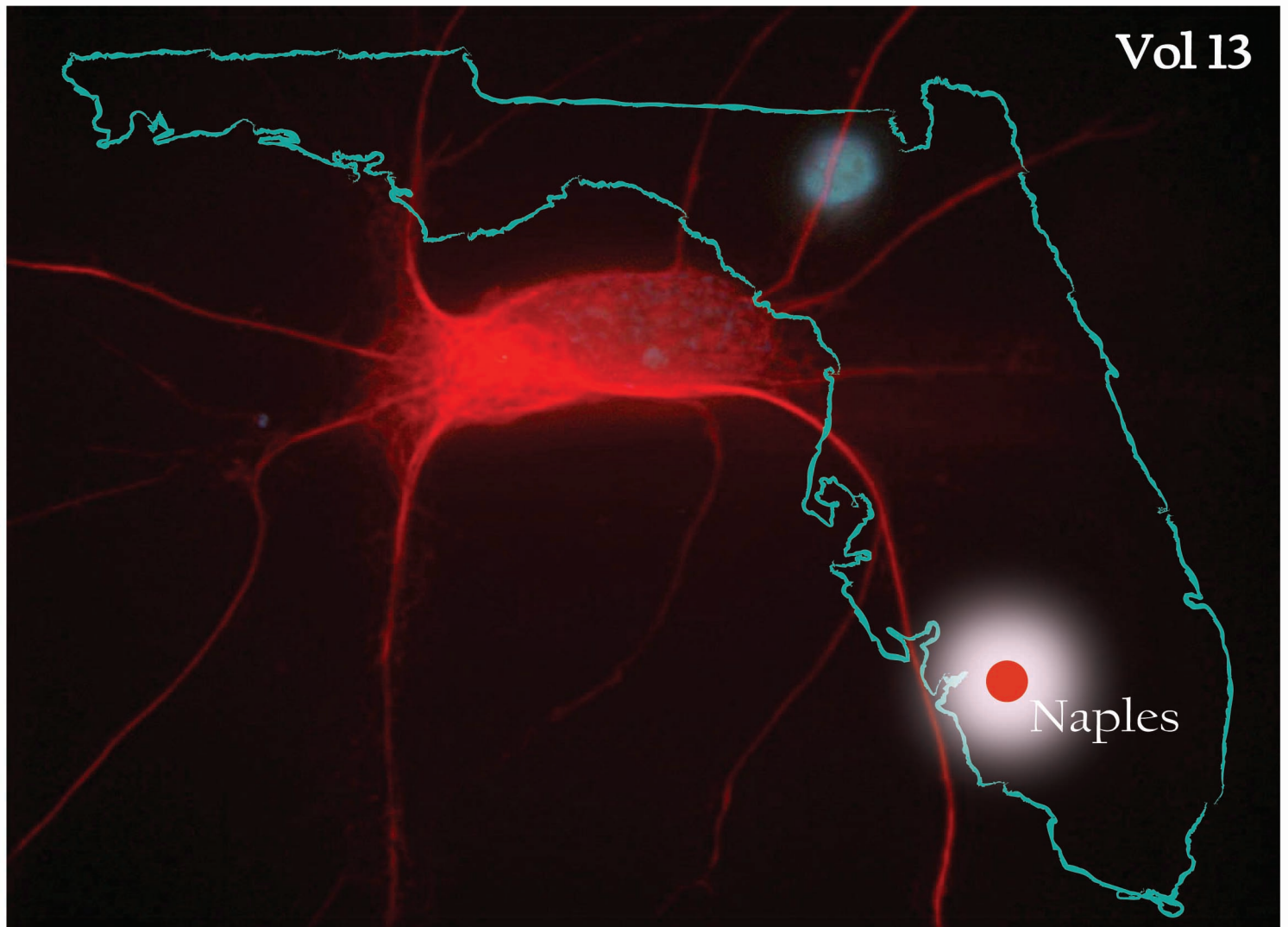




NEURAL CONTROL OF MOVEMENT

# 18th ANNUAL MEETING



Vol 13

Naples

**NAPLES, FL**  
Naples Beach Hotel & Golf Club  
April 29 - May 4, 2008

# NCM 2008 at a Glance

April 29 – May 4

	Tues	Wed	Thurs	Fri	Sat	Sun
7:00-8:00		<i>Breakfast</i>	<i>Breakfast</i>	<i>Breakfast</i>	<i>Breakfast</i>	
8:00-10:15		Panel Session 1 CORCOS	Panel Session 5 GDOWSKI	Panel Session 9 BURDET	Panel Session 12 TURNER	
10:15-10:35		<i>Break</i>	<i>Break</i>	<i>Break</i>	<i>Break</i>	
10:45-12:15		Perspective Session 2 KORDING	Perspective Session 6 SMEETS	Perspective Session 10 FLANAGAN	Open II Session 13	
12:30-3:00	<i>Arrive</i>	<i>Break</i>	<i>Break</i>  <i>Board I</i> <i>12:30 - 1:30</i>	<i>Break</i>	<i>Break</i>	
3:00-4:30		Open I Session 3	Tutorial Session 7 SMITH	Panel Session 11 KURTZER 3:30 – 5:45	Panel Session 14 TING 4:00 – 6:15	<i>Breakfast and Departure</i>
4:30-5:30		Poster I	Poster II			
5:30-6:30	<i>Registration</i>			<i>Business Meeting</i> 6:00 – 7:00		
6:30-7:00		Workshop Discussion Session 4 SCHIEBER	Workshop Discussion Session 8 KAUTZ		<i>Break</i>	
7:00-7:30				<i>Board II</i>		
7:30-10:00	<i>Reception</i>	<i>Reception Honoring Dr. Gottlieb</i> <i>7:30-9:00</i>			<i>Banquet &amp; Dance</i>	
- 12:00						

**NEURAL CONTROL OF MOVEMENT (NCM)**  
**18<sup>th</sup> Annual Meeting**  
April 29 – May 4, 2008  
**Naples Beach Hotel & Golf Club**  
Naples, Florida

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We are grateful to Sinauer Associates, Inc. and to Springer Publishing for their generous donation of textbooks, to be awarded by raffle to student members of NCM at the meeting.

## SPECIAL EVENTS

**All sessions will be held in the River of Grass Ballroom in adjacent, but partitioned space. Posters will be in a partitioned segment of the ballroom (Sections D & G).**

- Tuesday, April 29: 7:00-10:00 PM  
**Opening Reception, Ocean Lawn**  
 (heavy hors d'oeuvres, soft drinks and cash beer)  
*Note - Along with the Opening Reception ticket, each conferee will receive two tickets, valid for non-alcoholic beverages that may be upgraded at the conferee's expense to a beverage of choice. Please remember to bring your tickets.*
- Wednesday, April 30, through Sunday, May 4: 7:00-8:00 AM  
**Breakfast Buffet, Everglades Dining Room**  
*Note - Each conferee will receive 5 dated breakfast tickets with his/her registration packet. Tickets will be collected by hotel personnel as conferees enter the breakfast line. Please remember to have your ticket available.*
- Wednesday, April 30: 7:30-9:00 PM  
**Reception Honoring Dr. Gerald Gottlieb**  
 (hors d'oeuvres & cash bar), *Solarium North*
- Friday, May 2: 6:00-7:00 PM  
**NCM Business Meeting**
- Saturday, May 3: 7:30-8:15 PM  
**Reception (cash bar), Solarium North**  
 8:15-midnight  
**Banquet & Dance**  
*Note - Each conferee will receive a ticket for the Dinner/Dance with his/her registration packet. Tickets will be collected by hotel personnel at the dinner. Please remember to have your ticket available.*

## CONFERENCE INFORMATION

**Registration/Information Desk and Message Center Hours - Clubhouse Solarium North:**

	Tuesday	Wednesday	Thursday	Friday	Saturday
<b>AM</b>	N/A	7:00 – 10:30	7:00 – 10:30	7:00 – 10:30	7:00 – 10:30
<b>PM</b>	5:30 – 7:00	4:30 – 6:30	4:30 – 6:30	3:30 – 4:00	3:30 – 4:00

A bulletin board will be available for posting announcements.

**Breakfast**, Tuesday, April 29, through Sunday, May 4, is included in the registration fee.

**Posters for Session I** should be set up by **Wednesday, April 30, 8:00 AM**, and must be taken down by **Thursday, May 1, 8:00 AM**.

They may be remounted by **Saturday, May 3, 8:00 AM**, and must be removed by **4:00 PM**.

**Posters for Session II** should be set up by **Thursday, May 1, 10:30 AM**, and must be taken down by **Friday, May 2, 7:30 PM**.

**NEURAL CONTROL OF MOVEMENT**  
**18th Annual Meeting**  
**Naples Beach Hotel & Golf Club, Naples, Florida**  
**April 29 - May 4, 2008**

***DAILY MEETING SCHEDULE***

*All sessions will be held in the **River of Grass Ballroom** in adjacent, but partitioned space.  
Posters will be in a partitioned segment of the Ballroom (**Sections D & G**).*

**Tuesday, April 29, 2008**

**5:30 – 7:00 PM**                      **REGISTRATION**, Clubhouse Solarium North

**7:00 – 10:00 PM**                    **RECEPTION**, Ocean Lawn

**Wednesday, April 30, 2008**

**7:00 – 8:00 AM**                      **BREAKFAST**, Everglades Dining Room

**8:00 – 10:15 AM**                    **PANEL**     **Session 1**

TITLE:                                      ***REFLEXES AND VOLUNTARY MOVEMENT: THE LEGACY OF GERALD GOTTLIEB***  
ORGANIZER:                                *D. Corcos*  
PARTICIPANTS:                              Zev Rymer, J. Rothwell, Z. Hasan, J. Semmlow, M. Latash

**10:15 – 10:35 AM**                    **B R E A K**

**10:45 AM – 12:15 PM**                **PERSPECTIVE**     **Session 2**

TITLE:                                      ***BAYESIAN APPROACHES TO MOTOR CONTROL***  
ORGANIZER:                                *K. Kording*  
PARTICIPANTS:                              M. Berniker, D. Angelaki, P. Sabes

**12:30 – 3:00 PM**                      **B R E A K**

**3:00 – 4:30 PM**                      **OPEN PRESENTATIONS I**     **Session 3**

SPEAKERS:                                      *S. Sober, P. Celnik, H. Scherberger, K. Thoroughman, D. Sternad, B. Najafi*

**4:30 – 6:30 PM**                      **POSTER SESSION I**

**6:30 – 7:30 PM**                      **WORKSHOP - DISCUSSION**     **Session 4**

TITLE:                                      ***NOT YOUR FATHER'S RETICULOSPINAL TRACT ANYMORE***  
ORGANIZER:                                *M. Schieber*  
PARTICIPANTS:                              S. Baker, J. Buchanan, J. Buford, A. Davidson, T. Drew, J. Rothwell

**7:30 - 9:00 PM**                      **Reception Honoring Dr. Gerald Gottlieb**  
(hors d'oeuvres & cash bar), *Solarium North*

## ***DAILY MEETING SCHEDULE (Continued)***

**Thursday, May 1, 2008**

**7:00 – 8:00 AM**

**BREAKFAST**, *Everglades Dining Room*

**8:00 – 10:15 AM**

**PANEL** **Session 5**

TITLE:

***SENSORY REWEIGHTING, WHAT IS IT, AND HOW IS IT USED TO CONTROL POSTURE***

ORGANIZER:

*G. Gdowski*

PARTICIPANTS:

P. DiZio, E. Keshner, R. Peterka

**10:15 – 10:35 AM**

**B R E A K**

**10:45 AM – 12:15 PM**

**PERSPECTIVE** **Session 6**

TITLE:

***WHAT DOES VISUOMOTOR ADAPTATION DO TO OUR SENSES?***

ORGANIZER:

*J. Smeets*

PARTICIPANTS:

D. Henriques, P. Sabes

**12:30 – 3:00 PM**

**B R E A K**

**[12:30 – 1:30 PM**

**Board Meeting I ]**

**3:00 – 4:30 PM**

**TUTORIAL** **Session 7**

TITLE:

***ERROR CLAMPS FOR STUDYING MOTOR LEARNING: HOW THE ABILITY TO EXPERIMENTALLY CONTROL ERROR SIGNALS CAN GIVE NEW INSIGHTS INTO MOTOR ADAPTION***

ORGANIZER:

*M. Smith*

PARTICIPANTS:

R. Scheidt, F. Mussa-Ivaldi

**4:30 – 6:30 PM**

**POSTER SESSION II**

**6:30 – 7:30 PM**

**WORKSHOP - DISCUSSION** **Session 8**

TITLE:

***ALTERING LOCOMOTION THROUGH LEARNING AND CONSCIOUS CONTROL: WHAT ARE THE IMPLICATIONS FOR REHABILITATION?***

ORGANIZER:

*S. Kautz*

PARTICIPANTS:

A. Bastian, D. Reisman, C. Patten

## ***DAILY MEETING SCHEDULE (Continued)***

**Friday, May 2, 2008**

**7:00 – 8:00 AM**

**BREAKFAST**, *Everglades Dining Room*

**8:00 – 10:15 AM**

**PANEL** **Session 9**

TITLE:  
ORGANIZER:  
PARTICIPANTS:

***WHAT CAN ROBOTS TELL US ABOUT MOTOR CONTROL?***  
*E. Burdet*  
G. Cheng, H. Krapp, A. Ijspeert

**10:15 – 10:35 AM**

**B R E A K**

**10:45 AM – 12:15 PM**

**PERSPECTIVE** **Session 10**

TITLE:  
ORGANIZER:  
PARTICIPANTS:  
DISCUSSANT:

***ARE TWO-HANDED ACTIONS MORE THAN THE SUM OF THE PARTS?***  
*R. Flanagan*  
J. Diedrichsen, D. Nozaki  
J. Smeets

**12:30 – 3:00 PM**

**B R E A K**

**3:30 – 5:45 PM**

**PANEL** **Session 11**

TITLE:  
ORGANIZER:  
PARTICIPANTS:

***FLEXIBILITY AND COORDINATION OF UPPER LIMB REFLEXES***  
*I. Kurtzer*  
E. Perreault, R. Sainburg, R. Scheidt

**6:00 -7:00 PM**

**Business Meeting**

**[7:00 – 7:30 PM**

**Board Meeting II**

## ***DAILY MEETING SCHEDULE (Continued)***

### **Saturday, May 3, 2008**

**7:00 – 8:00 AM**

**BREAKFAST**, *Everglades Dining Room*

**8:00 – 10:15 AM**

**PANEL** **Session 12**

TITLE:

***“HOW FAST?” TRAJECTORY CONTROL, MOVEMENT ENERGY,  
AND THE BASAL GANGLIA***

ORGANIZER:

*R. Turner*

PARTICIPANTS:

*P. Mazzoni, Y. Niv, D. Vaillancourt*

**10:15 – 10:35 AM**

**B R E A K**

**10:45 AM – 12:15 PM**

**OPEN PRESENTATIONS II** **Session 13**

SPEAKERS:

*G. Blohm, J. Duque, M. Wagner, A. Suminski, C. Honeycutt,  
A. Pruszynski*

**12:30 – 4:00 PM**

**B R E A K**

**4:00 – 6:15 PM**

**PANEL** **Session 14**

TITLE:

***PARSIMONY IN NEURAL CONTROL: ARE THERE SHARED  
NEURAL MECHANISMS FOR FEEDFORWARD AND FEEDBACK  
CONTROL OF POSTURE?***

ORGANIZER:

*L. Ting*

PARTICIPANTS:

*T. Drew, P. Stapley, G. Torres-Oviedo*

**6:15 – 7:30 PM**

**B R E A K**

**7:30 – 8:15 PM**

**Reception** (cash bar), *Solarium North*

**8:15 – midnight**

**BANQUET & DANCE**, *River of Grass Ballroom*

### **Sunday, May 4, 2008**

**7:00 – 9:00 AM**

**BREAKFAST & DEPARTURE**



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- Synchronization with experiment control and video systems

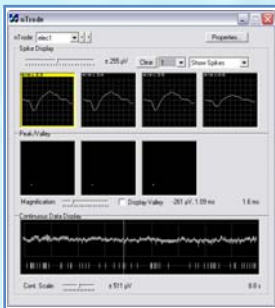
## Online Tetrode Processing

Online feature vs. feature plots for tetrode-wise identification of action potentials (units)



## Impedance/Crosstalk

Automatic impedance/crosstalk measurement *in vivo* for all electrodes



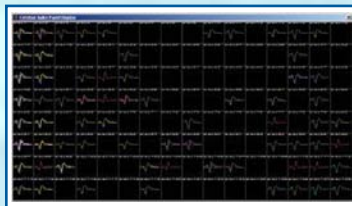
## Raster Plots

View spike events and field potentials for all channels



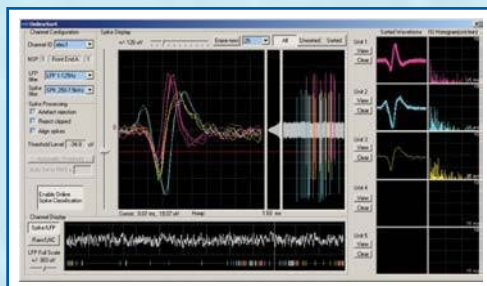
## Multi-Channel Display

See individual action potentials (units) on every channel



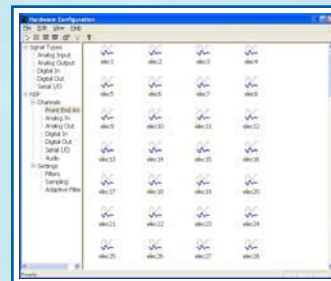
## Activity Map

Summary and display of spike-firing rates across channels



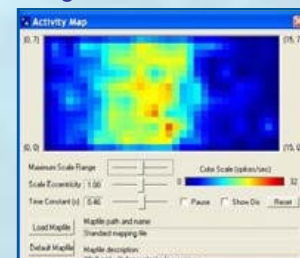
## Online Classification

Sort up to 5 units per channel (manual and automatic modes)



## Set-Up Window

Configure each electrode, auxiliary and experiment I/O channel



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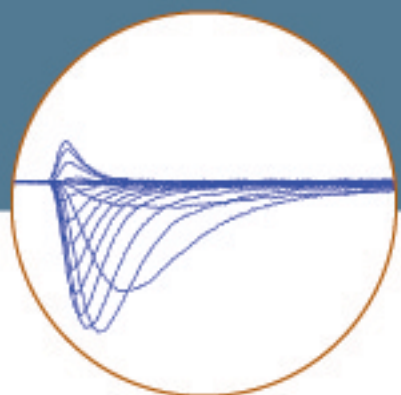
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Photo courtesy of VEPO, Temple University

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*Engages patient*

*Provides incentive and reward*

*Motivates volitional effort*

*Reduces tedious nature of therapy*

*Enhances sensormotor integration*

*Feedback indicates performance and results*

*Facilitates neural plasticity for recovery of motor and cognitive functions*

*Assists stroke patients with recovering reaching and grasping abilities*



Photo courtesy of Arizona State University



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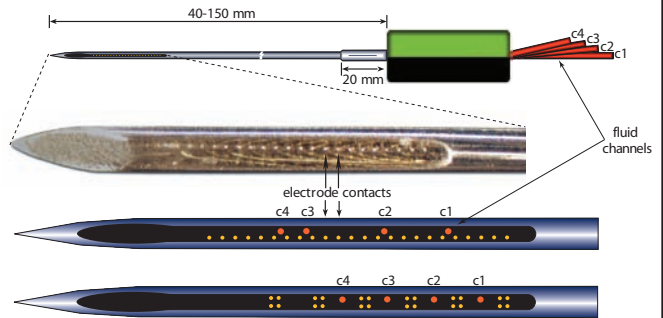
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#### Floating Microelectrode Array

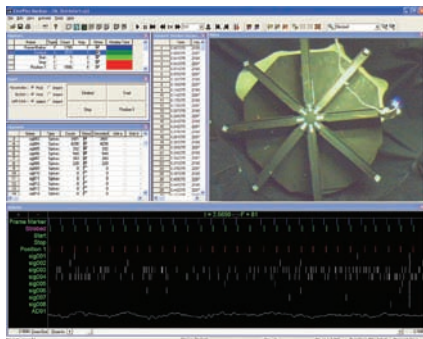
- User-defined electrode length (to 10 mm), impedance 10 kΩ to 2.5 MΩ and number of electrodes (up to 36)
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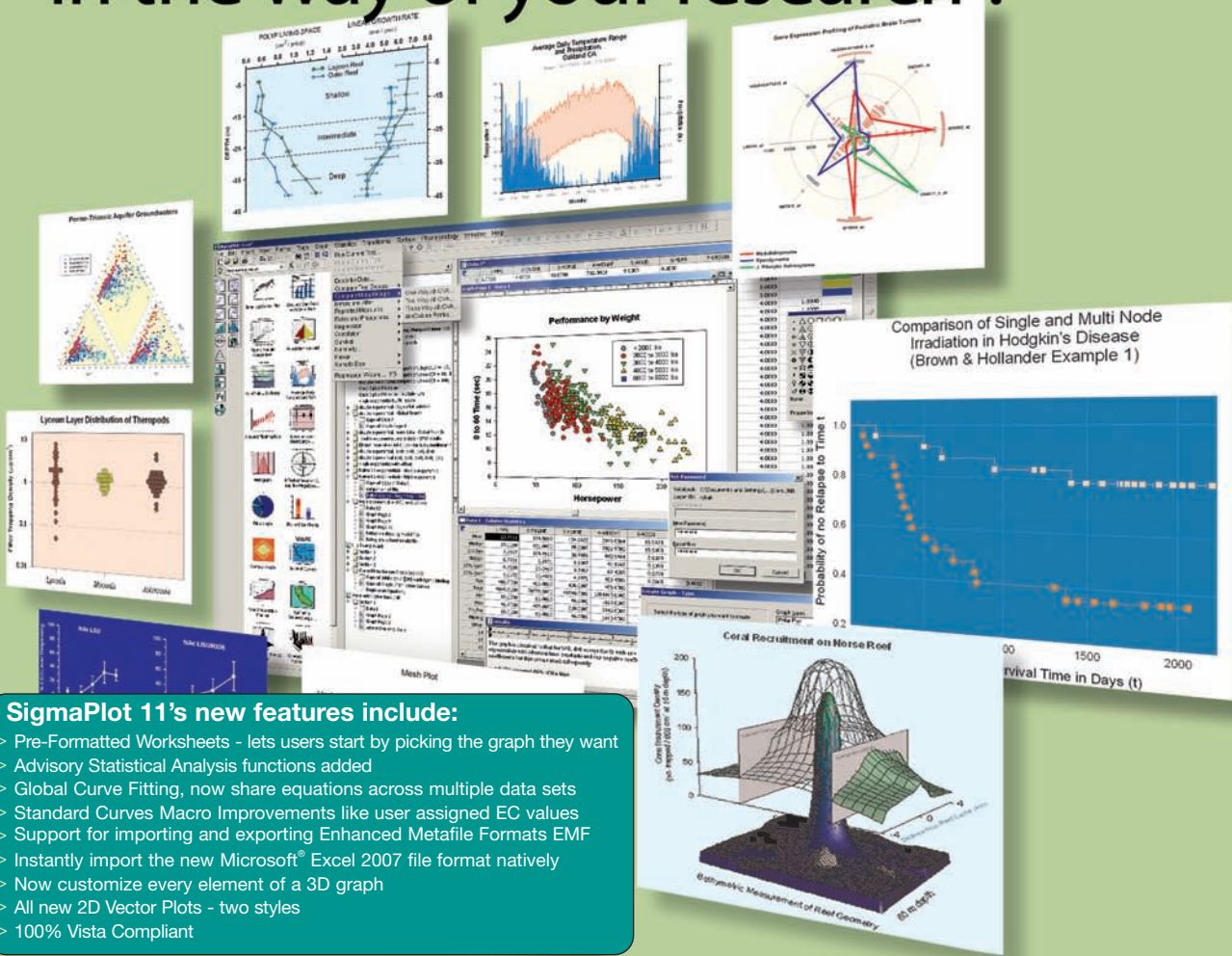
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**Poster Session I - April 30, 2008, 4:30-6:30 PM**

**A - WORKSHOP I: Not Your Father's Reticulospinal Tract Anymore**

**B - CLUSTER I: Prediction and Adaptation in the Saccadic System - Timing and Amplitude**

**C - Control of Eye and Head Movement**

**D - Posture and Gait**

**E - Fundamentals of Skeletomotor Control**

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**F - CLUSTER II: Cortical-brainstem Circuits for Smooth Pursuit**

**G - CLUSTER III: Modeling and Analysis of Ocular and Premotor Signals**

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# SESSION Abstracts, NCM 2008

## PANEL **Session 1**

Wednesday, April 30, 2008, 8:00-10:15 AM

### **Reflexes and Voluntary Movement: The Legacy of Gerald Gottlieb**

*Daniel Corcos*<sup>1</sup>, *Zev Rymer*<sup>2</sup>, *John Rothwell*<sup>3</sup>, *Zia Hasan*<sup>1</sup>, *John Semmlow*<sup>4</sup>, *Mark Latash*<sup>5</sup>

<sup>1</sup>Department of Nutrition and Kinesiology, University of Illinois at Chicago; <sup>2</sup>Sensory Motor Performance Program, Rehabilitation Institute of Chicago; <sup>3</sup>Sobell Department, Institute of Neurology; <sup>4</sup>Department of Biomedical Engineering, School of Engineering, Rutgers, The State University of New Jersey; <sup>5</sup>Department of Kinesiology, College of Health and Human Development

Gerry Gottlieb's career has been devoted to understanding reflexes, voluntary movement, and their interplay. Zev Rymer will pose the question: Segmental reflexes - do they matter? In the Sherrington era, segmental reflexes (including the tonic stretch reflex, reciprocal inhibition and flexion withdrawal) were regarded as responses built into the spinal cord, reflecting primitive circuitry and generating automatic responses, set largely outside volitional control. More recently reflex responses have been seen as integral to the control of voluntary motion, although the way in which such reflexes are integrated remains a matter of debate. We will review our current state of knowledge, making reference to Gerry Gottlieb's contributions to our understanding of the control of human voluntary motion. In 1989, Gerry Gottlieb published a target article in *Behavioral and Brain Sciences* in which he proposed the Dual-Strategy hypothesis as a way to understand how the electromyographic pattern changes for movements of different speeds and loads. John Rothwell will review recent research findings that shed light on the cortical mechanisms that underlie the triphasic pattern of muscle activation. For the control of multi-joint movement, Gottlieb introduced the idea of kinetic planning as a bold alternative to the seemingly self-evident necessity of kinematic planning. This idea stays clear of the need for solving complicated equations of motion and of dealing with their interaction terms. It also dispenses with feedback or equilibrium-point control, but treats kinematics as simply an emergent phenomenon. Ziaul Hasan will discuss how the idea has shown considerable explanatory power when applied to the initiation of movement, though it does not appear to suffice for the later stages of movement. John Semmlow will present a new analysis technique that applies Independent Component Analysis to motor responses that has been used to isolate two motor control components in the vergence eye movement response. The approach requires an ensemble of multiple motor responses to the same stimulus that is easy to obtain in most motor control research. While the approach has only been applied to eye movement data, it should be more broadly applicable to other dynamic motor responses. This talk will describe the promise of this approach to Gerry's type of data. Gerry Gottlieb has been the most vocal opponent of the equilibrium-point hypothesis since the early 1980s. His attempts at disproving the EP-hypothesis started with the demonstration that invariant characteristics did not have an invariant shape. Paradoxically, Gerry also co-authored half-a-dozen papers glorifying the EP-hypothesis. He contributed to works showing how the EP-hypothesis could handle issues of EMG patterns, variability, and the control of movements with different parameters. Mark Latash will discuss how, to avoid becoming an advocate of the EP-hypothesis, Gerry took the only reasonable strategy and escaped to Boston. This led to his complete recovery and new attacks on the EP-hypothesis. Finally, Gerry Gottlieb made important contributions to movement pathology. Daniel Corcos will briefly summarize some of these findings. He will then present some recent findings on muscle activation patterns in Parkinson's disease.

## PERSPECTIVE **Session 2**

Wednesday, April 30, 2008, 10:45 AM – 12:15 PM

### **Bayesian Approaches to Motor Control**

*Konrad Kording*<sup>1</sup>, *Dora Angelaki*<sup>2</sup>, *Philip Sabes*<sup>3</sup>, *Max Berniker*<sup>1</sup>

<sup>1</sup>Northwestern University; <sup>2</sup>Washington University, Saint Louis; <sup>3</sup>University of California, San Francisco

To control movement the nervous system relies on sensory perceptions from many modalities. The information provided by each of these modalities is noisy and uncertain. Vision alone provides us with an imperfect percept of the world, allowing for only limited acuity. Similarly neither our auditory nor our proprioceptive system provides us with perfect information about the world or our body. Choosing the appropriate motor command based on these percepts is further complicated by the fact that movement production is noisy. Even with perfect perception, noise inherent to neural computations may introduce uncertainty into the control of movement. A growing body of research suggests that noise and uncertainty play integral roles in the nervous system's functioning. Given the prevalence of uncertain information, understanding how it is processed is central to our understanding of the nervous system. Over the last decades many researchers have asked how the nervous system deals with noisy information. The framework of Bayesian statistics is progressively being used to predict how the nervous system could optimally deal with uncertainty. Many studies have found that the nervous system is actually quite good at combining uncertain pieces of information and is frequently close to the optima described by Bayesian statistics. A growing number of studies driven by Bayesian ideas have aimed at specifically understanding how the motor system processes noisy information. Ideas from Bayesian statistics have been used to model neural coding, eye movements, hand movements, posture, and the combination of multiple sources of information for movement execution and planning. In many cases it has been shown that human behavior is very close to the theoretical predictions. Furthermore, a range of phenomena in sensory-motor tasks that had been previously described can be reinterpreted in terms of decision making under uncertainty. Our panel will present this emerging research to the neural control of movement community. The topics will range from electrophysiology to sensory-motor tasks, revealing the wide applicability of this approach. Panelists will describe the Bayesian theory behind their approach and how it drives experimental work. The results presented will be interpreted in the Bayesian framework to emphasize the connections between the underlying theory and experimental observations of the motor system – both neural and behavioral. Dora Angelaki will discuss how neurons in the nervous system of monkeys are able to combine multi-modal sensory cues into a joint representation for motor planning. The salient properties of this representation are predicted by Bayesian ideas. Philip Sabes has analyzed how the predictability of targets influences movement variability. The observed reaching errors suggest the presence of an adaptive mechanism which can be explained with a simple Bayesian model and instantiated with a network utilizing Hebbian plasticity. Max Berniker's and Konrad Kording formulate motor learning as adapting to ongoing changes in the world and body. Their results explain many published findings on motor adaptation and generalization. The proposed panel will expose how Bayesian ideas can be useful to many studies of the control of movement, both behavioral and neural.



## **a.) The Dynamics of Sensorimotor Adaptation in Birdsong**

*Samuel Sober, Michael Brainard*

Keck Center for Integrative Neuroscience, University of California, San Francisco

What determines the efficacy of sensorimotor adaptation? Here we use the vocalizations of adult songbirds to study the dynamics of adaptation to experimentally imposed perturbations of sensory feedback. Both song learning (in which young birds learn to copy the song of an adult "tutor") and song maintenance in adult birds require auditory feedback, suggesting that these processes depend on a comparison of sensory feedback to an internal representation of the correct song. However, no studies have provided direct evidence that birds adjust their vocal output to minimize perceived song errors. We perturbed auditory feedback in adult Bengalese finches using custom-designed headphones that produced real-time distortions of pitch (fundamental frequency). Pitch shifts led to adaptive changes in song as birds adjusted the pitch of individual song elements (or "syllables") in the direction opposite the feedback shift. When normal feedback was restored, pitch returned to baseline levels. These data provide the first direct evidence that adult songbirds use auditory feedback to correct perceived song errors. To investigate the rules governing song adaptation, we applied pitch shifts of varying sizes. If birds shifted their behavior based solely on the magnitude of the disparity between expected and experienced feedback, larger feedback shifts would result in larger or faster changes in song output. Surprisingly, we found the opposite pattern – the larger the applied shift, the smaller and slower the adaptive change in song. While incompatible with the magnitude-based model described above, these results suggest that the strength of adaptation might depend on the overlap between the distributions of expected and experienced feedback. The pitch of each syllable over multiple renditions has a roughly Gaussian distribution. Small pitch shifts produce a high degree of overlap between the baseline distribution of pitch and the distribution of experienced pitch feedback for each syllable. Conversely, large pitch shifts result in little overlap between the baseline and shifted distributions. Smaller shifts might drive learning more effectively than larger shifts because the experienced pitch during small shifts more often falls within the baseline distribution, or because highly shifted auditory feedback (that is, shifted far beyond the baseline distribution) is given less weight when estimating vocal output. In summary, our results indicate that at least for some motor skills, the speed and efficacy of sensorimotor adaptation are greatest in response to small rather than large perceived errors in performance, and provide an account of how this might occur.

## **b.) Can Action Observation be used as a Strategy to Enhance Beneficial Effects of Motor Training in Neurorehabilitation after Stroke**

*Pablo Celnik<sup>1</sup>, Joseph Classen<sup>2</sup>, Katja Stefan<sup>3</sup>, Leonardo Cohen<sup>4</sup>*

<sup>1</sup>Dept. Physical Medicine and Rehabilitation, Dept. Neurology, Johns Hopkins University; <sup>2</sup>Dept. Neurology, University of Wuerzburg, Germany; <sup>3</sup>Dept. Neurology, University of Rostock, Germany;

<sup>4</sup>Human Cortical Physiology Section and Stroke Neurorehabilitation, NINDS, NIH

Performing a motor task or observing another individual performing the same motor actions (Action Observation, AO) activates "mirror neurons" in macaque monkeys. Indirect evidence of a somatotopically organized mirror neuron system also exists in humans. Because neurons in this system are active during performance of motor actions and observation of another individual performing the same motor task, we hypothesized that (1) AO could have similar qualitative effects as performing motor practice, as reflected by formation of motor memories, and (2) combining AO with physical practice could enhance training effects on formation of motor memories in healthy subjects and patients with chronic stroke. We investigated these hypotheses using a transcranial magnetic stimulation (TMS) paradigm capable of detecting TMS-evoked thumb movements directions changes consistent with formation of simple motor memories containing the kinematic details of the practiced movements. First, we tested a group of young healthy individuals and showed that observation of a video of another person performing motor training induced memory formation of the observed movements in the primary motor cortex. This process was associated with modulation of the cortical excitability balance favoring the muscle representations mediating movements in the observed direction. Then, we showed that AO combined with physical practice resulted in more prominent training effects relative to plain training in young healthy volunteers. More recently, we investigated whether the reduced effectiveness of motor training in healthy older adults was also present during AO and whether combining motor training with AO could compensate for this age-related deficit. Using a similar TMS paradigm, we found that, like motor training, the capacity of AO to

form motor memories in older adults is reduced. However, when motor practice was combined with AO the training effects were potentiated with clear formation of motor memories and corticomotor excitability changes favoring the trained muscle motor representation. These findings suggested that AO could be a valuable strategy to enhance motor training effects following brain lesions like stroke. In a final study, we tested this in a group of chronic stroke patients and found that congruent AO combined with motor practice resulted in an enhancement of training effects with similar changes in corticomotor excitability as healthy individuals. These studies suggest that AO could become a scientifically sound strategy capable of improving motor rehabilitation after stroke.

### **c.) Coding and Decoding of Hand Grasping Movements in the Macaque Parietal and Premotor Cortex**

*Hans Scherberger, Markus Baumann, Marie-Christine Fluet, Ben Townsend, Erk Subasi, Sebastian Lehmann*  
Institute of Neuroinformatics, Uni, ETH Zurich, Switzerland

Hand manipulations are crucial for human and non-human primate behavior. Neurons in the anterior intraparietal area (AIP) and the ventral premotor area (F5) have been shown to encode planning signals for hand grasping movements. We investigated the possibility to decode such grasping intentions from neural activity in AIP and F5 during a delayed grasping task, in which the presentation of a visual grasp target is separated in time from movement planning and execution. Macaque monkeys were trained to grasp an object (handle) that is positioned in one of 5 different orientations either with a power grip or a precision grip. Importantly in this task, the instruction of how to grasp the object (power vs. precision grip) as well as the object orientation in space was separated in time from movement preparation (planning) and movement execution. Results showed that individual neurons in AIP and in F5 represent the grip type and target orientation during memory-guided hand movements, and a Bayesian decoding simulation from these data demonstrated that the intended movement, grip type and grip orientation (10 conditions in total), can be predicted during movement planning in 96 % of all trials from the spiking activity of 116 AIP neurons and with an accuracy of 70 % from 84 F5-neurons. Encouraged by these results, we permanently implanted a total of 80 electrodes in AIP and F5 to implement a brain-machine interface for hand grasping. Using these implanted electrodes and a modified version of the delayed grasping task, we were able to decode the grip type and the object orientation in real time with an accuracy of 90% correct (in 4 conditions) and 72% correct (in 6 conditions) and without the animal moving its hand. These results suggest that neural activity from the parietal and premotor cortex is suitable for the real-time decoding of hand movements, as needed for the development of a neural prosthesis. Supported by SNSF, NCCR, EC-FP6 (Marie-Curie IRG), Forschungskredit UZH, SAMW, and ZIHP.

### **d.) Motor Adaptation, Generalization, and Computation in Preteen Children and Adults**

*Kurt Thoroughman, Michael Fine*  
Department of Biomedical Engineering, Washington University in St. Louis

Motor adaptation to externally applied forces has revealed important systemic properties of the human brain. We have recently discovered that both what and how people learn change rapidly in response to environmental demands. Here we investigate motor adaptation and trial-by-trial generalization in preteen children and adults. Children aged 9 to 12 years can demonstrate adult-like upper extremity control (see ESPN little league coverage) and impressive cognitive skills (see ESPN spelling bee coverage); here we use haptic forces to interrogate the ability of preteen nervous systems to transform sensorimotor feedback into updated prediction. We trained 20 preteen children and 20 adults to make reaching movements in two viscous haptic environments: a simple one that always pushed perpendicularly, and a complex one that featured parallel forces, perpendicular forces, and combinations thereof, dependent on movement direction. We examined self-paced reaction times in both groups in both environments; these reaction times indicated that children and adults attended similarly to the two environments. We first measured learning of the environments across many movements; to our surprise, children learned at the same rate as adults in the complex environment but more slowly than adults in the simple environment. We then quantified trial-by-trial generalization of error across movement direction. As expected, adults decreased both the magnitude and extent of generalization in the complex environment compared to the simple environment. Children, however, generalized narrowly and with equal magnitude in both environments. We modeled these behaviors with a neural network. Individual neurons' tuning width needed to change across environments to mimic adults' behavior, but remained narrow in both environments to mimic children's behavior. Lastly, we trained neural networks with a fixed learning rate



using neuronal tunings that best fit human trial-by-trial generalization. A network using narrowly tuned neurons, mimicking children's generalization, learned the simple environment more slowly than a network using broadly tuned neurons, mimicking adult's generalization. Our modeling demonstrates that fixed narrow tuning is necessary for a simple network to replicate children's trial-by-trial generalization; this same narrow tuning is sufficient to replicate children's adult-like learning of the complex environment and their relative difficulty learning the simple environment. We suggest that the ability to broadly generalize, and to flexibly change the breadth of generalization, is a developmental achievement that occurs between preteen childhood and adulthood.

### **e.) Variability, Covariation and Noise in Motor Learning and Retention**

*Dagmar Sternad*

Departments of Kinesiology and Integrative Biosciences, Pennsylvania State University

Reduction of random fluctuations or "motor noise" across practice is considered a major characteristic of motor learning evidenced in many demonstrations where improved accuracy correlates with decreases in variability over repeated movement executions. Variability is specifically informative when a task is redundant, i.e., the same result can be obtained by many different strategies. In recent experimental and theoretical work we developed a new method of decomposing variability in performance to allow further insights into determinants of change in behavior. Our approach permitted answers to three specific questions: Is it only random fluctuations that diminish with practice? Can variability be decreased in selected variables? How can variability be manipulated by interventions such as in rehabilitation practices? The basis for our studies is a decomposition of variability into three conceptually and quantitatively distinct factors: (1) Discovery of error-tolerant strategies (Tolerance); (2) exploitation of covariation between essential variables (Covariation); and (3) reduction of dispersion or "noise" (Noise). The so-called TCN-method quantifies the contributions of each of these components in task performance. In all experiments a throwing task served as our model system. Using a virtual set-up subjects threw a pendular projectile in a simulated concentric force field to hit a target. The movement was experimentally constrained such that only two variables, angle and velocity of ball release, fully determined the projectile's trajectory and accuracy of the throw. The set of successful solutions defines a nonlinear solution manifold. Importantly, different locations of the manifold are differentially sensitive to error. Experiment 1 examined performance changes with practice and showed that the largest contribution to learning was due to Tolerance, followed by Covariation, with reduction of Noise contributing the least. These results highlight that skill improvement consists largely of subjects' increasing sensitivity to subtle aspects of redundancy in execution, rather than simply reducing noise. Experiment 2 contrasted the hypotheses that variability is aligned with the solution manifold by covariation or that "signal-dependent noise" is minimized. In a task where successful strategies were redundant in the velocity dimension, results showed that executions exploited the redundancy of the task and rather than minimizing velocity, i.e., "signal strength". Experiment 3 examined how highly skilled performance can still be influenced by adding error-dependent noise. During practice sessions with added noise subjects could reduce their variability to maintain accuracy. Importantly, subjects maintained their low variability even after this noise was removed. The results have implications for training and rehabilitation.

### **f.) Passive and Active Decay Mechanisms in the Adaptive Processes Underlying Motor Skill Learning**

*Bijan Najafi<sup>1,2</sup>, Maurice A. Smith<sup>1</sup>*

<sup>1</sup>Harvard University, School of Engineering and Applied Sciences

<sup>2</sup>Rosalind Franklin University of Medicine and Science, Center for Lower Extremity Ambulatory Research

The ability to learn and retain information is one of the key features of a nervous system. While the decay in retention of declarative memories has been well studied, the mechanisms underlying the decay of motor skill memories are not well understood. If we understood these mechanisms, it might be possible to design better paradigms for learning and rehabilitating motor skills. Recently we proposed a computational model of motor learning suggesting that motor error engages multiple adaptive processes with different timescales: one process learns quickly but forgets rapidly (a fast learning process) while the other learns slowly but retains information well (a slow learning process). However this model does not address how the passage of time effects learning. We hypothesized that the two learning processes in our model might exhibit different temporal decay patterns. Specifically, the fast learning process might be highly volatile in time, while the slow learning process might be more temporally-stable and decay in a primarily experience-dependent manner. We tested this hypothesis for short-term motor adaptation

tasks. We trained groups of subjects to make reaching movements in a velocity-dependent force-field while grasping a robot manipulandum, and then studied the decay of this motor adaptation in three separate experiments. In the first experiment we tested for retention of a newly learned motor adaptation after time delays ranging from seconds to minutes. We found that adaptation decayed only partially with time and with a single exponential time constant of just 20 seconds. Interestingly the amount of decay matched the level of the fast learning process, and in a separate experiment which we removed the contribution of the fast learning process we were able to virtually eliminate this time-dependent decay. Furthermore, when zero-error active decay trials were studied, the time constant for decay of this fast learning process was unaltered suggesting that decay of the fast process is entirely passive. In a final experiment we found that zero-error active decay trials were able to substantially decay the slow learning process over the course of 10-20 minutes, although passive (time-related) decay caused no measurable decay in this slow learning process over the course of 20 minutes. These results suggest the decay of motor adaptation reflects the processes that constitute learning. The one learning process adapts quickly but and decays in a purely passive, time-dependent manner, while another learning process learns slowly and is temporally-stable, but decays in an active experience-dependent manner.

## WORKSHOP – DISCUSSION **Session 4**

Wednesday, April 30, 2008, 6:30-7:30 PM

### **Not Your Father's Reticulospinal Tract Anymore**

*Stuart Baker*<sup>1</sup>, James Buchanan<sup>2</sup>, John Buford<sup>3</sup>, Adam Davidson<sup>4</sup>, Trevor Drew<sup>5</sup>, John Rothwell<sup>6</sup>, Marc Schieber<sup>7</sup>

<sup>1</sup>Institute of Neuroscience, Newcastle University; <sup>2</sup>Department of Biological Sciences, Marquette University; <sup>3</sup>Department of Physical Therapy, Ohio State University; <sup>4</sup>Department of Neurobiology & Anatomy, University of Rochester; <sup>5</sup>Département de physiologie, Université de Montréal; <sup>6</sup>Sobell Department, Institute of Neurology, Queen Square; <sup>7</sup>Departments of Neurology & Neurobiology, University of Rochester

The reticulospinal system traditionally has been viewed as working with the vestibulospinal system to control postural reactions and locomotion. Surprisingly, recent work in mammals increasingly indicates that the reticulospinal system also contributes to voluntary movement of the proximal and even distal forelimb/upper extremity. Focused by a provocateur (SCHIEBER), a committee of experts spanning lamprey, cat, monkey and human will compare the role of the reticulospinal system in a rapid-fire, round-robin panel discussion exploring two questions: 1) Has the reticulospinal system evolved from controlling posture and locomotion to contribute to reaching and even grasping as well? Addressing this question, BUCHANAN will show how in the lamprey, which has no extremities, the RS system controls locomotion producing different effects on motoneurons innervating myotomal muscles located at different dorsal/ventral positions, DREW will show that the cat RS system controls both the standing limb and the reaching limb, BUFORD will show that in monkeys many reach-related RS neurons have preparatory period activity, BAKER will show monosynaptic connections to hand muscle motoneurons from monkey RF neurons, and ROTHWELL will show that the RS-mediated acoustic startle response indicates that humans too may have reticulospinal connections to hand motoneurons. Control from the reticulospinal system may have evolved further distally than you thought! 2) Are reticulospinal neurons primarily ipsilateral or contralateral, or do they contribute coordinated control to both sides? In this round, BUCHANAN will show that lamprey RS neurons project monosynaptically to ipsilateral motoneurons but influence motoneurons bilaterally, DREW will add how in cat the RS system coordinates control of the standing and reaching limbs, DAVIDSON will show that in monkeys single RS neurons influence motoneurons bilaterally in a double reciprocal fashion, BUFORD will show that in monkeys many RS neurons discharge similarly whether the right or the left arm reaches, BAKER will share preliminary evidence of monkey RS projections to both ipsilateral and contralateral motoneurons, and ROTHWELL will show that although the human startle response is bilateral, it can lead to early release of unilateral voluntary movement. Not simply ipsilateral, the RS system coordinates movements bilaterally!

(See Poster Session I for individual abstracts)

## PANEL Session 5

Thursday, May 1, 2008, 8:00-10:15 AM

### **Sensory Reweighting, What is it, and How is it used to Control Posture**

Participants: *Greg T. Gdowski*<sup>1</sup>, Paul DiZio, Emily A. Keshner<sup>2</sup>, and Robert Peterka<sup>3</sup>

<sup>1</sup>Dept. of Neurobiology & Anatomy, Dept. of Biomedical Engineering, University of Rochester;

<sup>2</sup>Dept. of Physical Therapy, College of Health Professions, Electrical and Computer Engineering, School of Engineering, Temple University; <sup>3</sup>Oregon Health Sci. Univ, Portland, Oregon.; <sup>4</sup>Brandeis University, Waltham, MA

It is well-known that visual, proprioceptive and vestibular sensory signals are used in controlling posture. Several studies have shown that the significance of a sensory signal depends upon the context in which posture is being controlled. It is thought that the central nervous system reweights sensory cues in order to optimally control posture in different contexts. The purpose and goal of this session is to provide examples of postural control systems that may rely on reweighting sensory signals and to shed light on how they might be used in controlling posture.

**Greg Gdowski** will address the utility of proprioceptive and vestibular signals in controlling the stability of the head with respect to the trunk during whole body rotations. We have used bilateral splenius EMG recordings in non-human primates to show that periods of cocontraction are produced during rotation when the head is free to move. We hypothesize that cocontractions are related to neck proprioceptive stretch reflexes and result in dynamic changes in the stiffness of the head/neck plant. A model was used to show that reweighting proprioceptive signals could produce dynamic changes in stiffness that are more effective in head stabilization than was previously thought.

**Paul DiZio** will address whether arm proprioception and the precision fingertip contact afforded by the arm's many degrees of freedom are necessary for postural stabilization by finger contact. Three experiments will be discussed. In the first experiment, we perturbed arm proprioception and control with biceps brachii vibration (120 Hz, 2mm amplitude). This degraded postural control, resulting in greater postural sway amplitudes. In a second study, we immobilized the touching arm with a splint. This prevented precision fingertip contact but had no effect on postural sway amplitude. In both experiments, the correlation and latency of fingertip contact forces to postural sway were unaffected. The third experiment showed that correlations of finger force with sway differ during quiet stance versus voluntary sway. We conclude that postural control is executed based on information about arm orientation and task as well as tactile feedback from light touch, although precision fingertip contact is not essential.

**Emily Keshner** will address how postural orientation is intimately related to one's percept of spatial orientation. For example, if we do not have a reliable internal model to indicate where we are relative to the gravitational vertical, then we will be unable to accurately calibrate the muscle torques necessary to maintain our position in space. The internal model for spatial orientation may be calculated through a summation of segmental feedback signals and accurate signals from the visual and vestibular systems are necessary to formulate a reliable model. We have explored how motion of the visual environment may affect the perception of vertical and, consequently, affect postural stabilizing responses.

**Robert Peterka** will address how subjects adjust or reweight their utilization of visual, proprioceptive, and vestibular sensory orientation cues used for stance control depending on environmental conditions. We have used soleus EMG recordings to gain insight into the sensory reweighting process during continuous surface tilts of varying amplitudes with and without accurate visual cues. EMGs show a short latency stretch reflex response that changes in direct proportion to stimulus amplitude and is not influenced by visual cues. However, the medium latency response shows systematic changes corresponding to the sensory reweighting process. These changes can be interpreted as a visual and/or vestibular suppression of an underlying proprioceptive response. The EMG timing of the suppression suggests that visual cues act with less time delay than vestibular cues.

### What Does Visuomotor Adaptation do to our Senses?

*Denise Henriques*<sup>1</sup>, *Philip Sabes*<sup>2</sup>, *Jeroen Smeets*<sup>3</sup>

<sup>1</sup>Centre for Vision Research, York University, Toronto; <sup>2</sup>Department of Physiology, University of California, San Francisco; <sup>3</sup>Faculty of Human Movement Sciences, VU University, Amsterdam

Visuomotor adaptation is a frequently used tool, for instance used to test cerebellar function and to alleviate effect from parietal dysfunction (neglect). But what is really happening during adaptation is far from clear. Is it a collection of clearly separated sensory and motor processes? Is the sensory part recalibration, or just re-weighting of information? In this perspective session, we will present several theoretical and empirical observations on visuomotor adaptation that challenges classical interpretations. We will discuss to what extent the different theoretical approaches to adaptation can deal with the various experimental results obtained in different paradigms.

**Denise Henriques** will show that recalibrating the arm motor system using false visual feedback of the hand does not recalibrate our proprioceptive estimate of hand path geometry, and does so only slightly when estimating hand position. That is, when adapting to distorted vision that shows the hand curving rightward when moving straight, subjects learn to move the hand along a leftward-curving path they do not afterwards feel that the hand path is curved when it moves along straight surface. These results are inconsistent with the idea that visual and proprioceptive information are globally realigned. She will argue that having the adapted hand path constrained is the best way to separate the effect of visual recalibration on the movement from that on proprioception.

**Philip Sabes** will show that visuomotor adaptation has multiple components, including sensory and motor. Sensory adaptation (SA) is composed of visual and proprioceptive adaptation. In his view, these sensory effects are “global”, i.e. they reflect a general realignment of the sensory signals. In addition, reach-specific effects of adaptation are observed, which are called “motor adaptation” (MA). He proposes that MA is likely to be cerebellar dependent, while SA is likely to be parietal. The lack of appreciation of multiple adaptation effects has led to a lack of clarity in the literature on visuomotor adaptation. He proposes that all of these effects are the result of error corrective learning. Such a model could be used to predict the balance we expect to see between these various adaptation effects, hopefully reconciling differences in the literature. For example, simple “prism-like” shifts of visual feedback are likely to drive SA, while visual rotation experiments are more likely to drive MA.

**Jeroen Smeets** will argue that the sensory component of visuomotor adaptation can be regarded as an example of optimal sensory combination, without any recalibration. He will argue that in order to determine the contribution of proprioception alone, one has to exclude not only visual information, but also updated visual memory of the hand’s location. In a similar way, we have an updated proprioceptive memory of positions in the outside world. As updating introduces uncertainty, the weight given to the updated information reduces with every movement made. The short periods of (false) feedback that are used to keep the adapted state will ensure that subjects keep giving weight to the remembered information. Various experimental predictions of this new view on adaptation will be discussed.

## TUTORIAL Session 7

Thursday, May 1, 2008, 3:00-4:30 PM

### **Error Clamps for Studying Motor Learning: How the Ability to Experimentally Control Error Signals Can Give New Insights into Motor Adaptation**

*Maurice Smith*<sup>1</sup>, *Robert Scheidt*<sup>2</sup>, *Ferdinando Mussa-Ivaldi*<sup>3</sup>

<sup>1</sup>Harvard School of Engineering and Applied Sciences; <sup>2</sup>Marquette University, Dept of Biomedical Engineering; <sup>3</sup>Northwestern University, Dept of Physiology

Performance errors are widely believed to drive many types of motor adaptation ranging from visuomotor rotations to saccade adaptation to force-field adaptation during reaching. However traditional paradigms for examining these motor adaptations have employed a controlled disturbance that produces (uncontrolled) performance errors that drive learning. In this session we will point out several powerful theoretical & practical advantages of directly controlling performance errors instead, and we will review the technical aspects of maintaining tight control over these errors. Just as the development of the ability to experimentally clamp membrane voltage led to a new level of understanding membrane physiology, the ability to clamp performance errors may lead to substantially improved understanding of the processes underlying motor learning. Although the use of this technique is in its infancy, its use is already enabling experiments which are substantially advancing the study of motor adaptation. Perhaps the simplest way to control performance error is to clamp it to zero. Although a perfect zero-error clamp will never be achieved, the ability to reduce these errors to less than 1% of the error magnitude that typically drives motor learning has already been achieved in some paradigms. There are two distinct ways in which zero-error clamp trials have been effectively used to date: The first way in which such trials were used was to understand how motor adaptation intrinsically decays in a force-field adaptation task, and to show that such decay is orders of magnitude slower than the washout of adaptation previously observed when the external disturbance (the force-field) is held at zero rather than kinematic error. Error clamp trials have been subsequently used to demonstrate that multiple distinct, simultaneously-active learning processes contribute to short-term motor learning, and that the interactions between these processes account for several leaning phenomena that had not previously been connected. An entirely different way that error clamp trials can be used is to understand the how the temporal structure of motor output evolves during learning. When error is not held at zero, online feedback responses to within-movement errors interact with learning-related feedforward changes in motor output, making it difficult if not impossible to recover the latter from the composite motor output. However if error is clamped at zero, feedforward changes in motor output can be directly measured. Such measurements are leading not only to more accurate measurements of learning curves, but to careful characterization of how the temporal properties of learned changes in motor output progress. This progression has several surprising features that give new insights into the motor primitives that underlie adaptation.

## WORKSHOP – DISCUSSION **Session 8**

Thursday, May 1, 2008, 6:30-7:30 PM

### **Altering Locomotion through Learning and Conscious Control: What are the Implications for Rehabilitation?**

*Steve Kautz*<sup>1,2</sup>, *Amy Bastian*<sup>3</sup>, *Darcy Reisman*<sup>4</sup>, *Carolynn Patten*<sup>1,2</sup>

<sup>1</sup>VA Brain Rehabilitation Research Center, Malcom Randall VA Medical Center, Gainesville, FL, USA; <sup>2</sup>University of Florida, Department of Physical Therapy, Gainesville, FL, USA; <sup>3</sup>The Johns Hopkins School of Medicine, Department of Neurology, Kennedy Krieger Institute, Baltimore, MD; <sup>4</sup>University of Delaware, Department of Physical Therapy, Newark, DE, USA

Locomotion is one of the most basic and essential of all human behaviors. It is often thought of as an automatic process that requires little conscious control. Yet, there are many instances when it is advantageous to change it (e.g. optimize a runner's form, restore function after CNS damage). This session will focus on the mechanisms used to change human locomotor patterns. We will explore how malleable the locomotor pattern is, discussing topics including: modulation of learning, context specificity, and conscious modulation of gait in health and disease. Amy Bastian will discuss work focused on modulation of motor learning. She will specifically address whether transcranial direct current stimulation (tDCS) applied over the cerebellum can augment locomotor learning processes in healthy individuals. Preliminary work suggests that anodal tDCS can improve adaptation rate and the retention of new walking patterns on a split-belt treadmill, as compared to sham or cathodal stimulation. These results will be discussed in terms of general motor learning mechanisms and potential application to individuals with locomotor deficits from stroke. Darcy Reisman will discuss work focused on the context specificity of adaptation. She will address how context can make a locomotor adaptation specific or generalizable. Her work shows that new walking patterns obtained following split-belt treadmill walking can transfer to over ground walking, and she will discuss the variables that influence the extent of this transfer. These results will be discussed in terms of the potential importance of generalizability for the application of adaptation paradigms in rehabilitation. Steve Kautz will discuss work focused on conscious modulation of locomotion. He will address the ability of controls versus persons with post-stroke hemiparesis to generate a voluntary step of longer length during steady state walking. Control subjects achieve this by increasing propulsion and swing speed using the stepping leg and increased propulsion using support leg. The same bilateral adaptations are not present after stroke, and interestingly the paretic leg differs in its ability to generate increased propulsion depending on whether it is the stepping or stance leg. These results are discussed in the context of deficits of voluntary control of specific elements of the locomotor pattern after damage to cerebral structures. Carolynn Patten will discuss work focused on the ability to modulate gait speed in persons affected with hemiparesis post-stroke. She will address the roles of biomechanical and neuromuscular power in gait speed modulation and demonstrate how modulation of ankle plantarflexor power affords a means to characterize hemiparetic locomotor dysfunction. On this background, she will discuss adaptations in gait dysfunction following therapeutic interventions, including alterations in the locomotor pattern that enhance ankle plantarflexor power production and improve gait speed modulation.

(See Poster Session II for individual abstracts)

## PANEL Session 9

Friday, May 2, 2008, 8:00-10:15 AM

### What can Robots tell us about Motor Control?

*Etienne Burdet*<sup>1</sup>, *Gordon Cheng*<sup>2</sup>, *Holger Krapp*<sup>3</sup>, *Auke Ijspeert*<sup>4</sup>

<sup>1</sup>Department of Bioengineering, Imperial College London; <sup>2</sup>Computational Neuroscience labs, ATR; <sup>3</sup>Department of Bioengineering, Imperial College London;

<sup>4</sup>School of Computer and Communications Sciences, EPFL

There is a close relation between robots and biological motor control, as both have to develop strategies for acting on the physical world. This relationship can be used in both ways. On the one hand, biomimetic control derived from neurophysiological models are implemented and tested on robots. Robotic systems, on the other hand, are used to physically interact with motion of humans or animals, and Virtual Reality workstations with computer-controlled visual and force feedbacks are now routinely used to investigate the neural control of movements. However, these last years have seen approaches in which robots are more closely associated with humans or animals in order to discover motor control principles. This panel will present four such approaches: *i*) The first presentation will explain how dedicated fMRI compatible interfaces are used in Etienne Burdet's group to explore motor learning and post-stroke rehabilitation (<http://www.bg.ic.ac.uk/staff/burdet/Home.html>). Simultaneous fMRI and EMG during movements performed in computer-controlled dynamics enables to control experimental conditions and to quantify human motor control accurately. *ii*) Most humanoid robots such as the famous Asimo from Honda are designed according to conventional robotics principles and controlled to reproduce recorded trajectories. The humanoid robots that Gordon Cheng and his group develop at ATR CNS, in contrast, are conceived as a tool to investigate principles and algorithms of human motor control and can physically interact with humans (<http://web.mac.com/gordoncheng/English/Welcome.html>). *iii*) Holger Krapp will outline how robots can help us studying multisensor fusion and dynamic range fractioning in insect gaze and flight control. Such closed-loop robot-insect interfaces, which aim at identifying general principles of biological sensorimotor transformation, may inspire the design of robots with sensor-rich feedback control (see <http://www.spectrum.ieee.org/print/2151> & <http://www3.imperial.ac.uk/people/h.g.krapp>). *iv*) Auke Ijspeert and his group (<http://birg.epfl.ch/page27899.html>) have developed a salamander's robot which swims and walks using central patterns generators (CPG) observed in its biological counterparts. Interestingly, the CPG model enabled them to predict a property of the spinal cord oscillatory centers that could be verified in real salamanders (Science 315(5817): 1416-20). Each presentation will be followed by a related discussion.



### Are Two-Handed Actions More than the Sum of the Parts?

Speakers: *Randy Flanagan*, Queen's University, Canada

Jörn Diedrichsen, Bangor University, U.K.

Daichi Nozaki, Research Institute National Rehabilitation Center, Japan

Discussant: Jeroen Smeets, Vrije Universiteit, Netherlands

Many arm movement studies have focused on single limb reaching and pointing movements. However, manual tasks often involve coordinated actions of different effectors; for example, the two hands in bimanual tasks or the thumb and index finger in grasping. Here we consider the extent to which the organization of multi-effector tasks emerges from the control of the individual parts. We will show that both predictive and reactive bimanual behaviour is influenced by task constraints related to the coordination of the two effectors. In short, the control of bimanual tasks is distinct from the control of the unimanual parts.

**Randy Flanagan** will provide evidence that the control of bimanual grasping differs from the control of unimanual reaching or touching movements. In bimanual grasping, participants moved the two hands to contact a virtual object and adapted to opposing visuomotor rotations applied to the two hands. In unimanual reaching, they contacted the virtual object with one hand and adapted to a visuomotor rotation. In unimanual reaching, adaptation was local to the training direction whereas, in bimanual grasping, adaptation involved a remapping between object width and grasp aperture. This result suggests the control of bimanual grasping involves high-level task constraints that affect the two hands.

**Jörn Diedrichsen** will then explore the influence of task constraints on bimanual feedback control. In a bimanual reaching task, participants move a cursor with each hand to two separate targets. In this case the feedback control of the two hands was independent. However, when participants moved a single cursor with both hand, feedback corrections of the two hands became dependent, with each hand correcting for a perturbation of the other. These task-dependent changes also influenced how the two hands adapt to a force field applied to one of the hands. He concludes that coordinate is highly flexible and is best investigated relative to the task constraints.

**Daichi Nozaki** will discuss his work showing limited interference (and transfer) of motor learning in the same limb between unimanual and bimanual movements. He will use a state-space model to illustrate how this limited transfer of learning may be generated if there is a partial, but not complete, overlap in neurons involved in unimanual and bimanual tasks.

Finally, **Jeroen Smeets** will discuss challenges to the idea that movements of multiple effectors are controlled through a coordinative control strategy and will consider evidence for the opposing view that multi-effector movements are to a large extent determined by the constraints of the task and the properties of individual effectors, leaving only a marginal role for specific control of coordination.

**Flexibility and Coordination of Upper Limb Reflexes**

*Isaac Kurtzer*<sup>1</sup>, Eric Perreault<sup>2,3</sup>, Robert Sainburg<sup>4</sup>, Robert Scheidt<sup>5</sup>

<sup>1</sup>Centre for Neuroscience Studies, Queen's University; <sup>2</sup>Departments of Biomedical Engineering, Northwestern University; <sup>3</sup>Department of Physical Medicine and Rehabilitation, Northwestern University; <sup>4</sup>Department of Kinesiology, Pennsylvania State University;

<sup>5</sup>Department of Biomedical Engineering, Marquette University

An increasing number of researchers are appreciating how the feedback control of the upper limb can incorporate sophisticated representations of the motor periphery and be flexibly tailored to the behavioral task, capabilities often reserved for feedforward control. Here we present recent experimental evidence that upper limb reflexes, the fastest feedback responses to an external perturbation, also exhibit this degree of motor intelligence under normal/non-clinical conditions. Thereby, these studies provide a stronger link between the historically contrasting concepts and experimental paradigms of feedback and forward control. Kurtzer will discuss how the arm's long-latency reflexes reflect an internal model of limb dynamics to decode the underlying torque perturbation whereas short latency reflexes are linked only to the local joint's motion. Perreault will discuss how long-latency reflexes are tuned to both the mechanical features of the environment and task demands, and that TMS disruption suggests distinct sites for task- and environment-dependent modulation. Sainburg will discuss how movement-related reflexes are reset prior to the overt movement reprogramming using a hybrid paradigm involving mechanical perturbations and a visual double-step. Scheidt will discuss how tonic multi-joint reflexes are compromised in stroke-afflicted patients and how these problems with spasticity also impact movement planning.

**“How Fast?” Trajectory Control, Movement Energy, and the Basal Ganglia***Robert S. Turner<sup>1</sup>, Pietro Mazzoni<sup>2</sup>, Yael Niv<sup>3</sup>, David Vaillancourt<sup>4</sup>*

<sup>1</sup>Department of Neurobiology and Center for the Neural Basis of Cognition, University of Pittsburgh; <sup>2</sup>Department of Neurology, College of Physicians and Surgeons, Columbia University; <sup>3</sup>Center for the Study of Brain, Mind and Behavior, Princeton University; <sup>4</sup>Department of Kinesiology and Nutrition, Departments of Bioengineering and Neurology, University of Illinois at Chicago

Recent models of motor control suggest the need for a general mechanism that regulates the effort or motor “energy” expended during a movement (Guigon et al. 2007; Todorov and Jordan 2002). This effort term may be related to the basal ganglia, because studies have shown that neural activity of specific nuclei scales with the velocity and amplitude of movement (Turner et al. 1998; Turner et al. 2003), and the rate and amplitude of force during grasping (Vaillancourt et al. 2004; Spraker et al. 2007). Recent theoretical accounts have linked movement-related expenditure of energy to the demands of the task (Mazzoni et al. 2007) and to an animal's previous experience of the cost/benefit contingencies of the task (Niv 2007; Niv et al. 2006). In this symposium, we will present several lines of research that implicate the motor circuit of the basal ganglia in aspects of motor control related to movement effort, energy expenditure or cost. **Yael Niv** will present results from a series of modeling studies that suggest the opportunity cost of time is a primary determinant of response vigor in action selection and motor control. Several lines of evidence implicate the tonic level of dopamine in the basal ganglia as a possible substrate for this opportunity cost term.

**Dr. Vaillancourt** will discuss a series of functional imaging studies performed in neurologically normal subjects. Together, these studies consistently implicate portions of the basal ganglia motor circuit in aspects of motor output that co-vary with rate of change of force, motor effort, or energy expenditure.

**Dr. Turner** will present results from studies in rhesus monkeys in which transient disconnections of the basal ganglia motor output produced discrete impairments in the animal's ability to appropriately scale movement velocity and extent. These aspects of task performance co-vary closely with the energetic cost of the task.

**Dr. Mazzoni** will present results from his recent psychophysical studies in patients with Parkinson's disease. He found that parkinsonian bradykinesia could be accounted for by increased sensitivity to the energetic costs associated with movements that require rapid accelerations and decelerations.

These disparate experimental approaches lead to a consistent theory that the basal ganglia motor circuit modulates an aspect of motor control that is related to the effort or energy expended during a movement. This concept is consistent with the more global hypothesis that the basal ganglia as a whole, together with its dopaminergic innervation, regulate action motivation and response “vigor.”

## a.) Pursuit Eye Movements Require a Geometric Transformation of Velocity Signals

*Gunnar Blohm*<sup>1,2</sup>, *Pierre Daye*<sup>1</sup>, *Philippe Lefevre*<sup>1</sup>

<sup>1</sup>CESAME and Lab. Neurophysiol., Universite catholique de Louvain, Louvain-la-Neuve, Belgium

<sup>2</sup>Dept. Physiology and Faculty of Arts & Science, Queen's University, Kingston, Ontario, Canada

It is well established that saccade planning requires a geometric transformation between the retinal stimulus and the desired motor plan to acquire the target (Crawford & Guitton 1997). However, this problem of reference frame transformations has never been considered for velocity signals. Therefore we asked whether a separate 3D visuomotor transformation of velocity signals was theoretically required by modeling the underlying geometry. We then tested our model predictions in a series of smooth pursuit experiments. We used quaternions to model the 3D eye-in-head geometry. Our model predicted that a visuomotor velocity transformation would require the use of extra-retinal eye-in-head position and should include three different components; (1) because of the eye's spherical projection geometry, the same retinal velocity should result in different interpretations of velocity direction depending on eye-in-head position, (2) false torsion due to off-axes eye positions must be compensated for and (3) ocular torsion (e.g. due to the VOR) must be accounted for. We tested these 3 predictions separately on human subjects. Subjects were required either to pursue an eccentric moving target viewed under different vertical eye positions (prediction 1), to pursue a target previously foveated at different oblique positions (prediction 2) or to make a fast head roll to either shoulder while maintaining fixation in order to obtain large eye torsion because of dynamic VOR and then to pursue a moving target (prediction 3). 3D eye-in-head position was measured at 400Hz using a Chronos Video head-mounted eye tracker and head-in-space position and orientation was sampled at 200Hz using a Codamotion active infrared marker tracking device. We analyzed the open-loop gaze pursuit response, i.e. the first 100ms after pursuit onset (velocity threshold detection). We then compared the observed pursuit response to the prediction of the model to determine whether 3D geometry was or was not taken into account in the visuomotor velocity transformation. We found that for all 3 components of the velocity conversion geometry, human behavior was accurate. This suggests that the brain indeed performs a complete 3D visuomotor velocity transformation for smooth pursuit eye movements that is different from the previously described visuomotor transformation of position signals for saccades. Since pursuit direction was accurate even for torsional values outside of Listing's plane in our head-roll condition (prediction 3), we rule out the possibility that the velocity transformation geometry we describe here could be accounted for by the mechanical properties of the plant, e.g. through pulleys.

## b.) The Consequences of Selection: Corticospinal Excitability Changes in the Non-Selected Hand during Unimanual Actions

*Julie Duque*<sup>1,2,3</sup>, *Ludovica Labruna*<sup>1</sup>, *Richard Ivry*<sup>1,2</sup>

<sup>1</sup>Department of Psychology, University of California, Berkeley; <sup>2</sup>Helen Wills Neuroscience Institute, University of California, Berkeley; <sup>3</sup>Laboratory of Neurophysiology, Université catholique de Louvain, Brussels, Belgium

A selection process underlies all actions, with one stage involving the choice of one hand rather than the other. Previous studies have shown that, at the time of movement onset, corticospinal excitability is increased in the non-selected hand. This facilitatory effect could result from residual activation of a potential response that was not selected. Alternatively, it could reflect the engagement of brain regions that are recruited in an effector-independent manner i.e. areas involved in movement preparation for either hand. To evaluate these hypotheses, we asked subjects to position their hands on a computer screen placed across their knees. They performed four choice-RT tasks in separate blocks, formed by the factorial combination of two variables. First, the choice was either within-hand (right index finger or right pinkie abduction) or between-hand (left or right index finger abduction). Second, we compared two types of imperative cues: symbolic cues in which a letter indicated the appropriate response and spatial cues in which a circle appeared at the target location of the response. Motor evoked potentials (MEPs), elicited by TMS over the right motor cortex, were measured in the left first dorsal interosseous (FDI) and the left abductor digiti minimi (ADM). Following a warning signal, MEPs from left FDI and ADM muscles were inhibited in all tasks; this effect was more prominent in the between-hand blocks (left hand was a potential responder) than in the within-hand blocks (left hand was irrelevant), a finding consistent with the hypothesis that inhibitory processes prevent premature responses in potential effectors. After the imperative cue, MEPs in the left hand rose rapidly when the muscle was the response agonist and to a

smaller extent when it was not the response agonist. MEPs in left hand muscles also increased when the response was made with the homonymous muscle in the opposite right hand (e.g. left FDI during right index finger abduction). Facilitation in the non-responding hand was more pronounced in the within- than between-hand selection task, likely due to the stronger preparatory inhibition in the latter condition. Interestingly, the facilitation was stronger when the response was signalled by a symbolic than spatial cue. This latter result shows that facilitation in the non-responding hand is modulated by the manner in which an action is cued. This modulation argues against a residual planning hypothesis and is consistent with the idea that facilitation could be related to effector-independent response planning.

### **c.) Task-Specific Error Feedback Control in Reaching Arm Movements: Feedforward Motor Adaptation Automatically Trains Feedback Responses**

*Mark Wagner<sup>1</sup>, Maurice Smith<sup>1,2</sup>*

<sup>1</sup>Harvard University School of Engineering and Applied Sciences

<sup>2</sup>Harvard University Center for Brain Science

There is a long-running debate over the precise nature and importance of cortically-modulated online error feedback, particularly in the limit of short, targeted movements. Some have posited that for these movements, control is almost entirely feedforward, based on a desired trajectory, and the influence of sensory feedback is minimal. More recently proposals have added to this a forward-model-based feedback controller, which uses real-time online state-predictions to issue corrective accelerations as needed. Generalized optimal feedback control goes even further to assert that these corrective accelerations are specific to and appropriate for the particular dynamics and goals of the current task. To date, however, empirical evidence that clearly supports these particular assertions has been somewhat scarce. Here we provide direct evidence that, following a new feedforward motor adaptation, motor feedback responses to unanticipated errors become precisely task-appropriate, even when such errors were never experienced during training. To study this ability, we asked how, if at all, do online responses to occasional, unanticipated force pulses during reaching arm movements change after adapting to altered arm dynamics? Specifically, do they change in a task-appropriate manner? In our task, subjects learned novel velocity-dependent dynamics during point-to-point reaching arm movements. Occasional force pulses, however, produced unanticipated changes in velocity. Therefore, after adaptation, a task-appropriate response to an unanticipated pulse must compensate the expected change in velocity-dependent dynamics. We found that after adaptation, a new component of the pulse-response precisely compensated expected effects of velocity changes—even though this response was never itself trained. These results provide evidence for a flexible optimal feedback controller which produces responses specific to the learned dynamics of the current task. In order to accomplish this, the neural processes underlying feedback control must (1) be capable of accurate real-time state prediction for velocity, and (2) have access to recently learned changes in internal models of limb dynamics.

### **d.) Trial Based Modulation of Neural Activity in Primary Motor Cortex during Adaptation to a Visuomotor Rotation**

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Previous studies of reach adaptation in non-human primates have demonstrated that neurons in primary motor cortex show learning related changes in response to constant perturbations over the course of many reaches (Li et al., 2001; Padoa-Schioppa et al., 2004). However, these studies have not addressed changes in neural activity that occurs on a much shorter timescale (i.e. from one trial to the next). We know that the adaptation of reaching movements to unpredictable environmental perturbations results from the ability to update motor commands based on performance information from only the most recent movement attempts (Scheidt et al., 2001). However, it is unclear how these trial-by-trial changes influence the activity of neural ensembles in primary motor cortex. One macaque monkey (*Macaca mulatta*) was trained to move a cursor appearing above its hand location from a central target to one of eight peripheral targets (6cm) using a two degree of freedom, planar robotic manipulandum. An electrode array composed of 100 electrodes (Cyberkinetics Neurotechnology Systems Inc) was used to record the spiking activity of single units in primary motor cortex during the experiment. Each session consisted of three phases. During the pre and post adaptation phases, the monkey made at least 5 unperturbed movements to each of the peripheral targets, which were pseudo-randomly selected on each trial. During the adaptation phase, all movements were directed to the 90 degree target and were perturbed by a clockwise rotation of the cursor position about the central target that varied in magnitude pseudo-

randomly from trial-to-trial. Movement error was calculated as the peak deviation orthogonal to the line connecting the center and peripheral target. As expected, we observed an inverse linear relationship between movement error and rotation magnitude. We binned trials in the adaptation phase by error magnitude to look at neural activity related to the errors that drive adaptation. We found that cells modulated their activity in proportion to the magnitude of the error at the end of the ballistic phase of movement. These responses were strongest when the corrective movement was directed in the cells preferred direction; thus the responses were involved in feedback correction. We also binned adaptation phase trials by the perturbation experienced on the previous trial to investigate how recent experiences might change neural activity. These responses showed no consistent pattern of activation, thus we are using additional methods to determine how past experiences drive present performance. Support: NIH NINDS R01NS048845

### **e.) The Effect of Cutaneous Feedback Loss on Tuned Muscle Responses to Support Surface Postural Perturbations**

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Intact and decerebrate cats are known to respond to horizontal support surface perturbations with tuned muscular responses of a specific direction and breadth (Macpherson 1988b, Honeycutt 2005). Studies using platform rotations have suggested that cutaneous feedback may be important in producing appropriate muscle responses to support surface perturbations (Ting and Macpherson 2004). In order to investigate the sensory mechanisms underlying these responses, we have developed a post-mammillary decerebrate cat preparation capable of responding to postural perturbations (Honeycutt 2005). To test the importance of cutaneous feedback on the production of appropriately directed and tuned muscle responses, we recorded from 15 muscles of the right hindlimb during horizontal support surface perturbations before and after right tibial nerve crush in the decerebrate cat. The right tibial nerve innervates the plantar surface of the paw. Preliminary data suggest that while there is a proportional decrease in amplitude, the muscle responses remain intact in direction and breadth after the loss plantar surface cutaneous feedback. This coupled with the knowledge that group Ia afferents respond to support surface perturbations with tuned responses of similar direction and breadth to muscles (Honeycutt 2007), suggests that muscle spindle feedback may mediate the directional tuning of individual muscle responses to postural perturbations while cutaneous feedback may scale those responses. We will further investigate this hypothesis using the reinnervation surgery to eliminate the monosynaptic group Ia feedback while preserving motor function.

### **f.) Long-Latency Reflexes of the Upper-Limb are Sensitive to the Metrics of a Visuo-Spatial Task**

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Recent theories of motor control posit that the extensive repertoire of volitional behaviour is accomplished via intelligent manipulation of sensory feedback. The implication is that rapid feedback-mediated responses (i.e. reflexes) will be tuned in accordance with behavioural demands. We have previously presented a paradigm to examine upper-limb reflexes under a wide range of behaviors akin to the prevalent methodology used to study the volitional motor system. Briefly, subjects are presented with a visuo-spatial target and are trained to respond to an unpredictable perturbation by rapidly placing their hand inside the target. This allows us to quantify how reflexes change with target metrics such as position, size and shape and expands on previous research using verbal instructions. We have shown that long-latency reflexes (50-100ms) of shoulder and elbow muscles are strongly modulated by target positions that require categorically different responses. Here we extend these results and show that long-latency reflexes, like volitional responses (120-180ms), are sensitive to the direction and distance of spatial targets in one- and two- dimensions. Our first experiment placed targets at five positions along one axis to determine whether reflexes are continuously graded by target distance in accordance with the behavioural task-demands or whether they are limited to categorical changes. Akaike's Information Criterion was used to compare four models relating reflex activity to target position (constant, step, linear and sigmoidal). Long-latency reflexes continuously increased their magnitude with target distance and

**Parsimony in Neural Control: Are there Shared Neural Mechanisms for  
Feedforward and Feedback Control of Posture?**

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The ability to maintain standing posture and balance during everyday movements requires a combination of both anticipatory and reactive postural control. When preparing to perform a voluntary task, such as reaching for an object, or taking a step, an *anticipatory postural adjustment* (APA) precedes the movement itself. The role of the feedforward APA is to change the body posture such that the desired movement can be performed successfully. In contrast, during unexpected perturbations to the body, which might occur when standing on an unstable surface, or when the foot slips during walking, an automatic postural response (APR) is evoked after the perturbation is sensed by the nervous system. This feedback APR changes the body posture to mitigate the destabilizing effects of the perturbation. Typically, these feedforward and feedback modes are studied independently. But, given that their common role is to stabilize the body's posture by coordinating multiple muscles, joints, and limbs, is it possible that there are common neural substrates underlying feedforward and feedback control of posture? In this panel, we will present some of the commonalities and differences between anticipatory and reactive postural control. Afterward, we hope to discuss the possibility of common neural substrates for these two modes of postural control. First, Lena Ting will present a general framework for understanding hierarchical control of posture and movement, whereby muscle synergies could be motor modules for task performance that could be accessed both by descending and feedback pathways. She will present musculoskeletal simulation results that suggest that muscle synergies in the cat constrain the possible force directions used for APRs, and that muscle synergies could be tuned for better feedforward or feedback postural control. Moreover, a neural controller that retains the same synergies for a range of postural configurations can predict changes in postural forces observed experimentally. Gelsy Torres-Oviedo will present data demonstrating that a common set of muscle synergies can reproduce inter-trial variability—presumably due to feedforward adaptive mechanisms—during human APRs across a variety of postural configurations. She will also demonstrate inter-subject differences in muscle synergy number and pattern, perhaps suggesting differential strategies for balance control. Paul Stapley will present directional tuning curves of human muscle activity during APAs preceding a reaching task, and compare them to tuning curves of APRs. He will also discuss interactions between APA's and APRs during human postural control. Finally, Trevor Drew will present data suggesting that the same reticulospinal neurons (RSN) in the cat that are activated during APAs preceding a reach, are also activated during APRs following an unexpected loss of the support surface in a single limb. This demonstrates that the same neurons may be involved in producing both anticipatory and compensatory postural adjustments. We hope to conclude by a discussion of the underlying organizational principles for feedforward and feedback postural control.