onto forelimb muscles for a whole-limb movement in the macaque monkey

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The magnocellular division of red nucleus (RNm) is a source of origin of the rubrospinal tract that constitutes a large body of the lateral descending motor pathway. In the monkey studies, the functional role of RNm has been inferred from anatomical and electrophysiological evidence. RNm neurons provide divergent connectivity onto virtually all levels of the spinal cord, particularly a direct projection to C8-T1 motor nuclei, which innervate distal forelimb muscles. RNm cells showed a strong burst when the monkey concurrently employed digits and other parts of forelimbs in a coordinated manner, such as reshaping of a hand in a reach-to-grasp movement (van Kan and McCurdy 2001). These results support a hypothesis that RNm neurons play a key role in coordinating distal and proximal musculature of a forelimb. However, the exact way that RNm contributes to the production of a coordinated spatiotemporal pattern of forelimb movement is still elusive, due to limited information regarding functional projection patterns of individual RNm neurons onto spinal motoneurons for forelimb muscles. To resolve the issue, we attempted to reveal functional linkages (post spike effects, PSEs) between a RNm neuron and forelimb muscles using the spike triggered averaging (STA) technique to identify rubromotoneuronal (RM) cells, thereafter examined the PSE distributions for the RM cells. For STA, we recorded the single-unit electrophysiological activities of rubral cells concurrently with electromyographic (EMG) activities from the 25 muscles including shoulder, upper arm, forearm, and hand muscles while a Japanese monkey was performing a sequence of whole-limb movements consisting of reach-to-grasp and pull of a ball-shaped object (i.e., whole-hand grip), precision grip of pellets, and transportation of pellets to mouth. To identify PSEs we analyzed neuron-muscle pairs with more than 2000 spikes for each rectified EMG signal using multiple fragment analysis. We identified 76 RM cells with 322 cell-muscle pairs. A large proportion of the cells (46/76, 60%) produced PSEs on multiple muscles rather than affecting a single muscle, and the mean muscle field was  $2.42 \pm 1.70$ . The obtained PSE distribution

was proximally biased as compared with a previous report (Sinkjaer et al. 1995). The divergent projection patterns are characterized as being distributed across functionally different muscles and interestingly, the relations of those muscles were predominantly reciprocal. This results suggests that RM system serves to coordinate proximal-to-distal joints by activating multiple inter-joint muscles in a reciprocal manner, which may contribute to producing a specialized muscle synergy pattern. van Kan, P.L. & McCurdy, M.L., 2001. Role of primate magnocellular red nucleus neurons in controlling hand preshaping during reaching to grasp. *J. Neurophysiol*, 85(4), 1461-1478. Sinkjaer, T. et al., 1995. Synaptic linkages between red nucleus cells and limb muscles during a multi-joint motor task. *Exp Brain Res* 102(3), 546-550.

## **2-D-34 The organization and extent of GABA inhibitory interneuronal networks in the spinal cord**

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The spinal cord is a complex network of excitatory/inhibitory interneurons and motoneurons with local organization according to functions. Here, by taking advantage of optogenetics tools, we investigate the question whether the inhibitory interneurons of the spinal cord are organized in a modular way. Furthermore, we study the extent by which we can control the motor behavior of freely moving animals by optogenetic manipulation of the inhibitory circuit of the spinal cord. We used transgenic mice expressing ChR2 in GABAergic neuronal populations (VGAT-mChR2-YFP) in which ChR2-EYFP expression was mostly confined to spinal lamina II and III. Extracellular recordings confirmed that blue light shone on the spinal cord was able to evoke single neuron responses. In anesthetized animals, we evoked movements by both intraspinal and cortical electrical stimulation and we monitored the produced hindlimb isometric force through a force sensor attached to the ankle. When intraspinal electrical stimulation was coupled with non-invasive light stimulation - delivered at the same location - the produced movements was strongly reduced ( $n = 8$  mice, median reduction 43 %,  $p < 0.05$  sign-rank test). Next, we evoked hindlimb movements by (contralateral) cortical stimulation. In this case, light was shone at different levels of the spinal cord (from middle thoracic to middle lumbar with about 0.5-1 mm steps) by means of a movable optical fiber. Movements produced by electrical stimulation of the motor cortex were strongly reduced when light stimulation was applied. Light stimulation of the middle-lower thoracic sector had the strongest suppression of all the hindlimb movements evoked by cortical stimulation (90% reduction,  $p < 0.05$  sign-rank test,  $n = 4$  mice). Taken together, these two experiments illustrate that optogenetic stimulation of the GABAergic interneurons effectively suppressed movements and further the suppressive effects propagates in a rostro-caudal manner. Finally, we tested the effect of light activation of GABAergic interneurons in awake freely moving animals by monitoring EMG activity and by behavioral testing (ladder walking). A brief period of optical stimulation of the spinal cord produced a loss of muscular tone (latency of EMG suppression 6.55 ms) in all of the muscles i.e. agonist and antagonist, caudal to the stimulated point. Furthermore, long trains of optical stimulation suppressed or strongly compromised the walking pattern (correct placement of the paws on the rungs in the period of light ON vs. light OFF, forelimb  $p > 0.05$ , hindlimb  $p < 0.05$ , ranks-sum test,  $n = 8$  animals), often resulting in the dragging of the affected hindlimb. As soon as the light was turned off, the animal immediately recovered his stance and normal walking behavior. In conclusion, the modular organization of the spinal cord observed in previous experiments for motoneurons and glutaminergic neurons, is not present for inhibitory interneurons. Furthermore, we have shown that it is possible to control the inhibitory circuit of the spinal cord in freely moving animals with a millisecond resolution.

## **2-D-35 Dissociating the role of motor cortex in the acquisition and control of learned motor sequences**

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Motor skill learning underlies much of what we do, be it hitting a tennis serve, playing the piano, or simply brushing our teeth. Yet despite its importance, little is known about the circuits that implement the learning process. Here we explore the role of motor cortex by lesioning it in rats trained on a motor skill. A possible confound of lesion studies is that they may conflate motor cortex's role in controlling the motor output with its role in learning it. To get around this we trained rats to produce temporally precise movement sequences, a skill that, once mastered, survives motor cortex lesions (results presented at last year's NCM). The task requires animals to press a lever twice with a specified inter-press-interval (typically 700 ms), with the interval range for reward narrowing with learning. While the motor control challenges of the task are deliberately modest, the movement sequences that emerge over months of training are both complex and exquisitely precise. The fact that motor cortex is not required for generating these learned motor sequences, allows us to disambiguate its role in learning from its role in production. To test its role in the acquisition and adaptive modification of learned motor sequences, we lesioned motor cortex, including both the primary and secondary forepaw representation. Animals lesioned after having learned the task to criterion were trained to shift the time interval between the lever presses. They were able to modify their motor output at a rate comparable to controls (i.e. animals with intact cortex), suggesting that motor cortex is not required for adaptive modification of already learned motor sequences. These modifications were typically confined to speeding up or slowing down existing motor gestures in the sequence to meet the new demands of the task. Animals lesioned before being exposed to the task, however, were incapable of learning or mastering the task to anywhere near the extent of controls. While lesioned animals could press the lever, and were able to slowly modify their mean intertap interval, they were unable to properly terminate the lever pressing after unrewarded presses, as required by the task. While lesioned animals converged onto motor sequences that showed some level of reproducibility across trials, they were significantly more variable than controls. Our results are consistent with motor cortex being necessary for organizing the overall structure of a learned motor sequence. Once this 'meta-structure' is acquired and consolidated, motor cortex does not seem to be required for adaptively shaping the timing and kinematics of the underlying motor elements.

## **2-D-36 Context-dependent changes in ventral premotor cortex grasping-related activity: effects of object orientation and multiple grip affordances**

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Ventral premotor cortex (PMv) is a key node in the parieto-frontal network specialized in transforming visual information representing the shape of objects into hand postures best suited for grasping them. In this project we analyze whether PMv neural activity associated with a given grip strategy is affected by features of the target object not related to the part being grasped. It has been theorized that PMv may represent archetypal 'grip affordances' linked to specific objects. This experiment explores how the presence of multiple possible affordances interacts with object orientation in PMv. Neural activity was recorded in a behaving monkey (*macaca mulatta*). Three objects were presented to the monkey using a motorized turntable. All of them had a central cylindrical shaft of identical

dimensions. A horizontal disk was attached at the top of object A. A vertical plate was attached to object B. Object C was identical to object B, except flipped upside down (with the vertical plate attached to the bottom of the object). All three objects were mounted on rods so that they could be lifted vertically. The positioning of the rods was such that the cylindrical shaft of each object was placed at exactly the same height. The monkey began each trial in the dark. After holding two hand-in-place contact switches for one second, an object in front of the monkey would be illuminated (objects were presented pseudo-randomly using the turntable). After one second, a grip instruction light was illuminated above the object. A red light was used as a power grip instruction, while a yellow light was associated with either a key grip (object A) or precision grip (objects B and C). After a 2 second delay, the grip cue light was extinguished and a green light was illuminated. The green light acted as a 'go cue' instructing the monkey to grasp and lift the object using the cued grip. After holding the object for 200ms the monkey was rewarded with a sip of fruit juice. Neural activity in PMv was recorded using a chronically implanted microelectrode array. The firing patterns of ~100 simultaneously recorded neurons were characterized using dimensionality reduction techniques based on spike train similarity. During the object presentation phase, three distinct patterns of activity were observed, associated with each of the test objects. Throughout the delay period these activity patterns gradually changed, evolving into six different states associated with specific object-action combinations by the time of movement execution. Our results demonstrate that a power grip executed within the context of different objects can be associated with different patterns of activity, even though the part of the objects being grasped is identical in terms of size, orientation, and position relative to the monkey. Such context dependent changes can be observed within a single object when it is presented at a different orientation, even though the part of the object being grasped with a power grip is symmetrical and does not require a different grasping strategy when the object is inverted. Our findings suggest that PMv neural activity is not simply a representation of either object geometry or grasping strategy, but instead gradually incorporates available information into dynamic activity patterns which ultimately lead to distinct network states associated with specific object-action combinations.

## 2-D-37 The tuning of human motor response to uncertainty and risk in a dynamic environment task

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The role of motor uncertainty in discrete or static space tasks, such as pointing tasks, has been investigated in many experiments. These studies have shown that humans hold a highly accurate internal representation of their intrinsic motor uncertainty and compensate accordingly for this variability. Furthermore, experiments imposing additional extrinsic motor and sensory variability have shown that subjects still respond near optimally, even as risk increases. While static conditions provide an important foundation to understanding the relationship between uncertainty, risk, and movement, they rarely appear in natural situations. The aim of this study was to investigate how humans respond to uncertainties in a dynamic environment despite indeterminate knowledge of the outcomes of specific actions. Our hypothesis was that subjects would maintain appropriate safety margins determined by uncertainty, noise, and risk, but more importantly, that they tune their statistical behavior to uncertainty based on cost. In this experiment, subjects maintained one-dimensional "steering" control of a vehicle in an iPad® driving simulation. The speed of the car was determined solely by position on a two-lane road. While on the road, driving in a lane yielded the maximum possible velocity, driving on the dashed line between lanes caused the vehicle to slow down, and hitting the grass along the side

of the road brought the car to a complete stop. The points earned were inversely proportional to the time taken to complete each trial. In addition to inherent motor variability, uncertainty was artificially enhanced by corrupting the responses of the subject with horizontal perturbations at a frequency of 30Hz. The baseline task contained five levels of uncertainty including no additional variability. A subsequent task introduced high risk into the scenario by replacing grass on one or both sides of the road with water, which if hit would incur a very high penalty. As expected, preliminary results depicted position as a bimodal probability density function at low uncertainty levels, implying that subjects tended to keep towards the center of a single lane. As uncertainty increased, the peaks of the bimodal distribution tended toward one another. At high uncertainty, most subjects' position distribution exhibited a well-fit Gaussian function, indicating that they spent most of the time in the center of the road. The position corresponding to a peak plotted against uncertainty level fit separate linear regressions for each task. In the task with high risk on both sides the linear regression was shifted down as compared to the low risk task, indicating that the rate of convergence toward the center of the road in terms of increasing motor variability did not change, but that subjects acted more conservatively at all uncertainty levels. Conversely, in the task with high risk on one side as compared to low risk, the linear regression was shifted up. Subjects drove in the lane opposite to the high risk and stayed farther away from the center of the road on average. These results demonstrate the awareness of subjects to dynamically changing task cost and provide evidence that they avoid risk even in the absence of errors. It is evident that humans tune their statistical behavior based on cost, taking into account entire probability distributions of possible outcomes with long tails in response to environmental uncertainty.

## 2-D-38 Effects of walking speed on intrastride electrocortical activity in humans

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High-density electroencephalography (EEG) and independent component analysis (ICA) can reveal electrocortical activity in humans during walking and running (Gwin et al. 2010, 2011). Previously our laboratory demonstrated that multiple cortical areas (anterior cingulate, posterior parietal, and sensorimotor) all exhibit significant intra-stride changes in spectral power coupled to the gait cycle. The purpose of this study was to examine how walking speed and cognitive dual-tasks affect the electrocortical activity using similar methods. Falls during ambulation and mobility disorders, more generally, are a clinically important issue for many elderly and neurologically impaired individuals. Our goal was to determine if high-density EEG and ICA could reveal how healthy young individuals adapt their cortical activity to deal with increasing challenges in walking speed and cognitive attention. 20 healthy young subjects walked on a treadmill at a range of speeds with and without a cognitive task. The cognitive task was a visual Brooks Spatial Memory task with a 3x3 grid of numbers to remember and put in order (Brooks et al. 1967). We recorded 256-channel EEG, motion capture data, ground reaction forces, electromyography (EMG), and cognitive task response data from a hand-held key pad. We used Adaptive Mixture Independent Component Analysis (AMICA) to separate EEG signals into maximally independent component signals representing brain sources, muscle sources, and artifacts (Delorme et al. 2012; Onton et al. 2006). We modeled each brain source with an equivalent current dipole using an inverse source modeling algorithm. We clustered these electrocortical sources across subjects based on similarities in dipole location, spectral power and scalp topography. Results indicated clusters of interest in the sensorimotor, anterior cingulate, and posterior cingulate areas. For each cluster, we created an event-locked plot of spectral power relative to a whole-trial baseline. In motor and motor

related areas, electrocortical sources primarily exhibited an increase in alpha power around double support. This alpha power increase at double support was more pronounced with increasing speed. We also found high-gamma power increases around double support for several motor clusters, potentially indicating increased attention and focus during double support. Furthermore, during dual-tasking, we found a significant increase in theta band power during memory retrieval in clusters associated with working memory. This is consistent with several studies showing that periods of intense cognitive activity increase theta activity in human cortex (Gevins et al. 1997; Krause et al. 2000; Burgess et al. 2000). Results did not demonstrate significant gait-locked spectral power differences in motor areas between walking with the cognitive task and walking without the cognitive task. Our findings indicate that the human sensorimotor cortex is actively involved in the control of gait and that cortical involvement likely increases with speed. The results of this and future studies could provide insight into the neural mechanisms of gait control and have important implications for the field of gait rehabilitation. The long term hope is to apply the separate techniques to elderly and neurologically impaired individuals to help with diagnosis and treatment. Supported by NIH R01 NS073649 and ARL W911NF-10-2-0022.

## **2-D-39 Response properties in ventral and dorsal premotor cortex during natural reach to grasp movements**

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The primate reach to grasp is a complex, ethologically relevant behavior that requires coordination between the proximal and distal segments of the upper limb. Electrophysiological data have provided some evidence for two networks supporting reaching and grasping movements: a dorsal network that is specialized for movements of the proximal segment of the limb, and, a ventral network to subserve grasping. The extent to which these two networks may topographically organize premotor cortex remains unresolved. Indeed, single unit recordings from ventral premotor cortex (PMv) show that cells in the rostral portion respond to distal movements whereas cells in the caudal portion modulate with proximal movements. Additionally, there is some recent evidence of grasp selectivity in dorsal premotor cortex (PMd). In this study, we explore responses in PMv and PMd during natural reach to grasp movements. Experimental procedures are described in detail in Saleh, et al., 2012, *J. Neurosci.*, and will be briefly recapitulated here. Two male rhesus macaques (monkeys J and L) were trained to reach and grasp objects with their left hand. The monkey's vision was blocked prior to object presentation. A manually controlled pneumatic piston would remove the vision block at the start of each object presentation. On a given trial, a robot would present an object at one of four preprogrammed locations. The set of objects consisted of five geometric shapes designed to evoke a variety of precision and power grips. While the animals performed this task, we monitored the kinematics of the arm and hand using a 10 camera motion tracking system (Vicon). Unit spiking activity as well as local field potentials were collected from PMd and PMv using 96 channel microelectrode arrays (Blackrock Microsystems) implanted in each area. Spike waveforms were sorted offline using software (Plexon). A variety of discharge patterns was observed in each area's spiking activity. We performed a metric space analysis to test the extent to which populations of neurons in PMv and PMd encode information about object type and location. We found that both areas convey information about object location, with PMv being slightly more informative. Based on our preliminary metric space analysis, neither PMd nor PMv carried a significant amount of information about

object type. However, the response profiles of single units are visually distinct, suggesting that at least some object type information is available.

## **2-D-40 Increased motor output is associated with M1 motor map expansion during isometric finger contraction**

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Precise control of finger movement is vital for activities of daily living and relies on finely graded contraction of agonist-antagonist muscles. This is not trivial from a neural control perspective because in the motor cortex (M1), corticospinal neurons innervating muscles that are primary movers of individual fingers (e.g. intrinsic hand muscles) are intermingled with those innervating multi-finger complexes (e.g. long forearm muscles). As such, previous studies measuring motor evoked potentials (MEP) with transcranial magnet stimulation (TMS) to assay corticomuscular excitability, have reported increased MEP amplitude in synergistic muscles, and decreased MEP amplitude in relaxed nonsynergistic muscles during movement initiation of a neighboring muscle. One possibility that has been proposed is that M1 muscle fields are akin to visual receptive fields, and use a mechanism akin to surround inhibition (SI) to achieve the desired muscular activation. Indeed, empirical data suggest that SI in M1 may be associated only with low motor output such that decreases in MEP size of nonsynergistic muscles is diminished when a contraction is maintained or forces of >40% of maximum voluntary contraction (MVC) are required. Yet no study has described the mechanism behind this switch, and it remains unclear how the distribution of corticospinal muscle fields in M1 change as a function of motor output during sustained contraction. In order to examine the relationship between SI and motor output, we quantified the amplitude and distribution of TMS-evoked M1 maps of intrinsic hand and long forearm agonist-antagonist muscles during isometric contractions involving graded force levels. Five healthy right-handed subjects participated after providing institutionally approved informed consent. Subjects were seated with their right arm-hand stabilized and the index finger pressing a force sensor. Using frameless neuronavigated TMS, each subject's contralateral M1 "hotspot" and resting motor threshold for the right first dorsal interosseous (FDI) muscle was determined. For mapping, TMS (110% of resting threshold) was applied to a broad territory spanning the sensorimotor cortex extending from the FDI hotspot by 2.5 cm in all directions. Subjects were required to exert force to move a cursor on a screen toward a target corresponding to 0% (rest), 20%, and 40% of MVC. TMS stimulation was triggered automatically by a TTL signal when the target force was maintained >500ms, ensuring that MEPs were systematically recorded at constant force levels and muscle spindle lengths (contraction was isometric). MEPs were recorded from two "single-mover" agonist-antagonist pairs (FDI and extensor indicis) and two extrinsic "multi-mover" agonist-antagonist pairs (palmaris longus and extensor digitorum). We quantified the "motor map" for each muscle by interpolating MEP values onto a 5x5cm grid (0.5 cm spacing). Outcome measures included map area, volume, and mean excitability. Comparison of motor maps across the graded force levels revealed an active expansion of the excitable area with minimal change in position of the hotspot. This was evident for both the FDI and long forearm muscles in all subjects. Our data suggest that increased motor output is associated with expansion of cortical activation involving multiple muscles, perhaps due to the loss of surround inhibition.

## 2-D-41 Towards the human ethome

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Natural human interaction with the physical environment depends crucially on voluntary movement of our limbs. In turn, many neurological disorders affect normal movement, making changes in movement behaviour a good candidate for biomarker. Yet, quite unlike genetic diseases which we can easily pinpoint thanks to our knowledge of the human genome, we have no equivalent “ethome” to help quantifying changes in daily motor behaviour. In this work, we present a new experimental data making use of state-of-the-art, wearable and wireless motion capture suits (45 DOF) and data gloves (18 DOF per hand) to capture human movement at high resolution over prolonged periods of time in a naturalistic settings. Subjects are placed in environments of their natural life such as a bedroom, a workplace, their living room and a breakfast/kitchen and free to behave as they naturally would. We annotate the behaviour online using custom-written software. Video recordings are used for double-checking of annotations and offline analysis. We tested this new experimental paradigm on 44 healthy subjects aged between 20 and 30. Results show that both average movement durations and inter-movement intervals (IMI) follow an exponential distribution such as observed in a multitude of other natural phenomena. Furthermore, preliminary analysis of the data suggests that the true dimensionality of natural movement is much lower than the actual degrees of freedom of the body. This observation suggests that the brain might correlate the movement of various joints in order to reduce computational complexity of movement and take advantage of pre-wired or learnt movement synergies of building blocks. To the best of our knowledge, this work represents the first data collection and analysis paradigm allowing to capture natural human movement data in unconstrained settings, which were going to make public shortly.

## 2-D-42 Proprioceptive representations of the hand in primary somatosensory cortex

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The vestibular system senses head motion produced by linear acceleration or rotation and generates compensatory motor adjustments that assure posture, balance and gaze. Sensory information routed through the lateral vestibular nucleus (LVN) provides ipsilateral excitatory input to all segmental levels of the spinal cord. Moreover, physiological studies have shown that LVN neurons selectively activate motor neurons innervating extensor muscles while inhibiting flexor motor neurons, so preserving posture and balance. Nevertheless, the principles that bind sensory-motor organization to the function of LVN neurons have remained unclear. We have applied molecular genetic and recombinant viral tracing techniques to explore the organizational rules by which LVN neurons encode and transform sensory input, and the motor behavioral consequences of inactivating sensory-defined sets of LVN neurons. We explored the specificity of LVN inputs to functionally defined motor pools by injecting an AAV2/1-GFP expression vector into the LVN and its descending spinal axons, and in parallel visualizing motor neuron somata and dendrites by injecting a AAV6-Cre vector into individual hindlimb muscles in a conditional floxed ROSA-tdTomato reporter line. Analysis of ankle and knee extensor motor neurons revealed that ~89% of gastrocnemius and ~60% of vastus lateralis motor neurons received direct synaptic contacts from LVN neurons, whereas tibialis anterior and biceps femoris flexor motor neurons lacked LVN input. Conversely, retrograde rabies transynaptic tracing studies revealed labelled LVN neurons after rabies injection into extensor but not flexor hindlimb muscles. These studies document a

striking anatomical specificity of motor neuron innervation by LVN neurons, and our current studies are exploring the developmental origins of extensor specificity. To gain genetic access to LVN neurons defined by specific sensory input we used rabies virus-based anterograde trans-synaptic tracing from sensory neurons supplying individual semicircular canals or otolith organs. This method permits identification of subsets LVN neurons that receive direct input from individual sensory organs, and the tracing of their projections to motor neurons in the lumbar spinal cord. In addition, we eliminated sensory-defined LVN neurons by semi-circular canal injection of a rabies virus vector encoding the diphtheria toxin receptor, combined with focal diphtheria toxin injection in lumbar spinal cord. Preliminary studies have begun to define vestibulo-motor behavioral defects associated with acute elimination of sensory-defined subsets of LVN neurons.

## 2-D-43 Sensory-motor organization of vestibulospinal circuits

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The vestibular system senses head motion produced by linear acceleration or rotation and generates compensatory motor adjustments that assure posture, balance and gaze. Sensory information routed through the lateral vestibular nucleus (LVN) provides ipsilateral excitatory input to all segmental levels of the spinal cord. Moreover, physiological studies have shown that LVN neurons selectively activate motor neurons innervating extensor muscles while inhibiting flexor motor neurons, so preserving posture and balance. Nevertheless, the principles that bind sensory-motor organization to the function of LVN neurons have remained unclear. We have applied molecular genetic and recombinant viral tracing techniques to explore the organizational rules by which LVN neurons encode and transform sensory input, and the motor behavioral consequences of inactivating sensory-defined sets of LVN neurons. We explored the specificity of LVN inputs to functionally defined motor pools by injecting an AAV2/1-GFP expression vector into the LVN and its descending spinal axons, and in parallel visualizing motor neuron somata and dendrites by injecting a AAV6-Cre vector into individual hindlimb muscles in a conditional floxed ROSA-tdTomato reporter line. Analysis of ankle and knee extensor motor neurons revealed that ~89% of gastrocnemius and ~60% of vastus lateralis motor neurons received direct synaptic contacts from LVN neurons, whereas tibialis anterior and biceps femoris flexor motor neurons lacked LVN input. Conversely, retrograde rabies transynaptic tracing studies revealed labelled LVN neurons after rabies injection into extensor but not flexor hindlimb muscles. These studies document a striking anatomical specificity of motor neuron innervation by LVN neurons, and our current studies are exploring the developmental origins of extensor specificity. To gain genetic access to LVN neurons defined by specific sensory input we used rabies virus-based anterograde trans-synaptic tracing from sensory neurons supplying individual semicircular canals or otolith organs. This method permits identification of subsets LVN neurons that receive direct input from individual sensory organs, and the tracing of their projections to motor neurons in the lumbar spinal cord. In addition, we eliminated sensory-defined LVN neurons by semi-circular canal injection of a rabies virus vector encoding the diphtheria toxin receptor, combined with focal diphtheria toxin injection in lumbar spinal cord. Preliminary studies have begun to define vestibulo-motor behavioral defects associated with acute elimination of sensory-defined subsets of LVN neurons.

## E - Integrative Control of Movement

### 2-E-44 Interception of a ball falling on an inclined plane

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Interceptive and avoidance actions often involve interactions with accelerating objects; successful actions versus these moving objects need predictive estimates of their motion to overcome our sensory-motor delays. Studies in neurophysiology and psychophysics have shown that whereas vision is able to provide critical information about the direction, position and velocity of moving objects, human vision estimates accelerations very poorly (threshold for speed changes is at least four-times worse than threshold for speed discrimination). Such a limited ability to process optical acceleration should adversely affect interaction with accelerating objects. We have previously shown that when intercepting vertical free-falling objects, an internal model of gravity (1g model) is used to predict object motion. Here we show that the internal representation of a falling object is a more general model, constructed upon experience and taking into account also air drag and surface friction. This internal model of fall is applied not only in the case of 1g motion (vertical free-falling motion) but also when object acceleration is a fraction of g. A real ball rolled downward on a plane that could take one of three different inclinations relative to the horizontal: 30°, 45°, 60°. For each inclination, the ball descended with different acceleration profiles. In a first series of experiments, subjects were asked to hit the falling ball in a fixed position below the lower border of the inclined plane after the ball had left the plane. Visual information of the whole trajectory (over the inclined plane and the subsequent path in air) and haptic information at contact were provided (i.e. information on mass, velocity, direction of ball motion). In a second series of experiments, subjects performed a task similar to that of the first series of experiments, but visual information of ball trajectory was provided only on the plane, because ball motion was suddenly stopped prior to exit from the plane. In a third series of experiments, subjects had the same visual information as in the second series of experiments, but they were required to draw in air the prosecution of ball trajectory once the ball left the trailing edge of the inclined plane; visual or haptic feedback about ball trajectory in the air were not provided. All series of experiments showed that subjects were able to construct a model of fall taking in account gravity effects on object motion, air drag and surface friction. On-line visual information was used to adjust 1g predictive model.

### 2-E-45 Strong positive correlations between variability and sensitivity promote homogeneous linear motion detection thresholds across a heterogeneous otolith afferent population

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As we navigate through the world, our brain relies on multisensory cues originating from visual, vestibular and proprioceptive systems in order to maintain our balance, posture and stable gaze as well as to perceive self-motion. Specifically, otolith organs of the vestibular system function as linear acceleration detectors at the earliest stages of processing and provide a vital source of information about the linear motion of the head in space. Loss of vestibular input can lead to an increase in the propensity to fall, postural instabilities, as well as deficits in motion perception. To date however, despite a fairly mature body of research on self-motion perception, our knowledge about how the vestibular periphery contributes to perceptual abilities is quite limited. Here, we recorded the activity of single afferents in

macaque monkeys during linear motion along their preferred directional axes. We directly measured how well an ideal observer could discriminate between different head accelerations based on neural activity (i.e. detection thresholds) over a wide range of frequencies (0.5-16Hz) corresponding to physiologically relevant stimulation. We found that neuronal threshold values for single otolith afferents were substantially higher than perceptual values even when an optimal filter was used to provide an estimate of neuronal firing. Surprisingly, we further found that afferents with large differences in resting discharge variability and response sensitivity showed no significant differences in neuronal thresholds. We found that this was because increases in variability were effectively offset by increases in sensitivity; a coding strategy which markedly differs from that used by canal afferents to encode rotations (Sadeghi et al., 2007). Finally, using Fisher information, we show that pooling the activities of multiple otolith afferents gives rise to neural thresholds that are comparable with those measured for perception. Taken together, our results provide unexpected insight into the influence of neuronal discharge variability on sensory encoding, and strongly suggest that higher order structures integrate inputs across afferent populations to provide our sense of linear motion. References: Sadeghi SG, Chacron MJ, Taylor MC, Cullen KE (2007) Neural variability, detection thresholds, and information transmission in the vestibular system. *J Neurosci* 27:771-781.

### 2-E-46 Differential modulation of inter-hemispheric interactions during maximal force production and submaximal force control tasks

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Submaximal force control and maximal force production involve distinct motor requirements. Specifically, submaximal force control involves ongoing regulation of both the magnitude and timing of force production to meet a task goal. In contrast, maximal force production involves generation of force without explicit requirements of force modulation. How the neural control mechanisms for these distinct motor tasks differ remains unclear. Here we investigated task-related differences in inter-hemispheric interactions during: (a) maximal force production and (b) submaximal force control. Eleven, right handed, young adults (age  $28.36 \pm 5.2$  yrs) performed unimanual and bimanual isometric power grip during maximal voluntary contraction (MVC) and submaximal force control with visual feedback. The bimanual MVC was determined as the maximum total force produced when contracting both hands simultaneously. Submaximal force levels (30% & 60% MVC) were calculated for unimanual and bimanual conditions as a relative percentage of each participant's MVC. We used the ipsilateral silent period (iSP) (i.e., the duration of interruption of voluntary muscle activity by focal transcranial magnetic stimulation (TMS) of ipsilateral motor cortex) to study inter-hemispheric interactions. Our data identified two novel findings. First, iSP duration was significantly ( $p < 0.05$ ) increased during submaximal force control ( $43 \pm 4.8$  ms) relative to MVC ( $32 \pm 3.1$  ms). This finding suggests that the precise spatio-temporal modulation of forces during submaximal force control is mediated by an increase in inter-hemispheric inhibitory processes. Second, iSP duration was greater in bimanual ( $39 \pm 3.4$  ms) as compared to unimanual ( $34 \pm 2.9$  ms) tasks. Increased inter-hemispheric inhibition may account for the specific differences in motor performance during bimanual relative to unimanual tasks. Together, these findings demonstrate task-specific modulation of inter-hemispheric interactions. Importantly, the extent of inhibition between hemispheres is influenced by the nature and the complexity of motor control requirements.

## 2-E-47 Fitts' Law relationships of single-muscle myocontrol with Bayesian-filtered surface EMG in healthy adults and children with dystonia

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Myocontrol, the control of electromyographic (EMG) signals, holds great promise because it has the potential to provide flexible and accurate control of prosthetics that approaches the quality of normal movement. Surface EMG (sEMG) is a non-invasive way to capture EMG, but the high level of noise makes it difficult to use in real-world applications. This issue may be addressed with Bayesian non-linear filtering of sEMG, which responds rapidly to sudden increase in force but changes little during periods of low variability in the sEMG input signal. We have developed a Fitts' Law paradigm to assess the information transmission during myocontrol under different filtering schemes. Previous work has shown that movement times in healthy and naive young adults resembles a Fitts' Law relationship, and single-muscle myocontrol with Bayesian-filtered sEMG has a performance level comparable to that of force control. In our work, we further explore the characteristics of myocontrol using Bayesian-filtered sEMG through two tasks. In task 1, we further examined the applicability of Fitts' Law to myocontrol in young, healthy adults to determine if Fitts' Law holds in myocontrol or if movement time depends more heavily on 1 of the 2 parameters (distance or width). In task 2, we conducted a double-blinded randomized study comparing Bayesian-filtered sEMG to linear-filtered sEMG in healthy adults, children with dystonia, and age-matched control children. For both tasks, subjects were asked to control isometric contractions of the FDI muscle of their dominant hand with visual feedback of filtered sEMG. Vertical position of a cursor was proportional to the level of contraction of the FDI. Subjects were instructed to move the cursor into targets of different sizes as fast and accurately as possible and maintain the position for 500 ms. Trials where this 500 ms hold time was not accomplished within 3 seconds were considered unsuccessful. For task 1, targets were divided into 2 groups of 10. In one group, 5 distances were selected for 2 widths, and in the other group, 5 widths were selected for 2 distances. We found that Fitts' Law holds under most conditions, however, targets at a small distance required more movement time. This suggests that baseline sEMG noise makes stabilizing around low contraction levels more difficult and movement time may approach a lower limit as index of difficulty decreases due to small distances. In task 2, indices of performance of the Fitts' Law relationship were calculated for six targets, and overflow was measured in the children with dystonia. Preliminary results suggest the quality of myocontrol with Bayesian filtering will be improved enough over linear filtering to allow the potential for myoelectric device control, even though error rates and movement times are higher in children with dystonia. Increased error rates and movements times may imply that children with dystonia need more time to reach targets, more lenient target parameters, or both. In summary, we have found that myocontrol using Bayesian-filtered sEMG tends to follow Fitts' Law for most levels of muscle contraction, and the performance level is good enough to warrant explorations into using sEMG with Bayesian filtering as a way for children with motor disorders to control devices.

## 2-E-48 Intermediate EMG prediction from M1 discharge improves online cursor control performance

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With the increasing use of neural recordings to control prostheses, the theoretical question of the relation between primary motor cortex (M1) activity and movement parameters has taken on practical

importance. Although most current neuroprosthetic systems focus on the extraction of kinematic signals from M1 activity, it has been long established that M1 contains a significant amount of muscle activity (EMG)-related information. We have recently demonstrated that the tuning of M1 neurons changes with posture in much the same way that muscles do, and that neuron-to-EMG predictions generalize better across postures than do predictions of extrinsic force direction. Here we compare further, the neuron-to-muscle and neuron-to-force relation through analysis of the quality of both offline predictions and online neuroprosthetic cursor control by a monkey. The monkey was trained to move a cursor to targets on a computer monitor by applying 2D isometric torque about the wrist. We compared the monkey's normal 'hand-control' performance with that of a 'brain-control' paradigm using two types of linear decoders: a direct neuron-to-force model and a neuron-to-EMG-to-force model cascade. The models were computed by linear regression from offline data. The EMG decoder cascade consisted of an initial prediction of seven forearm EMG signals through a neuron-to-EMG model, which then served as the inputs for an EMG-to-force model. The direct force decoder and the EMG cascade decoder yielded approximately equivalent force prediction in terms of variance accounted for during hand control. However, during brain control, the EMG cascade decoder was superior for all performance metrics analyzed, including the time to target, path length and success rate. Importantly, the EMG cascade decoder significantly reduced the cursor jitter. This effect was consistent with the transfer function of the EMG cascade decoder, which matched that of hand control more closely than did the force decoder. Applying an appropriate low-pass filter to the force decoder output eliminated the difference in frequency content, but unavoidably introduced a delay that affected the monkey's performance. We are continuing to investigate the properties of these predictions that give rise to superior control. Our results show that we can take advantage of the intrinsic relationship between M1 neurons and muscles to develop better decoders for neuroprostheses.

## F – Posture & Gait

### 2-F-49 Varying body weight support in bipedal stepping rats: Changes in locomotor behavior are partially related to alterations in hindlimb posture

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Alterations in body weight support (BWS) have been shown to result in changes in locomotor performance during treadmill stepping in rats following spinal cord injury (SCI). It is thought that changes in weight assistance primarily affect stepping through alterations in load-related stretch of the plantarflexors and activation of cutaneous afferents on the plantar surface of the foot. However, locomotor behavior may also be affected through additional mechanisms, including changes in hindlimb posture brought about by changing the orientation of the rat's torso relative to the stepping surface, as often occurs with increased levels of BWS. The purpose of this study was to investigate the extent to which differences in stepping performance between a high loading condition (60% BWS) and low loading condition (90% BWS) can be attributed to mechanisms unassociated with load-related afferent information. Sixteen female, Sprague-Dawley rats underwent spinal cord transection surgery as neonates and received four weeks of bipedal locomotor training using a robotic device that included a BWS mechanism, two robotic arms that attached to the animals' shank, and two reciprocating platforms that served as the stepping surface. The reciprocating platforms were instrumented with force sensors to determine ground

reaction forces generated by the stepping animal. Following 2 and 4 weeks of training, step length, step height, swing velocity, and a novel measure of stance duration were evaluated for all animals while stepping under 3 conditions: 90% BWS, 60% BWS, and 90% with a load applied directly to the animal's hindlimb via robotic arm. The hybrid 90% BWS + robot applied stance field presented a condition in which the animal experienced both a change in hindlimb posture due to increased BWS and a plantarflexion load that approximated stepping under the 60% BWS condition. The results indicated that loads applied via changes in BWS vs those applied directly to the animals' hindlimbs did not result in similar stepping behavior. In particular, stance duration was significantly increased when load was increased by reducing BWS, but was unaffected when load was increased through the use of the robotic arms. In addition, horizontal swing velocity was significantly increased under the 60% BWS condition when compared to both of the 90% BWS conditions. These results suggest that under the conditions studied here, mechanisms unassociated with plantarflexion load were important factors in the determination of the timing and duration of stance, hindlimb extension during stance, and forward swing velocity. These results might be explained by differences in hindlimb posture, as trunk orientation angle was significantly different between the 60% and 90% BWS conditions when a small subset (n=5) of these animals was analyzed. Hindlimb posture and trunk orientation should therefore receive careful consideration in future experiments involving body weight support and bipedal stepping in rats. This work was supported by NSF 85688.

## **2-F-50 The role of attention in fall avoidance: Evaluation of dual task interference with postural and visual working memory tasks in young and older adults: Does capacity limitation influence postural responses?**

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Increased incidence of falls among older adults has been associated with balancing and walking under dual task conditions (performing two tasks at once). Young adults readily perform motor and cognitive tasks simultaneously (e.g. reading e-mail on a hand held device while walking) with little impact on performance of either task; however similar activities among older adults more commonly result in a fall. Studies showing interference patterns under postural dual task conditions, in which postural and high-level cognitive tasks are paired, suggest a sharing of attentional resources between the two independent modalities. Not all of the postural research, however, shows interference in the performance of postural and cognitive tasks under dual conditions; both the degree of difficulty of the tasks and the nature of the attentional resource targeted during the cognitive task influence the presence of an interference pattern. Some cognitive tasks have increased processing demands such that information stored in working memory must be manipulated to complete the task (e.g. Brooks spatial memory task - requires maintenance and updating of a mental matrix). The visual change detection task (detection of color change in 1 square from arrays of 2, 4, or 6 squares) used in the current study requires only that information be stored in working memory, thus we propose it provides a more sensitive tool to study the nature of the interaction between cognitive processing and the control of posture. An estimate of visual working memory capacity (VWMC) can be contrasted between single and dual task conditions. Extensive evidence shows the decline in cognitive function associated with aging; however no previous research has evaluated the effect of aging on visual working memory capacity using the visual change detection task and/or examined how this may interfere with postural control in complex tasks. Based on declines in cognitive function

associated with aging we hypothesized that there would be a decline in visual working memory capacity among older adults (OA) and that performance in both the postural and cognitive tasks would be altered. The change detection task was paired with balance tasks of varying challenge: control (sitting), isolated stance, isolated stance intermixed with perturbations and perturbation of the support surface. Results showed that VWMC was significantly reduced in OA 2 ( $1.8 \pm 0.7$ ) as compared to young adults (YA) 3 ( $2.8 \pm 0.6$ ). Reduction in VWMC was greatest between the control (sitting) and perturbation conditions for both groups, YA ( $p < 0.001$ ) and OA ( $p < 0.001$ ). A significant decline in VWMC was seen between the control (sitting) and "expectation" (isolated stance intermixed with perturbations) conditions with YA ( $p < 0.05$ ) and not OA ( $p < 0.32$ ). No significant difference was seen in the number of steps or the use of an up on toes pattern between single and dual task conditions among YA ( $p < 0.2$ ;  $p < 0.33$ ) but there was a significant increase in OA ( $p < 0.05$ ;  $p < 0.05$ ). In addition OA showed a significant increase in tibialis anterior amplitude following perturbations in the dual task condition ( $p < 0.01$ ), which could be associated with the increased number of trials in which an up on toes pattern was used during balance recovery.

## **2-F-51 Coordination of leg muscles related to footpath stabilization during over ground walking post-stroke**

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People with hemiparesis following stroke often demonstrate impaired balance during walking and high incidences of falls. Appropriate placement of foot during swing phase of walking is critical to maintain stability and prevent falls. The central nervous system is hypothesized to use the available flexibility provided by abundant degrees-of-freedom to maintain a consistent footpath by co-variation of muscle activations and joint motions. Muscles have been shown in postural studies to be organized into a smaller number of groups termed muscle modes, and these muscle modes co-vary to form muscle synergies to produce a stable location of the center of pressure or center of mass. Recent studies propose that the central nervous system uses the synergies at the level of joints to stabilize the foot position in antero-posterior (AP) and medio-lateral directions during walking. Nevertheless, the use of functional synergies by the nervous system to control the foot position in the vertical direction, which is important for foot clearance during swing phase of walking and critical in preventing falls due to trips, has not been investigated directly. The purpose of current study is to investigate the role of muscle synergies in stabilizing the footpath during the swing phase of walking within stroke population. In this study, seven stroke survivors have been recruited and studied to date. Subjects walked over ground at their comfortable walking speed while kinematic and electromyographic (EMG) data was collected from their affected limb. A linear envelope was created from the EMG data and non-negative matrix factorization (NNMF) was applied to the linear envelopes obtained during over ground walking to estimate the muscle modes. Then, uncontrolled manifold (UCM) analysis was used to determine how the variance of the muscle modes across cycles was structured, i.e., how much of the variance was associated with flexible combinations of muscle modes used to stabilize the vertical and AP footpaths (Vucm or "good" variance), or muscle mode variance leading to footpath variability (Vort or "bad" variance). These measures were then averaged across the swing phase and subjected to statistical analysis. The results indicated that 'good' variance was significantly greater than 'bad' variance ( $p < 0.05$ ). The relative difference ( $\Delta V$ ) between the two variance components also was computed as  $\Delta V = (Vucm - Vort) / (Vucm + Vort)$ . The closer the value of  $\Delta V$  is to one, the more the muscle mode variance contributes

towards footpath stabilization.  $\Delta V$  for all the subjects was positive and statistical analysis showed that  $\Delta V$  was significantly different from zero ( $p < 0.05$ ), suggesting that more of the muscle mode variance across cycles represents flexible combinations of the muscle modes to stabilize the footpath. The current results support the hypothesis that the central nervous system uses the abundant degrees of freedom available at the level of muscle modes to stabilize the footpath during the swing phase of walking, even in stroke survivors. Concurrent studies in our lab are examining how this use of flexibility differs from that of non-neurologically impaired individuals.

## 2-F-52 The dynamics of online corrections determine the mode of posture and movement coordination

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We have previously shown that online corrections of reaching movements performed in standing evoke postural adjustments that occur before corrections to the arm muscles (Leonard et al. 2011). When visual target shifts are presented during a reaching movement in the direction opposite to the on-going reach (ipsilateral target shift), postural adjustments in the limb contralateral to the reaching arm decelerate and subsequently re-orient the body to the new target before corrective muscle activity in the arm muscle occurs. However, it is possible that the biomechanical conditions determine the precise mode of control adopted for coordinating adjustments in posture and voluntary movement. To this end, we compared postural adjustments and arm muscle adjustments to both ipsi- and contralateral shifts in target position. We hypothesized that the biomechanical constraints of modifying planned arm movements during stance determine the mode of postural control adopted. Using an online correction paradigm, we investigated the postural adjustments in standing humans exposed to unexpected changes in final target position during reaching. 8 right-handed subjects stood barefoot on 2 triaxial force plates within a light array consisting of 7 LED targets spaced at 15° intervals, with the central target oriented to their midline (90°) and 3 targets to the left (ipsilateral targets: corr75, corr60, corr45) and right (contralateral targets: corr105, corr120, corr135) of the midline, respectively. All targets were placed at shoulder height and at a distance of 130% of their reach length. During unperturbed reaching (reach), subjects were asked to reach and point to a central target aligned with their midline (90°) with their right hand upon random illumination of the target at a self-selected speed. In perturbed trials (corr), subjects initially pointed to the 90° target and after a variable delay from the onset of the arm movement, the final light position unexpectedly shifted to any of the other targets. EMG was recorded bilaterally from soleus (SOL), tibialis anterior (TIB), peroneus longus (PER), rectus femoris (RFEM), biceps femoris (BFEM), and tensor fascia latae (TFL), and from right biceps (rBIC), triceps (rTRIC), and anterior (rADEL) and posterior deltoids (rPDEL), as well as whole body kinematics. Subjects performed unperturbed 'reach' movements to the central target (90°) by extending their right arm towards the target, which induced a slight counter-clockwise (CCW) rotation of the trunk. Deceleration of the body and stabilization of the hand at the target was achieved with bilateral activations in the extensor leg muscles that preceded deceleration of the reaching hand. In contrast, in response to contralateral shifts in the visual target to the left, subjects re-accelerated their reaching arm in the direction of the on-going body rotation. Onset of the target shift was quickly followed by large corrective burst of rBIC, and subsequent activations in the lower ipsilateral limb that created the necessary shear forces to accelerate the body and arm towards the new target position. In the context of our previous findings, these results suggest that adjustments in posture are not always predictive with respect to modifications in

voluntary movements and that the coordination between posture and movement depends on the dynamics of the upcoming movements.

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## 2-F-53 Does postural adaptation to moving platform transfer across voluntary sway and arm raising tasks?

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Postural control can be performed consciously or unconsciously. Consciously performed motor commands are called focal movement, and voluntary sway is a good example. On the other hand, compensatory backward control of trunk and lower limbs before voluntary arm raise is known as anticipatory postural adjustments (APA), which is unconsciously performed. It has been reported that focal (arm raise) and postural (backward shift of body) components are relatively independent control processes (Slijper et al. 2002). However, little is known about motor learning mechanisms for postural control performed as focal movement (voluntary sway) and that performed as APA. The question arises if these postural tasks share neural representation. This preliminary study investigated the question by using motor learning and transfer paradigm. Predictive motor commands to compensate for an external perturbation learned through one task will be transferred to another task if motor learning mechanism is shared between these two tasks. Hence we exposed subjects to a moving platform during voluntary sway trials and tested if learned motor commands were transferred to APA trials. Six healthy males stood on a platform were asked to move their center of pressure (CoP) in a forward or backward direction (voluntary sway task). Amplitude of the sway was set as 35% of his anteroposterior limit of stability (approx. 4.8 cm) for each subject. After 30 baseline trials on a stable support surface (10 trials for each of forward sway, backward sway and arm raise tasks), the platform was moved rightward or leftward (acceleration: 0.5 m/s<sup>2</sup>, peak velocity: 0.2 m/s, duration: 800 ms, amplitude: 8 cm) associated with forward sway or backward sway, respectively. Eighteen catch trials in which the platform was not moved (6 trials for each of forward and backward sway and arm raise tasks) were interleaved in 108 (54 trials for forward and backward sway) adaptation trials. Subjects learned to predictively shift the CoP in mediolateral directions to compensate for the platform movement associated with anteroposterior voluntary sway, which was confirmed by the presence of aftereffect in the catch trials (1.3 ± 0.7 cm rightward shift for forward sway and 1.2 ± 0.3 cm leftward shift for backward sway). If this predictive mediolateral shift of CoP transferred to APA during the arm raise task, one could say that motor learning system for the postural tasks was overlapped between voluntary sway and APA. However, no mediolateral shift was observed during arm raise tasks (0.0 ± 0.1 cm), suggesting that anteroposterior postural controls for voluntary sway and APA associated with the arm raising task are relatively independent.

## G - Theoretical & Computational Motor Control

### 2-G-54 Using path integrals to learn neuromotor controls of reaching movements

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Predicting or imitating human motions is a very difficult but important problem both for aiding in the research and clinical treatment of movement and neurological disorders as well as developing safe, useful humanoid robotics. One of the primary challenges is the large number of degrees of freedom for movement; the human skeleton

has many joints, some simple and some very complex with wide ranges of motions such as the shoulder or hip joints. The physiology and biomechanics of the musculoskeletal system introduce many more complications; muscles can only contract, thus each joint is actuated at very least two muscles, increasing the control dimensionality greatly. Each muscle itself is complex, as its contractile force is highly non-linear in many meters such as muscle length or contraction velocity. A detailed model of a mammalian muscle contractions in response to electrical stimulation captures these essential features of muscle dynamics (Brown and Loeb, 2000). This high dimensionality and complexity makes this an intractable problem for most conventional learning algorithms, either because they require differentiability, an internal model of the whole system or cannot scale to large dimensionality efficiently. Using the Brown and Loeb muscle model, we apply a novel reinforcement learning algorithm, “Policy Learning through Path Integrals” (PI2) to find optimal neural controls for the muscles in the upper arm that actuate the elbow and shoulder in the horizontal plan. This learning algorithm uses a stochastic method to find an optimal muscle control policy by evaluating a number of movement attempts (rollouts) using the current policy plus some injected noise. The search through policy space is made efficient by sampling noise from a distribution inversely proportion to the control costs; policy updates are computed by probability weighted sum over the noisy parameters of these rollouts. As a result this algorithm is capable of learning efficiently in high dimensions without requiring differentiable controls or costs (Theodorou et al., 2010). An important biological parallel captured in this model is the control-dependent noise found in human motor systems; the noise in signals measured at the neuromuscular junction is proportional to the mean signal delivered by the nerve ending. In our model, the noise applied to the control policy in each rollout results in control-dependent noise at the muscle model level and thus minimal neural signals become a natural optimization criterion. We perform a qualitative analysis of the movement policy adaption of our model by recreating the force field reaching experiments presented in (Shadmehr and Mussa-Ivaldi, 1994). The model is first trained to reach in a point to point motion, then a hand-velocity dependent curl field is applied to the model and the motion is re-trained. After removing the force field, the same reaching movement produces an after image of the adaptation. We compare these after-images of adaption our model produces to those observed in humans subjects.

## 2-G-55 A modified random walk describes the low dimensional structure of motor variability in reaching trajectories

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The ever-present movement-to-movement variations in our motions prevent us from exactly repeating our actions. This motor variability is a fundamental feature of our motor system, yet little is known about how it evolves during the course of movement. Here we investigated the nature of this evolution during rapid point-to-point reaching arm movements, and discovered a surprisingly low-dimensional structure to the variability that was highly consistent across subjects. Moreover, we found that a simple model based on a random walk describes several key features of this variability with remarkable accuracy. The ability to accurately model the propagation of motor variability with such a simple model may prove to be a valuable tool for further understanding both the nature of motor variability and its consequences for motor control. In this experiment, subjects attempted to quickly (300-450ms) trace a smooth 20cm path displayed on a monitor, without visual feedback about their hand position. Despite tracing the same path repeatedly, subjects demonstrated considerable trial-to-trial variability in their hand paths. However, this variability had a surprisingly low-dimensional structure,

as over 99% of the variance in hand path shape was explained by just 3 of each subject's principal components (PCs). This structure was consistent across individuals, both in terms of the shapes of the 1st three PCs (correlation coefficients consistently above 0.96 between each subject's PCs and the average PCs) and the fraction of variance each accounted for ( $90\% \pm 3\%$ ,  $8\% \pm 3\%$ , &  $1\% \pm 0.5\%$ , respectively). Remarkably, we found that a simple random walk could largely explain the structure of the variability we observed in hand path shape. This model predicted (1) the shape with which variability expanded during the course of movement (average  $R^2 = 0.81$  when fitted to each subject), (2) the shapes of the 1st three PCs of the variability (average  $R^2 = 0.83, 0.89$ , &  $0.86$  across subjects for PC1, PC2, PC3 respectively), and (3) the fraction of the variability in hand path shape that each accounted for (85%, 8%, & 3%, respectively). Despite the apparent success of the random walk model in describing subjects' variability, we noticed a small but consistent difference between a key feature of the experimental data and the model predictions: The total variance in subjects' hand paths often evolved superlinearly with time, whereas the variance of a pure random walk increases linearly. We thus explored whether adding a simple “momentum” term to the model, representing the motion conservation present in viscoelastic dynamics, could account for this difference. In this modified random walk model (Model:  $x(n+1) = x(n) + A*(x(n) - x(n-1)) + \text{Gaussian noise}$ ), each step of the walk ( $x(n+1)-x(n)$ ) is supplemented with a single “momentum” factor ( $A$ ) that propagates the previous step ( $x(n)-x(n-1)$ ). We found that this revised model with only a single additional parameter accounted for the vast majority of the remaining variation in the hand path shapes unexplained by the pure random walk model. In particular, (1) the shape of how variability evolves during the course of subjects' hand paths (average  $R^2$  across subjects = 0.99), (2) the shapes of the 1st three PCs (average  $R^2$  across subjects = 0.99, 0.97, & 0.99 for PC1, PC2, and PC3 respectively), and (3) the dimensionality of the variability (the 1st three PCs accounted for 93%, 5%, & 1% of the modeled motor variability).

## 2-G-56 Dynamic predictability in rhythmic object manipulation

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Previous studies on discrete reaching movements in dynamic environments have advocated several kinematic, kinetic and energetic criteria (Takahashi et al., 2001; Huang et al., 2012). For manipulating objects with internal degrees of freedom optimality principles of both accuracy and force has been proposed (Nagengast et al., 2009). These criteria were formulated for discrete tasks, not explicitly addressing the characteristics of object dynamics in continuous rhythmic interactions. We hypothesize that particularly in rhythmic movements the complexity and nonlinearity of the object's dynamics play a dominant role in shaping the performer's strategy. More specifically, we hypothesize that humans avoid unpredictable or chaotic solutions and favor control strategies that afford predictable interactions with the object. This hypothesis was tested using the exemplary task of carrying a cup of coffee, simulated in a virtual set-up as a cup with a ball (coffee) in 2D (dynamics based on non-linear cart-and-pendulum model, Hasson et al, 2012). Subjects interacted with the virtual object via a robotic manipulandum. In Experiment 1, subjects ( $n=10$ ) oscillated the cup between two target locations (distance=10cm) at a metronome pace of 1Hz (40 trials, 45s each). Thus, the movement amplitude and frequency were specified; however, subjects could choose different relative phases between the ball and cup. In Experiment 2, subjects ( $n=8$ ) could choose their movement amplitude (corresponding to the distance in Experiment 1) and relative phase, while producing 1Hz back-and-forth movements; hence, solutions defined a 2-dimensional space. The result space of ball-and-cup kinematics (assuming sinusoidal cup trajectories) was

defined by amplitude, frequency, and relative phase between ball and cup. Inverse dynamics simulation results showed that the same task performance, defined by instructed frequency (and amplitude), can be achieved in different regions of the result space with strategies that differ in "effort" (mean squared force per cycle) and predictability. Predictability was quantified by an index defined as normalized average cycle-by-cycle variance of force, and by mutual information between the cup kinematics and the applied force profile; both provided matching measures of predictability. Results of Experiment 1 showed that with practice subjects changed their strategies from in-phase to anti-phase, which corresponded to changing from low- to high-predictability regions of the result space, based on predictability index. However, this change was coincident with effort minimization. Experiment 2 was designed to dissociate solutions with predictability and minimal effort. Results showed that with practice the movement amplitude, effort level and predictability index increased, i.e., the subjects chose regions in the 2D result space with higher predictability, even though these regions were associated with higher effort, a measure typically expected to be minimized in human movements. The simulations highlighted that complex tasks may have solutions with differing levels of chaotic or unpredictable behavior. Experimental results supported the hypothesis that humans prefer to maximize dynamic predictability when rhythmically manipulating objects with complex dynamics. The quantification of predictability expresses that humans seek solutions where rhythmicity of force and kinematics are synchronized, yielding overall rhythmic performance.

## 2-G-57 Error amplification improves performance by reducing motor noise

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Performance improvement in learning a new task typically proceeds by iteratively decreasing errors. In the presence of noise error correction gains should be conservative ( $<1$ ) to prevent overcorrection/instability, but if too small, performance improvement will be slow. In this case, an increase in gain, which may be elicited by error amplification, can improve performance (Abe & Sternad, submitted). As gain and noise are interrelated, an alternative route to performance improvement is decreasing subjects' intrinsic noise. This study used a virtual throwing task to explore the mechanisms underlying performance improvement with error amplification. Three hypotheses were tested: H1: Error amplification elicits larger performance improvements than veridical feedback. H2: Error amplification elicits changes in both gain and intrinsic noise. H3: Added extrinsic noise leads to further reduction in intrinsic noise and thereby even greater improvement. Subjects manipulated a lever arm to throw a virtual ball to hit a target as accurately as possible (error = minimum distance between ball trajectory and target). Subjects practiced "skittles" for 3 days without amplification (240 throws/day); on 3 more days, visual feedback was altered showing amplified errors. Three groups ( $n=6$ , per group) received deterministic error amplification (DEA) with amplification factors of 1.5, 2.0, and 2.5. Three additional groups received the same DEA levels, but with added noise (stochastic error amplification; SEA). A control group received veridical error information. To estimate each subject's feedback gain and noise, performance was modeled as a simple error-updating system with independent noise sources at planning and execution stages. Relative noise magnitudes were defined by the parameter  $K$  ( $K=1$  only execution noise;  $K=0$  only planning noise). System identification was used to estimate the feedback gain  $B$ , overall motor noise variance  $N$ , and  $K$  for each subject on practice Day 3 and 6 (before and with manipulation, respectively). The optimal  $B$  was calculated for each subject as the one giving minimum average error. Results showed that both DEA and SEA groups

decreased error from Day 3 (no amplification) to 6 (amplification) more than controls (H1). Neither DEA nor SEA groups showed significant changes in  $B$  compared to controls (counter H2). Non-systematic changes in  $K$  were observed for all groups, except DEA-2.5. At the end of Day 3, most DEA and SEA groups had gains above the optimal gain. Since  $K$  and  $N$  changed across practice, the optimal  $B$  changed, and the effect of error amplification was to raise subjects' gains even farther from optimal. This alone would have made performance worse, however this was offset by significant reductions in noise  $N$  for both DEA and SEA at amplifications  $>1.5$ , consistent with H2. Counter to H3, there was no additional performance benefit with added extrinsic noise. The results showed that error amplification improved task performance, in agreement with previous reports (Wei, Scheidt, & Patton, 2005). Error amplification caused correction gains to increase beyond the optimal value that would give the least average error, but this was offset by decreased intrinsic noise. Thus, error amplification did not improve performance by changing subjects' error correction gains, but by decreasing the overall magnitude of motor noise. Counter to expectations, this result was similar for both deterministic and stochastic amplification.

## 2-G-58 A model of saccade control that emulates both healthy and clinical populations

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The primary goal of this work was to develop a new computational model for saccade control that is constrained by neurophysiology and emulates complex eye movement behaviors. Our model is an extension of a neural field model of the primate superior colliculus (SC) introduced by Trappenberg et al. 2001. The main advance presented here is the addition of numerous input signals. These inputs represent visual, visual-motor, motor, pre-tory, and inhibitory activity seen in several areas of the thalamus, cortex, and the basal ganglia (BG) known to affect SC activity and subsequent saccadic behavior. We tested our enhanced model using the anti-saccade task as it involves both exogenously driven (e.g., visual input) and endogenously driven (e.g., rule based) aspects. Our ultimate goal is to 'lesion' the inputs and determine if the altered model output replicates known behavioral deficits of several patient groups with BG and/or frontal cortex pathologies. METHODS: We modeled 8 signals entering the SC: 1) a visual transient; 2) a visually guided saccade signal; 3) a visually guided fixation signal; 4) a saccade preparation signal; 5) a voluntary guided saccade signal; 6) a voluntary guided fixation signal; 7) a spatially specific motor gate signal; 8) and a global dampening signal. These signals were all based on a fixed kernel across 100 nodes. To introduce controlled variability signals 2, 5, 6, 7, & 8 were given three possible growth rates and signals 4, 6, 7, & 8 were given three maximum value levels. Signals 4, 5, 6, 7, & 8 also shared 3 onset delay variations. The other signals were fixed for neurophysiological reasons. This created 118,098 unique combinations of inputs and as the variability was controlled we could determine which input combinations directly caused which behaviors. RESULTS: We replicated the behavior of normal human controls performing pro- and anti-saccade tasks. For example, pro-saccades had shorter reaction times and reduced variability, compared to anti-saccades. The model also produced express pro-saccades, triggered by the sudden appearance of a visual target, and express direction errors on anti-saccade trials, due to robust visual signals over-riding weak voluntary motor signals. There were also longer reaction time errors, when the automated visual-motor signal was stronger than the voluntary motor signal. We also investigated behavioral changes across development and within various patient groups. When we "knocked-out" signals that represent the direct and indirect pathways of the BG, the resulting effects mimicked specific patient groups with BG disorders. Reducing the direct pathway (signal 7) produced more late errors resembling

patients with Parkinson's disease, while reducing the indirect pathway (signal 8) produced more express saccades and fast errors in the anti-saccade task resembling patients with attention deficit hyperactivity disorder. Our biologically constrained saccade model is valuable to study how specific deficits in saccade behavior can be linked back to pathologies in the oculomotor circuit for several clinical groups. -Supported by CIHR.

## 2-G-59 Changes in reward landscape modulate motor learning

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Recent findings have demonstrated that reward prediction errors alone can drive motor learning. However, only binary reward was provided depending on whether the trial was successful or not. Further, the learning task (a visuomotor rotation) was introduced gradually. It is not yet clear whether reward only can lead to learning in a task that is introduced abruptly, or how it can modulate the time course of learning. Here, we provide a more informative reward feedback which decays continuously in magnitude with increasing error. We asked: 1) whether it is possible to learn an abrupt visuomotor rotation by reward feedback alone, and 2) whether we can modulate the time course of learning by manipulating the rate of decay of the reward landscape. Seated subjects made 15 cm horizontal reaching movements to a target while grasping the handle of a robotic arm. Error on a trial was defined as the difference between the initial reaching angle and the angle that would correspond to a straight-line reach. Feedback was presented to the subjects after each movement and was reported as a trial score which ranged from 0 to 1000. Subjects were assigned to one of two groups which differed only in how the trial score was calculated. The first group (Linear) received a score that decayed linearly with the error. The second group (Cubic) received a score that decayed cubically with the error. Both the Cubic (N = 9) and Linear (N = 9) groups were then divided into subgroups which consisted of a group that received visual feedback of the cursor (Vision, N = 3) and a group that did not (No Vision). The protocol consisted of 600 trials beginning with 50 familiarization trials. Familiarization trials were followed by 50 trials (Baseline) in which subjects either received visual feedback (Vision) or no visual feedback (No Vision) as per their group assignment. After Baseline, a 30 degree abrupt visuomotor rotation (Rotation) was implemented for 450 trials. The remaining 50 trials returned to a zero rotation (Washout). During the Baseline, Rotation, and Washout portions of the experiment the subjects in the No Vision subgroups could only rely on the trial score to learn the rotation. Initial reaching errors for each subject were fit using a generalized logistic function, which included terms for the growth rate and the time of maximum growth (an indicator of exploration). Subjects learned the abrupt rotation with reward feedback alone and that the reward landscape did influence learning. The Cubic No Vision group learned the rotation earlier than the Linear No Vision group as indicated by a reduction in the reaching error in the first fifteen trials of the Rotation block. Results of the model fits support this finding, indicating that the Cubic group began exploring earlier than did the Linear No Vision Group ( $P < 0.05$ ). However, they did not reduce their error at a faster rate as indicated by similar values for the maximum growth rate model parameter ( $P > 0.05$ ). Additionally, no differences were found between the final learned angle of the two groups ( $27.01 \pm 3.75$  deg,  $P = 0.45$ ). No differences were found between the Cubic Vision and Linear Vision groups. This study is novel in its investigation of the changes in motor learning in response to different reward landscapes which decay gradually as a function of performance. We have shown that by manipulating the structure of the reward landscape, we can change the time course of the motor learning process.

## 2-G-60 Efficient codes for multi-modal pose regression

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Redundancy reduction, or sparsity, appears to be an important information-theoretic principle for encoding natural sensory data. While sparse codes have been the subject of much recent research in machine learning and neuroscience, sparsity has primarily been evaluated using readily available datasets of natural images and sounds. In comparison, relatively little work has investigated the use of sparse codes for representing information about human movements and poses, even though the "manifold hypothesis" provides a common motivation for using sparsity in both sensory and motor codes. According to the manifold hypothesis, the space of all possible instances of an information modality (e.g., all possible 1000x1000 images, or all possible configurations of an articulated body containing 50 degrees of freedom) is not uniformly covered by the samples that we encounter in the natural world (e.g., retinal inputs or human poses). Instead, many types of natural data appear to lie in a low-dimensional manifold embedded within the higher-dimensional space. Sparse codes have been observed to be effective for representing data on such manifolds, and so should be useful for coding human pose information. In this work, we propose a basic architecture for evaluating the impact of sparsity when coding data representing human poses. We test the performance of several coding methods within this framework, with a particular emphasis on the task of computing a regression from a kinematic (i.e., joint angle) modality to a dynamic (i.e., joint torque) one for each pose. We show that, for pose data, sparse codes can be more effective than dense codes like PCA, especially when measured in terms of the information contained in each nonzero code coefficient. In addition, sparse codes are more effective than dense codes for mapping between modalities, possibly because a sparse code allows the regression task to factorize more cleanly than a dense representation.

## 2-G-61 An optimal control framework for studying action-based decision making

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Imagine that you are faced with the challenge of deciding where to go for dinner tonight. You have either the option to drive to a fancy restaurant downtown or to walk to a nearby fast food place. How do you decide between these alternative options? Classical economic theories suggest that humans make decisions by integrating all decision variables into a single factor that characterizes the subjective value of an offer and select the one with the highest pay-off. Only once a decision is made, the action planning begins. Recent experimental findings argue against this view, providing evidence that decisions are made through a biased competition between actions associated with alternative options. This is in line with the "action-based" theory suggesting that when people are faced with many alternative options, the brain generates several concurrent policies associated with each one. These policies compete for action selection and perceptual information is used to bias this competition, until a single policy is selected. Despite the strong experimental evidence, "action-based" theory is vague on how decision variables modulate the competition and how they are integrated in the process of action selection. In the current study, we propose an optimal control framework that provides a computational instantiation of the "action-based" theory, showing how value information should be integrated in a manner that is both online and can be updated during execution of actions. We show how the complex problem of action selection in tasks with competing goals can be decomposed into a

weighed mixture of individual policies, each of which produces a sequence of actions to achieve a particular goal. The framework integrates online information associated with action-related (i.e., action cost, accuracy) and goal-related (i.e., expected reward, outcome probability) variables into an evolving assessment of the “desirability” of each goal. This value reflects how desirable it is to follow a policy at a given time, with respect to the alternative options, and acts as a weighting factor on the individual control policies. Because it is time- and state- dependent, the weighted mixture of policies produces a range of behaviors from “winner-take-all” to “spatial averaging”. We evaluated the performance of this framework in a series of visuomotor tasks and found that it explains many aspects of human/animal behavior. We show that the spatial averaging behavior observed in rapid reaching tasks with competing goals can be qualitatively predicted by our framework. The model also provides insights into how decision variables affect the motor plan competition and how the competition between actions can lead to poor decisions. Finally, the framework provides insights into how lesions in brain regions that are involved in planning actions bias the decision process. Recent studies showed a contralesional bias in saccadic/reaching decision tasks after inactivation of parietal areas LIP and PRR, respectively. Our framework suggests that this effect may occur due to either devaluation of the contralesional side of the visual field or increase of action cost towards that side.

## 2-G-62 Integration of dynamic neural fields and an optimal control framework for action-based decision making

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Every moment the natural environment presents people with multiple potential goals that compete for action selection. How do we decide which action is the best to follow at a given time? A series of recent neurophysiological and behavioral studies suggest that when we are faced with more than one potential goal, we initiate parallel and partially prepared plans that compete for action selection and use perceptual information to bias this competition, until a single policy is selected. A recent optimal control-based framework showed that the complex problem of action selection can be decomposed into a weighted mixture of individual control policies associated with the alternative goals. The framework integrates online information about action- and goal-related variables into an evolving assessment of the “desirability” of each goal. This value provides an estimate of how desirable each policy is at a given time with respect to the alternative policies, and acts as a weighting factor of the individual policies. Although this framework predicts many aspects of human and animal behavior, it is limited only to behavioral data and does not provide any information on how neural circuits perform the computations underlying them. In this study, we integrate a dynamic neural field model with this optimal control-based framework in order to address both neurophysiological and behavioral data related to action selection. The neural field performs the online integration of action- and goal-related variables and provides the weighting factor to each control policy. Neural field models simulate the activity of a network of neurons over a continuous space with a local excitation and surround inhibition. In our model, the neural field encodes direction in an egocentric frame. Initially only sensory information is available such as the direction of possible targets and goal-related variables such as expected reward and outcome probability. The neural field integrates these variables and activates the corresponding policies for planning actions to the targets. Each policy computes action-related variables such as cost and accuracy for the action it represents, and projects these values back to the neural field. The neural field integrates this input, resulting in a dynamic encoding of the “desirability” of each goal. The field’s activity is used to weight

the influence of each control policy on the final action. Depending on the inputs to the field and its dynamics, this can result in winner-take-all selection of a policy or a weighted average of several competing policies. We evaluated the performance of the model in a series of visuomotor decision tasks that involve reaching and saccadic movements to multiple goals and found that it predicts qualitatively many characteristics of neurophysiological and behavioral data. Consistent with experimental data, we show competitive interactions between populations of neurons associated with potential targets prior to movement initiation in reaching tasks with more than one potential target. We also make novel predictions as to how these neural populations interact in rapid reaching tasks with uncertainty about the target location. Finally, we make predictions concerning how these competitive neural dynamics can result in erroneous or poor decisions, such as the “global effect” paradigm in express saccades with multiple targets.

## 2-G-63 “Causal” coordination between reaching and grasping related neural trajectories in primary motor cortex

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The coordination of transport and grasp components of reach-to-grasp behavior has been extensively studied psychophysically (Jeannerod, 1984, *J. Motor Beh.*, 16, 235-254; Haggard & Wing, 1995, *Exp. Brain Res.*, 102, 483-494). This work has indicated that reaching of the proximal arm is temporally and spatially coordinated with distal hand preshaping as the object is approached. However, it is not clear how populations of motor cortical neurons representing proximal and distal joints of the upper limb participate in this coordination. In this study, we examined single-trial neural trajectories related to either reach or grasp components of movement and found evidence of coordination and statistically inferred “causal” relationships between these two classes of neural activity. We simultaneously recorded from multiple single units in primary motor cortex (MI) while monkeys performed reach-to-grasp movements to four different objects presented in seven different locations by a robot. A 6-camera, Vicon motion capture system tracked the kinematics of a set of infrared reflective markers placed on the arm, wrist and fingers from which the kinematics of 17 joints were reconstructed. A total of between 33 and 50 MI neurons were isolated using spike sorting in each data set. We developed a linear encoding model to parse out neural activity related to reaching (defined as non-grasping related activity) and grasping (defined as non-reaching related activity). Single-trial “reach” and “grasp” neural trajectories were examined in a reduced neural subspace via principal components analysis and then compared. We found that the coupling between “reach” and “grasp” neural trajectories varied over the course of the movement such that the variance across multiple trials was reduced during the course of movement. Moreover, when one trajectory type started to lag the other, the other trajectory appeared to compensate such that the trajectories would once again be synchronized. By shuffling the trial order between reach and grasp neural trajectories, we found that these neural coordination patterns were destroyed. In addition, we found evidence of statistically inferred “causal” interactions between both types of single-trial neural trajectories.

## Notes

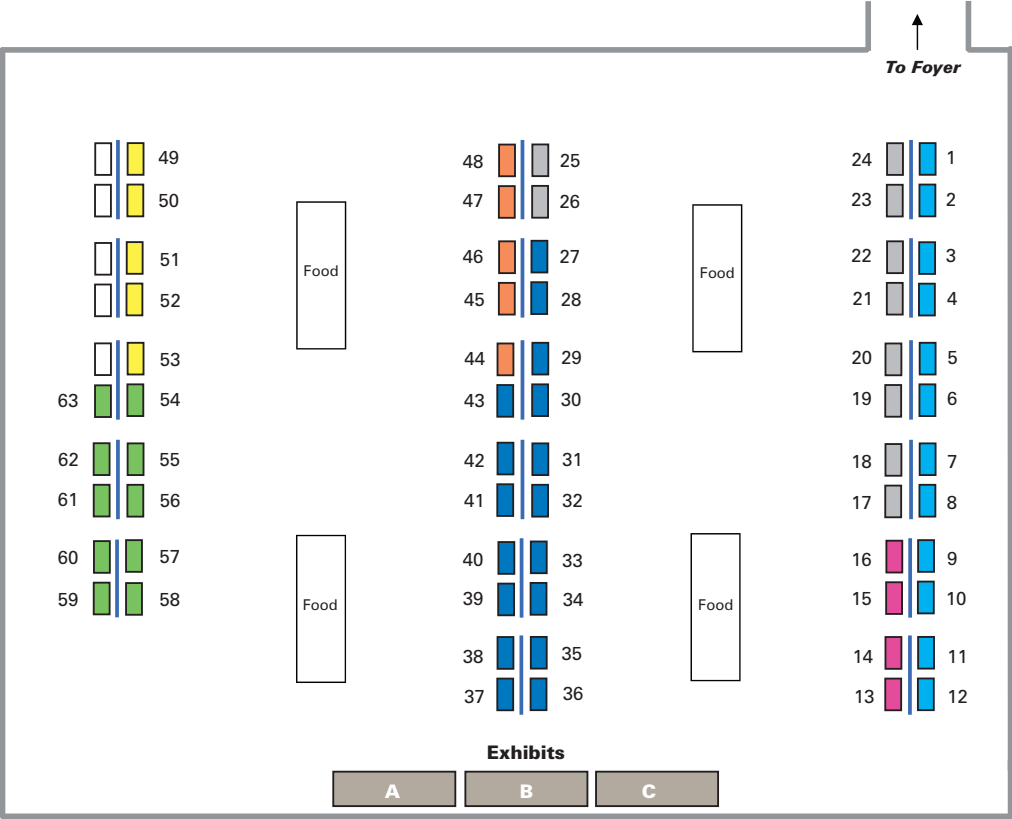
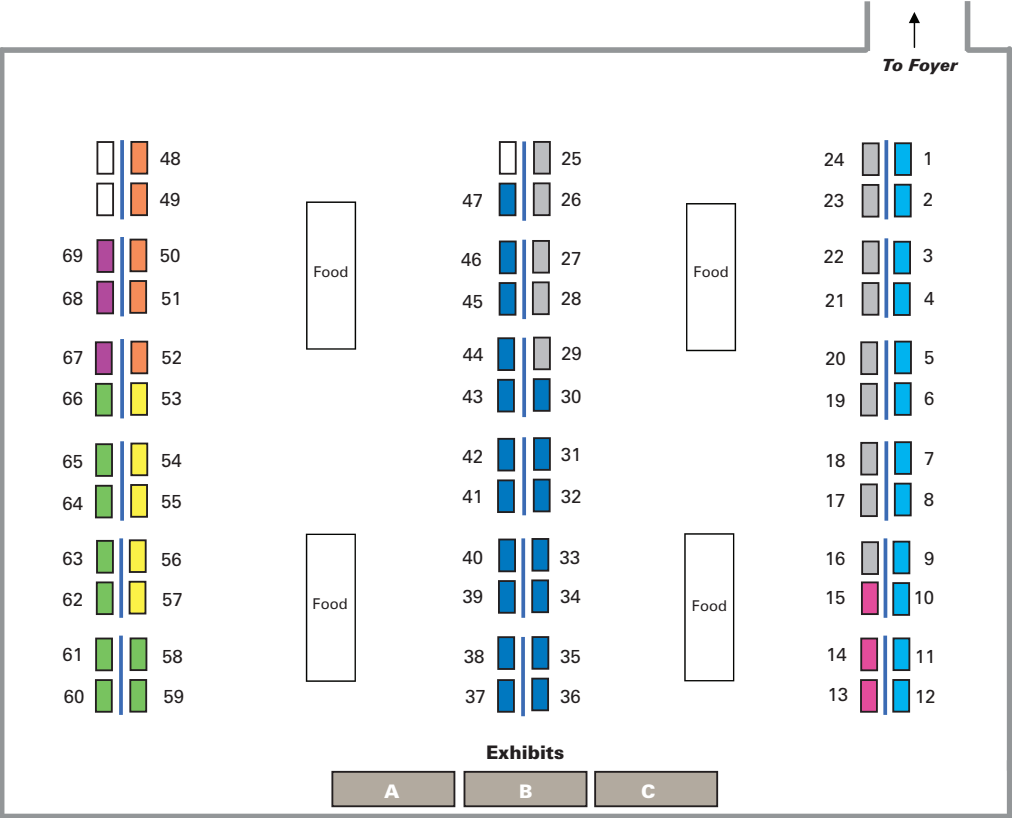
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