The Ninth Computational Motor Control Workshop at Ben-Gurion University of the Negev

May 9, 2013, W.A. Minkoff Senate Hall, BGU Marcus Family Campus, Beer-Sheva, Israel

http://www.bgu.ac.il/cmcw

Invitation Letter and Call for Posters, the ninth BGU-CMCW May 9, 2013

Dear Colleagues,

In what has now become a tradition, we wish to invite you to participate in the ninth annual Ben-Gurion University Workshop on Computational Motor Control on May 9th 2013, in the W. A. Minkoff Senate Hall at Ben-Gurion University of the Negev, Beer-Sheva, Israel. The following information is also available on our website: http://www.bgu.ac.il/cmcw

Thank you for your attention,
Opher Donchin and Amir Karniel
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Overview: The nervous system analyses sensory information and orchestrates motor commands. In so doing, it faces challenges that it shares with many artificially engineered systems. In the spirit of the classic field of cybernetics, the field of computational motor control makes scientific and technological progress simultaneously by exploring the differences between artificial control theory and biological motor control.Computational motor control is a multidisciplinary research program in which mathematics, engineering, biology, medicine and the cognitive neurosciences all play important roles. This workshop will bring together world leaders in the field of computational motor control including Israeli researchers and distinguished guests. The goal will be to learn about the current state of the field and to identify the directions that will provide the medical and scientific breakthroughs of the next decades.

Call for Posters: The posters will be available throughout the day near the lecture hall to facilitate fruitful discussions.Please submit a one-page abstract of up to 400 words by March 25 th through the website or by email to cmcw@bgu.ac.il with the subject heading "CMCW abstract submission". An email should clearly contain your name and affiliation. Notification of acceptance and abstract books will be mailed out on April 10 th. In addition, all accepted abstracts will appear on our website prior to the conference. Poster's should have a maximum width of 90 cm and a maximum height of 120 cm.

Best Poster Award: The award committee will choose the best poster(s) which will be announced at the end of the day. The Best Poster Award Committee will be chaired by Opher Donchin, Ben-Gurion University.
To be considered for the best poster award, authors must submit a file with their poster to the Best Poster Award Committee by May 1 th, 2013. The poster can be submitted in PDF, TIFF, or Power Point formats by e-mail to cmcw@bgu.ac.il. Please use the subject heading “CMCW best poster submission” and include in the text of the message the name of the main author. The Best Poster Award Committee members: Opher Donchin, Lior Shmuelof, Sandro Mussa-Ivaldi.

The Best Poster Award Sponsors:

- Alpha Omega
- SenseGraphics / Geomagic
- NanInsturments

Travel Award: In special cases we will also consider a travel award to partially cover the expenses of international researchers/students. The criteria for the travel award will be: (i) The scientific quality of the proposed poster and its relevance to the topic of the workshop (ii) An interest in pursuing a PhD, post doc or faculty position at Ben-Gurion University. Those interested in receiving a travel award should submit an abstract for the poster they will submit and a short description of their circumstances by March 25 th by e-mail to cmcw@bgu.ac.il with the subject heading "CMCW travel award."

Tour to the Judean lowland: On wednesday, May 8th , we plan a hike to the Judean lowland. The hike will leave from Ma'ale Hachamisha hotel at 8:30. Anyone who want to take a part in the hike is asked to arrive at the hotel on the morning of May 8. Please be sure to indicate your interest in the tour in the registration forms. The payment form will be sent by e-mail.

Dinners: We will have a festive welcome dinner on the evening of May 8, before the workshop that will take a place near Beit-Shemesh. People intersted in joining the diner, but were not on the hike, will be picked up at the Beit Shemesh rail way station at ~18:00 by the bus. Speakers and chairmen will be guests of the workshop at the dinner. For others wishing to join us, the dinner will be subsidized and will cost no more than 100 NIS per person. We will also have a more modest dinner and discussion in the evening following the workshop that will be payed by the participants.

Registration: Please register on our website http://www.bgu.ac.il/cmcw before March 25 th. Registration is mandatory but free. Space may be limited. Please indicate in your registration whether you are interested in particpating in the hike, the welcome dinner and the discussion diner.

Sponsors:

- The President, Ben-Gurion University
- The Zlotowski Center for Neuroscience, BGU
- The Dean of the Faculty of Health Sciences
- The Dean of the Faculty of Engineering

The Ninth Computational Motor Control Workshop
May 9, 2013
W. A. Minkoff Senat Hall, BGU Marcus Family Campus,
Beer-Sheva, Israel

Zlotowski Center For Neuroscience

Department of Biomedical Engineering and
the Zlotowski Center for Neuroscience at Ben-Gurion

Wednesday, May 8
Last day of EU C7 workshop
See www.bgu.ac.il/cmcw for links and details

- 9:00-17:00 Hike to Judean lowland
  starts from Ma'ale Hachamisha hotel
  Guide Eitan Krokovski
- 18:00 Festive Dinner

Thursday, May 9

- 8:30-8:50 Registration, Poster placement and coffee
  8:50-9:00 Opening Remarks **Amir Karniel**, BGU, Head of the organizing committee

Cerebellum: single units
Chair: Maarten Frens, Erasmus MC, Netherlands

- 9:00-9:30 **Javier Medina**, University of Pennsylvania, USA
  "Cerebellar control of movement timing: insights from eyeblink conditioning"

- 9:30-10:00 **Erik De Schutter**, OIST, Japan
  "Coding in silence: cerebellar Purkinje cell pauses control eye cascade endings"

- 10:00-10:30 **Tim Ebner**, UMN, USA
  "Still Searching with an Electrode for Internal Models in the Cerebellum: Encoding Kinematics, Errors and Learning"

- 10:30-10:40 Discussion
- 10:40-11:20 Coffee break and Posters

The Clinic: From Stimulation to Therapy
Chair: Miriam Zacksenhous, Technion, Israel

- 11:20-11:50 **Chris Miall**, University of Birmingham, UK
  "Stimulating the cerebellar contribution to cognition"

- 11:50-12:20 **Opher Donchin**, BGU
  "Motor hierarchy in the cortex and cerebellum"

- 12:20-12:50 **Simona Bar-Haim**, BGU
  "Training teenagers with cerebral palsy on a split-belt treadmill: insights to guide rehabilitation"
- 12:50-13:00 Discussion
- 13:00-14:30 Lunch and Posters

Motor control on multiple levels
Chair: Tzvi Ganel, BGU

- 14:30-15:00 **Lior Shmuelof**, Weizmann Institute, Israel
  "The puzzle of motor learning: from skill learning to adaptation"

- 15:00-15:30 **Reza Shadmehr**, Johns Hopkins University, USA
  "Movement vigor, impulsivity, and the cost of waiting in the human brain"

- 15:30-16:00 **Joern Diedrichsen**, UCL, UK
  "Adaptation vs. Skill learning: Lessons from visual rotation and mirror reversal learning."
- 16:00-16:10 Discussion
- 16:10-16:20 Poster awards
  Sponsors: Sensegraphics/Geomagic, NanInsturments, AlphaOmega
- 16:20-16:50 Coffee break

Sensory-motor systems
Chair: Opher Donchin, Ben-Gurion University

- 16:50-17:20 **Ilan Lampl**, Weizmann Institute, Israel
  "Adaptation and coding of stimulus intensity in the somatosensory system"

- 17:20-17:50 **Maarten Frens**, Erasmus MC, Netherlands
  "Enhancing Motor Learning"

- 17:50-18:20 **Andrew Jackson**, Newcastle University, UK
  "Optimizing control of Brain-Machine Interfaces"

- 18:20-18:30 Discussion
- 19:00 Diner

Talks

Precise control of movement timing by optogenetic inhibition of Purkinje cells.

Javier F. Medina

University of Pennsylvania, USA

Eyeblink conditioning is a simple form of motor learning that provides a great opportunity to examine how the cerebellum controls the timing of our movements. In the first part of my talk, I will present data from a series of behavioral experiments that examine the timing of the conditioned eyelid movement in head-fixed mice. The findings clearly demonstrate that mice learn to make well-timed blinks, not by regulating the onset of the eyelid movement, but by controlling its speed with high precision. To follow up on these findings, in the second part of my talk I will examine whether transiently inhibiting Purkinje cell activity in awake mice is sufficient to control the speed of eyelid movements. I will present data from a series of experiments using an optogenetic strategy to suppress the high spontaneous activity of Purkinje cells in an eyeblink microzone of cerebellar cortex. The findings demonstrate that a brief and synchronized decrease of Purkinje cell activity can be used as a signal to sculpt the timing and kinematics of eyelid movements via graded disinhibition of downstream neurons in the deep cerebellar nuclei.

Coding in silence: cerebellar Purkinje cell pauses control eye saccade endings.

Erick De Schutter

TBD

Still Searching with an Electrode for Internal Models in the Cerebellum.

Timothy J. Ebner, Laurentiu S. Popa and Angela L. Hewitt

Department of Neuroscience, University of Minnesota, Minneapolis Minnesota

Internal models provide for representations of the input-output properties of the motor apparatus or their inverses. The cerebellum has been hypothesized to acquire and store internal models of the motor apparatus. The results of behavioral, functional imaging and transcranial magnetic stimulation studies in normal subjects and in patients with cerebellar dysfunction support this internal model framework. However, only a few single unit studies have directly tested whether neurons in the cerebellar cortex have the signals compatible with either an inverse or forward internal model. Our studies in the monkey performing manual pursuit tracking under various force fields and loads demonstrate that the simple spike discharge of Purkinje cells in lobules IV-VI does not encode the dynamics-related signals required to be the output of an inverse dynamics model. However, recent studies of Purkinje cell firing during both tracking and reaching movements show that these neurons have characteristics expected of the output of a forward internal model of the arm. These characteristics include a robust, task independent representation of limb kinematics that leads the movement. The concept that the cerebellum is generating the signals needed to compute a sensory prediction error, that is, the difference between a prediction about the upcoming movement and the resulting sensory feedback, is also central to how a forward internal model operates. New studies in monkeys trained to manually track a pseudo-randomly moving target show that the simple spike firing is significantly correlated with the position, distance and directional errors. Importantly, the error encoding is independent of the kinematic encoding. Regression analyses determining the optimal timing at which the errors signals occur found bimodal temporal representations in which the simple spike firing encodes both prediction and feedback about an error. Decoding analyses show the population of Purkinje cells contains sufficient information to generate highly accurate estimates of the upcoming errors. For the majority of the bimodal profiles, the predictive and feedback error signals have opposing simple spike modulation. This opposing modulation could be used to compare the predictions with the consequences of motor commands, consistent with the neural signals needed to generate sensory prediction errors. Therefore, there is accumulating electrophysiological evidence that the cerebellum is involved in integrating the current state of the motor system with internally generated motor commands to predict the future state, consistent with a forward internal model.

Supported in part by NIH grants: NS18338, NS071686, and GM008244.\

Stimulating the cerebellar contribution to cognition and action.

Chris Miall

Birmingham, UK

In this talk, I will present results from 4 studies using TMS and TDCS to block the normal operation of the cerebellum. We have shown that TMS can disrupt reaching actions, such that there are directional errors after TMS to the cerebellum that are consistent with a reaching movement planned with out-of-date estimation of the state of the moving limb. We also show that rTMS of the right lateral cerebellum can disrupt predictive language processing. However, using cathodal TDCS to depress cerebellar cortical activity paradoxically leads to improved performance in an exploratory task, and to improved performance in cognitive and language tasks. I will argue that the negative effects of TMS are due to short term disruption of cerebellar predictive processes, while the positive effects of TDCS are due to disinhibition of cerebral cortical areas.

Motor Hierarchy in the cortex and cerebellum.

Opher Donchin

Ben-Gurion University of the Negev

I will review briefly the ideas surrounding hierarchy in the motor system, and relate these ideas to the notion of parallel distributed loops that seem to underlie parts of how the motor system is wired. These ideas will be placed in the context of recent experimental results in human subjects showing that heirarchy in the motor system can be revealed in the cerebellum that parallels the hierarchy in the cerebral cortex. Finally, I will discuss our findings and the theoretical ideas in terms of a research agenda focused on clarifying how movements really are structured by the nervous system that controls them.

Training Teenagers with Cerebral Palsy on a Split-Belt Treadmill Insights to Guide Rehabilitation.

Simona Bar-Haim

Faculty of Health Sciences
Ben-Gurion University of the Negev

The motor, cognitive and behavioral deficits that characterize cerebral palsy (CP) are caused by damage to the brain before the age of 2 years. Decades of neurorehabilitation research have shown that the damaged brain, just as the healthy brain can learn, and that motor recovery occurs in the setting of intensive task-specific practice. Methods for achieving optimal, engaging, meaningful intensive practice continue to be a source of research.

Today the physical and motor treatment of the child with cerebral palsy still includes, and is based on, contact of the physiotherapist's hands, encouragement and enablement of normal components of movement to facilitate normal development. The physical contact creates stimulus and a response from the child. The significance of this is that treatment today depends mainly on the neurophysiological approach of the beginning of the 20th century, which is based on the reflexive theory of Sherrington.

In this talk I will first raise the questions that we ask today concerning the clinical significance of the researches that we conduct today in the field of motor control and learning. I will then present the study we are now conducting on training teenagers with CP on a Split Belt Treadmill as part of a large RCT clinical trial, and discuss the phases of adaptation, retention and transfer of acquired walking functions to everyday life of the teenager with CP.

The study is supported by MERC USAID TA-MOU-09-M29-023

The puzzle of motor learning: from skill learning to adaptation.

Lior Shmuelof

Weizmann Institute, Israel

Motor learning tasks in the lab fail to capture essential components of real world motor learning behaviors. I will argue that motor learning should be decomposed into 2 components: action selection and improved execution (motor skill). In the first part of my talk, I will present a study about the kinematics and neuronal changes associated with improved motor acuity, a neglected component in motor skill research in humans. I will show that skill acquisition generalizes across difficulty levels and is associated with a reduction in trial-by-trial variability and with an increase in task representation in the primary motor cortex. In the second part I will show evidence of competition between error-based and reward-based learning mechanisms during an action selection (adaptation) task, and that reward-based learning drives the long-term retention of the adaptive patterns. I will present preliminary fMRI results suggesting that this competition takes place in the motor cortex. These results suggest that learning of complex motor tasks is likely to be driven primarily by model-free reinforcement processes.

Movement vigor, impulsivity, and the cost of waiting in the human brain.

Reza Shadmehr

Johns Hopkins School of Medicine

There is consistency in how health people move their eyes, arms, and legs. What is good about this way of moving, and why has our brain settled on this pattern? Here, I focus on the control of eye movements and suggest that the purpose of any movement is to acquire a more rewarding state. I suggest that the way the brain discounts reward in time strongly affects why we move the way that we do. This framework has the potential to explain why disorders that affect processing of reward in the brain, like Parkinson's disease, depression, and Schizophrenia, result in changes in control of movements.

Adaptation and Skill learning: Lessons from visual rotation and mirror reversal learning.

Jörn Diedrichsen & Sebastian Telgen

Institute of Cognitive Neuroscience, University College London

In this talk I will compare the learning of two different visuo-motor transformations during reaching: the rotation of the visual feedback by a certain angle and the mirroring of visual feedback around one axis. I will show that the human motor system learns these two transformations using separate mechanisms and that these are dissociable in the observed speed-accuracy tradeoff. For mirror-reversals there is a strong dependence of accuracy onto the reaction time (RT). For short RTs, participants still move into the wrong direction even after 2 days of training and only for longer RTs do they show the correct response. No such dependence is observed during visuo-motor rotation learning. Parallel observation are made in the fast feedback responses to visual displacements of the cursor that indicates the hand position. Together, these findings indicate that mirror reversals are learned by establishing a new control policy, which requires additional processing time, while visual rotations are learned through a recalibration of the existing control policy, thereby taking advantage of the automaticity of normal reaching. Furthermore, I will show that these two tasks differ in the way in that they consolidate between sessions. For visual rotations we observed consistent forgetting overnight, while mirror reversal learning showed substantial gains in the performance between sessions, which are sleep-dependent. Thus, with shifting speed-accuracy tradeoffs and offline consolidation gains, mirror-reversal learning shows common characteristics with many other skill-learning tasks, such as sequential finger movements. In contrast, visuo-motor rotation only requires the recalibration of a control parameter in an existing control policy. Therefore, we believe that the reaching under different visuo-motor transformations may provide new insights into the neural mechanisms underlying adaptation and skill learning.

Adaptation and coding of stimulus intensity in the somatosensory system.

Ilan Lampl

Weizmann Institute, Israel

Tactile information ascends from the brainstem to the somatosensory cortex via two major parallel pathways, lemniscal and paralemniscal. Although parallel processing of sensory information is not unique to this system, the distinct information carried by these pathways remains unclear. Using in vivo intracellular recordings at their divergence point, the brainstem trigeminal complex, we found that increasing the intensity of vibrissa stimulation entailed opposite adaptation effects in these nuclei. Whereas lemniscal neurons adapted less, paralemniscal neurons adapted more. This indicates that stimulus intensity is differently coded by these pathways. Indeed, using sets of noise stimuli covering different dynamic ranges we found that coding of intensity is greatly improved at the higher range of intensities for lemniscal neurons, whereas paralemniscal neurons better encoded the weaker range of stimuli. We suggest that parallel adaptive channels are a framework for increasing the dynamic range of intensity coding during sustained sensory stimulation.

Enhancing Motor Learning.

M.A. Frens

In this talk I will discuss various recent experiments from our lab in which we increased the speed of learning by cerebellar stimulation. These include environmental enrichment and transcranial direct current stimulation. I will speculate about a common underlying mechanism.

Optimizing control of Brain-Machine Interfaces.

Andrew Jackson

Institute of Neuroscience, Newcastle University

Brain-Machine Interfaces (BMIs) decode electrical activity directly from the nervous system to provide new communication channels for paralysed patients to interact with the environment. However, despite technological advances, the quality of 'brain control' has yet to match the speed, accuracy and efficiency of natural movements. Most current interfaces use a 'biomimetic' approach to decode motoric information, despite profound differences in biomechanical and sensory properties of artificial effectors. In this talk I will argue that BMIs should instead be conceived as abstract tools offering new sensorimotor affordances that the brain must learn to exploit. Primates have evolved remarkable tool-using abilities, but these are traditionally mediated through movements of the limbs. I will describe experiments using 'myoelectric control' in humans and 'brain control' in monkeys that explore the extent to which we are constrained by naturalistic patterns of neuromuscular activity, or can transcend these limitations to produce behaviour that is optimal for abstract goals dissociated from limb movement. Understanding the mechanisms by which abstract sensorimotor skills are acquired, and the limits of motor cortical flexibility, will be essential for developing abstract neural interfaces that are compatible with the computational architecture of the motor system.

Posters

Riemannian geometric approach to human hand tracing movements along planar contours.

Armin Biess *

Max-Planck-Institute for Dynamics and Self-Organization and Bernstein Center for Computational Neuroscience, 37073 Göttingen, Germany

Recently, a differential geometric approach to model human arm movements has beensuggested by the author and co-workers (geodesic model). This formulation is appliedhere to human hand tracing movements along planar contours by endowing arm con-figuration space with a Riemannian metric that is conformally related to the Euclidean metric. The conformal factor is given by the curvature of the contour. Speed-curvature relations are derived from the geodesic model for periodic and non-peridoc hand tracing movements and the compatibility with the empirical one-third power law is shown. Interestingly, this geometric approach leads to a generalization of the one-third power law to non-periodic boundary conditions and provides a new interpretation of the gain-factoras time-derivative of the Riemannian arc-length. Preliminary experimental data are presented and compared with model predictions. It is hypothesized that the sensorimotor system shapes arm configuration space by learning metric structures through sensorimotor feedback.

* currently at General Motors, Advanced Technical Center, Herzliya 46733, Israel

Savings in locomotor adaptation task explained by a dual-rate context-dependent learning process.

Firas Mawase[1], Lior Shmuelof [2], Simona Bar-Haim[3] and Amir Karniel[1]

[1]Department of Biomedical engineering, Ben-Gurion University of the Negev, Beer-Sheva, Israel

[2]Department of Computer Science and Applied Mathematics, Weizmann Institute of Science, Rehovot, Israel

[3]Department of Physiotherapy, Ben-Gurion University of the Negev, Beer-Sheva, Israel

Savings, defined as a faster relearning process of an external perturbation, offers a behavioral linkage between motor learning and memory. Recent perspectives suggest the motor learning is composed of multiple learning components, showing different learning and forgetting properties. Interestingly, there is currently no consensus about the learning components that underlie savings. In particular, the learning process that underlies savings during locomotor adaptation remains poorly understood. Here, we show that the basic error-based multiple timescales state space model is not sufficient to explain savings during locomotor adaptation. Instead, we found that error-based dual-rate context-dependent learning processes can explain adaptation and savings in locomotor adaptation. We confirm the model predictions in two experiments. In the first, subjects adapted to speed perturbations during walking on a split-belt treadmill, briefly de-adapted and then readapted. In a second experiment, subjects readapted after a prolonged period of washout of initial adaptation. Interestingly, we found inter-subject correlation between initial learning and savings measurements in the two experiments, suggesting that the multiple learning components share learning parameters. Our results suggest: (1) large initial errors during de-adaptation allowed spawning of new memory whereas savings during relearning occurs by switching to a previously protected memory (2) the learning parameters of the slow and fast learning components are not independent. Together, these findings suggest that parameter estimation for fast and slow learning components in locomotion may depend on a subject-specific shared inference process.

Kinematic bias causes decision bias in a perceptual decision making reaching task.

Jason Friedman[1,2] and Matthew Finkbeiner[1]

[1]*Department of Cognitive Science, Macquarie University, Sydney, Australia*

[2]*Physical Therapy department, Tel Aviv University, Tel Aviv, Israel*

When reaching to visual targets in front of the body in a speeded task, biases in the initial directions of reaching movements have been observed and depend on the initial posture of the arm (Ghilardi, Gordon, & Ghez, 1995). These biases, which vary across individuals, may be due to kinematic reasons. For example, when the right hand is directly in front of the midline of the body, movements in a forward-right direction are "easier" than movements in a forward-left direction. This is because movements to the forward-right require primarily rotation at only one joint (the elbow) whereas movements to the forward-left require rotations at both the shoulder and elbow.

In this study, we tested whether this kinematic bias in reaching causes a response bias in a perceptual decision making task. Biases in perceptual tasks are known to be under cognitive control (Wagenmakers, 2009), and can be manipulated by the task (e.g. by changing the probability or payoff of different options).

Subjects reached out to a target on a touch screen based on random dot kinematogram stimuli (e.g., if the dots are moving more to the left, reach out and touch the left target). We quantified kinematic bias by the ratio of movements that initially headed to the right of the sagittal plane, compared to movements that initially headed to the left of the sagittal plane. Perceptual response bias in this task was quantified using signal detection theory (Green & Swets, 1966). We found that there is a significant correlation between the kinematic bias and the perceptual response bias in this task. This correlation was found both when the stimuli were completely uninformative and when the stimuli contained perceptual information. Based on these findings, we propose that the kinematic bias, which seems to be a function of arm posture, causes a decision bias for this task.

Ghilardi, M. F., Gordon, J., & Ghez, C. (1995). Learning a visuomotor transformation in a local area of work space produces directional biases in other areas. *Journal of Neurophysiology*, *73*(6), 2535–2539.

Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York, USA: Wiley.

Wagenmakers, E.-J. (2009). Methodological and empirical developments for the Ratcliff diffusion model of response times and accuracy. *European Journal of Cognitive Psychology*, *21*(5), 641–671. doi:10.1080/09541440802205067

Amygdala response to an aversive stimulus is inhibited by cerebellar output.

Ari Magal and Matti Mintz

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An aversive challenge triggers two stage learning according to the two stage theory of classical conditioning. The first stage involves a fast acquisition of fear-CRs following CS-US association in the amygdala complex. The second stage involves a slower acquisition of motor-CRs in the cerebellum. Based on the observed interaction between the cerebellum and the amygdala, being that an adaptive rate of cerebellar motor-CRs was associated with decreased amygdala-based fear-CRs, a *third stage* of classical conditioning was hypothesized. This hypothetical third stage suggests that cerebellar output has an inhibitory influence upon fear-related amygdala activity. To explore this hypothesis, we mimicked the natural cerebellar output (i.e., neuronal-CR) using electrical stimulation of the cerebellum's interpositus and fastigial nuclei, and examined how the amygdala response to an aversive periorbital electrical stimulus (i.e., mimicking the US) was influenced by the cerebellar stimulation compared to no cerebellar stimulation. The results of the study show that cerebellar output had a differential inhibitory effect upon the amygdala response to the periorbital stimulation, depending on the laterality of the cerebellar nucleus stimulated and the latency at which stimulation was triggered. These results provide a neurophysiological basis for extinction of a learned fear response by adaptive cerebellar motor responses.

Experimental closed-loop motor-sensory control for the study of active perception.

Avner Wallach, Goren Gordon, Knarik Bagdasarian and Ehud Ahissar

Department of Neurobiology, Weizmann Institute of Science, Rehovot, Israel.

Rats actively acquire tactile information about their proximal surroundings by moving arrays of long hairs (whiskers) on both sides of their snout. The movements are exclusively controlled by the facial nucleus of the brainstem, via the facial nerve. This motor nerve may be exposed and electrically stimulated in anesthetized animals, thus inducing whisker movements quite similar to those observed in awake, behaving ones. In previous studies such 'artificial whisking' was performed in an open-loop manner, using a pre-defined stimulation pattern. Hence, activity in the vibrissal sensory pathway (conveyed by the trigeminal cranial nerve) was characterized only in response to narrowly distributed, stereotypical movements of the whiskers. Moreover, the context of feedback and control, central to the subject of active perception, cannot be implemented in open-loop experiments.

Here we present a novel experimental set-up which allows for closed-loop control of whisker-pad motion. Using fast video capture, on-line whisker tracking and real-time control of the stimulation pattern, we demonstrate that natural, dynamically rich whisker trajectories, as well as interactions with external objects, may be executed in anesthetized rats. This set-up allows for a systematic characterization of the motor-sensory system in a natural-like, closed-loop context. Moreover, the system serves as an accessible test-bed for theories of motor control and active perception.

Climbing fiber activity during trial-by-trial adaptation in the oculomotor vermis of rhesus monkeys.

M. Junker[1], D. Endres[12], P. W. Dicke[1], P. Thier[1]

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[2]Werner Reichardt Centre for Integrative Neuroscience, Tübingen, Germany
Eberhard-Karls Universität, Tübingen, Germany

The cerebellum plays a key role in motor learning, i.e. the optimization of motor behavior by considering the consequences of the behavior. It is usually assumed that information on the quality of the behavior is provided by climbing fibers, one of the two afferents reaching cerebellar cortex. Purkinje cell complex spikes (CS), the hallmark of climbing fiber activity, have been varyingly suggested to encode the motor error driving learning or, alternatively, a signal reflecting the adaptational state of the system.

In an attempt to clarify if CS encode the error driving learning, we resorted to visually guided saccades, a convenient model of goal directed motor behavior. Three Rhesus monkeys participated in the experiments, performing 10° center-out saccades in 1 out of 8 randomly chosen directions, separated by 45°. On one third of the trials, chosen at random, the visual target was stepped back by 3° during the saccade, on a second third it was stepped out by 3° or, on the final third, stayed at its initial location, thereby inducing a performance error or a regular visually guided saccade respectively. When analyzing the primary saccades, we found a tiny but nevertheless significant effect of the preceding performance error on the amplitude of the subsequent primary saccade. Its amplitude changed in a manner that would have reduced the error for this saccade if the same target shift would have taken place a second time. In an attempt to unravel the specific information, CS recorded in conjunction with the behavior might convey on the error or the changes of the behavior, we resorted to an analysis of mutual information (MI) with Bayesian binning (Endres & Földiák, IEEE Transactions, 2005). The MI analysis compared trials without error with those with errors in the one or the other directions. In ~33% of all n=129 CS subjected to this analysis, we found evidence for a significant difference between trials with errors and without. Importantly, the difference in CS activity between adapted and non adapted saccades occurred most frequently before the primary saccade, suggesting that the CS might reflect a memory trace of the error in the preceding trial. In other words, these findings support the notion that the climbing fibre offers a signature of the quality of past behavior in order to improve future manifestations of the same behavior.

Acknowledgements: Supported by the Werner Reichardt Centre for Integrative Neuroscience and the Bernstein Cluster for Computational Neuroscience, Tübingen

The building blocks of curved trajectories: studying the effect of shortened preparation time on execution.

Dovrat Kohen, Matan Karklinsky, Tamar Flash, Lior Shmuelof

Department of Computer Science and Applied Mathematics, Weizmann Institute of Science, Rehovot, Israel

The timed response (TR) reaching task allows delineation of movement controlled variables by investigating the effect of shortening movement preparation on the performed trajectories (Henning et al. 1988). Using the TR paradigm, Favila et al. (1989) showed different default plans for magnitude and direction of straight trajectories, suggesting that these variables are controlled separately. Nevertheless, in curved trajectories direction and magnitude are intertwined, and thus controlled variables are likely to differ. In the current study we adjust the TR paradigm to study the formation and controlled variables of curved trajectories. Fifteen subjects made reaching movements to 4 targets presented 15 cm from origin, while avoiding obstacles presented halfway between the origin and the targets. Subjects had to initiate the reaching movement in synchrony with a predicted auditory cue. Targets were presented at three different time points before the auditory cue (25, 100 and 350 ms), imposing different preparation time conditions. While subjects successfully reached the targets for all tested conditions, movements in the short preparation condition showed increased directional variability and a difference in average direction compared to the long preparation condition. Furthermore, average angular deviation and angular variability were correlated with reaction time in the short condition. Deviations of average trajectory may indicate that in the short condition subjects executed an initial task-insensitive default plan, and only later adjusted the trajectory to reach the target. The existence of a default plan is supported by the lack of target effect in the initial segments of the short but not the long preparation conditions. We argue that the increased trajectory variability in the short condition, which was not associated with decreased accuracy, indicates that curved trajectories are composed of multiple components that may be controlled separately. We further explore this claim using superposition and minimum jerk modeling approaches.

Motor Adaptation during locomotion on a split-belt treadmill in Cerebral Palsy, a novel concept in NeuroRehabilitation.

Lihi Rubin[1], Firas Mawase[1], Simona Bar-Haim[2] and Amir Karniel[1]

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The motor deficits that characterize cerebral palsy (CP), results from brain damage of the motor area that occurs before the age of two years. Decades of neurorehabilitation research have proven that the partially damaged brain can efficiently relearn, and that optimal recovery requires intensive task-specific practice. In the current study, we assessed the transfer of motor adaptation to skill learning and rehabilitation of teenagers with CP by exposing them to repetitive adaptation sessions to speed perturbation, using a split-belt treadmill. We then follow the over-ground transfer and motor retention of this novel intervention into the adolescent's natural environments by monitoring their walking functionality and physical activity level using accelerometers and functional tests. We found that teenagers with CP do not impair the ability to make predictive feedforward motor adaptations and showed intact motor after-effects. Interestingly, CP subjects significantly improved their motor functionality and predictive control throughout the repetitive adaptation sessions. In particular, results obtained from the last session showed significant improvement in symmetry and variance during walking on a split- belt treadmill compared to the first session. Furthermore, improvement in gait, symmetry and stability in everyday activities was evident in most of the CP subjects. Our results support the efficacy of long–term neurorehabilitation in improving walking in teenagers with cerebral palsy. We hypnotize that motor learning through repetitions of locomotor adaptation to a split-belt treadmill, yields substantial motor improvement and impairments recovery.

Computational implications of the hypothesis of muscle synergies.

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A prominent hypothesis in motor neuroscience suggests that the central nervous system generates desired muscle activations by combining a parsimonious set of predefined primitives called synergies. Most of the evidence for this modularity is based on the analysis of recorded muscle activations, and the results are often descriptive in nature. The implications of this control strategy are still far from understood, and its relations to the task and the dynamical system to be controlled are still under debate. Our work investigates these issues by considering the problem of controlling a simulated mechanical system in accordance with the model of time-varying synergies. In this scenario, the main challenge is the synthesis of a small set of actuations (i.e. synergies) that can be combined to generate effective control signals. This problem leads to a new definition of synergies that is grounded at the level of task, and that is demonstrated in a series of simulations. Further insights are provided by the Dynamic Response Decomposition (DRD), a novel method that is instrumental for the synthesis and the adaptation of a set of synergies. Our results show that the actuations corresponding to a handful of ``proto-tasks" represent useful synergies for solving qualitatively similar problems. This suggests that synergies are strictly tailored to the dynamics of the system and to tasks to be solved. The direct mathematical relation between task-constrains and the minimum required number of synergies confirms such an observation. Additionally, DRD reveals that a kinematic solution to the desired task can be obtained by linearly combining the kinematic trajectories corresponding to the synergies. Further, there exists a non-linear mapping between the coefficients of this linear combination and the ones of the synergies. Finally, our results demonstrate that the sole approximation error of the desired input signals does not provide direct information on the task performance, thus promoting a task-based assessment of the hypothesis of muscle synergies.

Handedness and the Perception of Stiffness.

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Handedness is characterized by a preference for using one hand rather than the other to perform most manual tasks and activities. We tested the effect of handedness on stiffness perception of both right and left handed subjects. Thirty three healthy participants were asked to choose the stiffer of two virtual elastic force fields after probing it using wrist joint movements of one hand. At the next day they repeated the task using the other hand. One field had varying stiffness levels; its force feedback was delayed by 50 msec in half of the trials. The second had a constant stiffness level and no delay. As previously reported, we found that entering a delay between force and position alters perception; subjects underestimated the stiffness levels of the delayed fields. This result was repeated across subjects in both hands. However, we found that the amount of underestimation of the right handed subjects differed substantially between dominant and non-dominant hand probing. Subjects underestimated the delayed stiffness to a greater extent while using the dominant right hand in comparison to the non-dominant left hand. On the contrary, left handers showed mix results and no specific tendency between hands. It was suggested that the estimation of stiffness emerges from the control policies that guide the hands using a force/position regression based model. Optimization of the hybrid model and the weighting factor between both control policies in right handed subjects was consistent with a preference for using position control in the dominant hand and force control in the non-dominant hand.

The 2/3 power law originates in the motor plan.

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The 2/3 power law $v = \gamma\kappa^{-1/3}$ expresses a robust local relationship between geometry and timing of human movement. Given its equivalence to moving at a constant equi-affine speed it is an important example of motor invariance. Whether this reflects central planning or peripheral biomechanical effects is greatly debated.

Motor imagery (MI), forming mental images of a motor action, is hypothesized to be functionally equivalent to the covert part of motor execution, without the following overt movement. Thus MI is a unique tool allowing access to the temporal structure of the motor plan. It is known that MI follows some kinematic properties of execution such as Fitts's law. We extend this approach by investigating MI's compliance with the 2/3 power law.

We constructed a novel experimental paradigm for recording sparse MI data from a continuous cyclic task, involving MI of tracing movements for some specified geometric shapes. For each trial we recorded and normalized the extent and duration of MI.

Using a likelihood ratio test we concluded that for most subjects (23 of 35) distributions of marking time dependent positions of the MI trajectory were significantly ($p<0.05$) better explained by the 2/3 power law than by constant velocity. Nonlinear regression for the values of the β parameter in a generalized power law $v = \gamma\kappa^{-\beta}$ resulted in mixed results, for some subjects (16 of 35) the confidence interval (for $p<0.05$) for β was entirely above 0.1.

Our results suggest that as is qualitatively expected from the 2/3 power law, MI does slow in curved portions of the trajectory, supporting the conclusion that the coupling between velocity and curvature originates in CNS trajectory planning. Due to its noisiness and sparseness, however, it is inconclusive whether the 2/3 power law provides a quantitatively exact description of the MI data.

Formation of Stiffness Perception: Evidence from Grip Force Modulation.

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During daily interaction with objects, we form internal representation of their mechanical properties. This representation serves us for forming perception and guiding actions. For example, a surgeon may use perception of mechanical properties of a tissue for diagnosis as well as to determine how strong she needs to grip a scalpel while cutting it. It is well documented that, in precision grip, the grip force is modulated with predicted load force, including inertial, viscous, and elastic loads. Interestingly, there is evidence for discrepancies between declarative reports of mechanical properties and grip force modulation. For example, Flanagan and Beltzner (2000) showed that subjects learned to adjust the appropriate grip force when lifting objects while still being affected by the size-weight illusion.

In the current study, we explore the relation between grip force adjustment and declarative perception during interaction with elastic force field using a tool. As in object lifting, during probing of an elastic force field, to avoid tool slippage, we need to adjust our grip of the tool based on prediction of the forces that we would encounter. We suggest that during the exploratory probing, users adjust their grip force as their perception of the field impedance forms, and that the grip force in the last probing cycle of each of the interactions with the field is correlated to their perception.

Five participants held a custom-designed gripper with an embedded force sensor attached to a haptic device, and probed virtual elastic force fields. In a forced-choice paradigm, we asked them to probe two fields, and answer which force field was stiffer. We show that the grip force at the last probing cycle can serve as a predictor of participant's perception of the stiffness of the elastic force field. We further discuss this prediction ability when force feedback is delayed.

Studying Human Motor Control in Robot-Assisted Surgery.

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In teleoperated robot-assisted surgery (RAS), a surgeon moves a master manipulator that sends commands to a patient-side robot. This practice provides many advantages to both the surgeon and the patient, but has not yet realized its full potential in terms of patient outcomes. We hypothesize that considering the surgeon's motor system can improve robot design, control, and surgical skill assessment and training. In addition, because RAS facilitates movement data collection, it provides an opportunity to test novel hypotheses about human control of movement and skill acquisition.

We explored the effect of teleoperation on movements of novices and experienced surgeons, in comparison with freehand movements. We instrumented an RAS system (da Vinci Si, Intuitive Surgical, Inc.) with a grip fixture and pose trackers on participants' arms. Participants sat at the master console and made planar center-out movements, freehand and via teleoperation. To ensure consistent visual feedback, a monitor placed on the surgical table presented to the user, via the endoscopic camera, the experimental view and a cursor representing the planar position of the master manipulator.

We found 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 are related to the dynamics of the manipulator and to the adaptation of experienced surgeons to these dynamics. We also analyzed mechanical redundancy using the Uncontrolled Manifold framework, and calculated the ratio between joint angle variability that does and does not result in hand trajectory change. We found that participants exploited redundancy to stabilize their horizontal (task-relevant) but not vertical (task-irrelevant) movements. Interestingly, this stabilization was stronger for experts than for novices, and weaker in teleoperated movements than in freehand.

Adaptation to Visuomotor Rotation in Isometric Virtual Reach Task.

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The ability to adapt to changes is a remarkable quality of our motor system. Adaptation to altered arm dynamics and kinematics during movement has been extensively studied, and it was found that perturbation of arm dynamics is learned in joint coordinates, whereas perturbation of the kinematics of a cursor is learned in hand coordinates. However, adaptation in isometric reaching, where the user controls a virtual cursor via force input, has not received as much attention. We explored two aspects of adaptation to visuomotor rotation in isometric virtual reaches: (1) the time-course, and (2) the coordinate frame in which the rotation is learned.

We built a planar, cable-driven, manipulandum with linkages that can mechanically lock. In the isometric configuration, force applied on the handle is mapped to the movement of a virtual cursor using either *position* or *velocity* control. In each experiment session, participants performed center-out reaches in three phases: *baseline*, *training* of counter-clockwise 45 degrees cursor rotation, and *washout*. In Experiment 1, they performed a movement session, followed by an isometric session. In Experiment 2, they performed only isometric reaches to one of two training targets in the left workspace and a washout testing target in the right workspace.

We found that the time-course of adaptation to visuomotor rotation in both position- and velocity-based cursor mappings resembles that of movement adaptation. Surprisingly, the transfer of adaptation depends on the mapping, and is different from movement. In position and velocity mappings, we observed transfer of adaptation in joint-coordinates; in velocity mapping, we also observed transfer in hand coordinates, but smaller than in joint coordinates.

Training of virtual movements using force/torque input and transfer of this learning to movement could be a transformative approach to restoring motor function that can engage individuals of a wide range of abilities using simple, cost-effective devices.

Inferior Olivary signal modulation by cerebellar and extracerebellar inputs.

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One possible approach to treating localized brain tissue loss is substituting the affected brain area with a synthetic neuroprosthesis interfaced to the affected area's inputs and outputs, thus creating a closed-loop system. In the EU-based ReNaChip project, we constructed a closed-loop system composed of a biomimetic chip interfaced to the inputs and output of a cerebellar microcircuit, which successfully rehabilitated cerebellar motor-conditioning in anesthetized rats (Prueckle et al, 2011; Bamford et al, 2012). A pivotal part of designing the system was characterizing the unconditioned stimulus (US) input to the neuroprosthesis. In classical conditioning, the somatosensory US is relayed to the cerebellum by the inferior olive (IO) and is often referred to as a sensorimotor "error signal" or as a "teaching signal" driving cerebellar plasticity involved in the acquisition of conditioned responses. Moreover, cerebellar output can modulate IO activity - including firing rate and synchronicity, and IO activity can modulate cerebellar output (De Zeeuw et al., 1998; Marshall and Lang, 2009).

We examined the effects of cerebellar and extracerebellar IO inputs on the IO-US signal: i. Using a combination of *in vivo* and *in silico* methods, we demonstrated that the IO's population response to sustained periorbital airpuff-USs is shaped by an olivocerebellar negative feedback loop, interacting with intrinsically-driven subthreshold oscillations in IO neurons to transform sustained somatosensory inputs into a phasic IO output. ii. We examined the effect of cerebello-olivary inhibition on the rate and latency of conditioned motor responses in behaving rats undergoing over-learning, and suggest that this inhibition may play a role in stabilizing cerebellar plasticity. iii. Using fear conditioning in anesthetized rats, we examined the effect of emotional background on the saliency of the IO-US signal, with implications for the interactions between emotional and motor learning mechanisms (Neufeld and Mintz, 2001; Lee and Kim, 2004; Taub and Mintz, 2010).

We conclude that the IO's response to somatosensory stimuli is shaped by cerebellar and extra-cerebellar inputs, with potential implications for the acquisition and execution of conditioned motor responses. From the perspective of a closed-loop neuroprosthetic system, these olivocerebellar interactions must be taken into account in designing brain-neuroprosthesis interactions.

Modeling fast sensory feedback which shapes whisker touch.

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Rats repeatedly sweep their facial whiskers back and forth to explore their environment. Such explorative whisking is driven by pattern generators that can operate independently of direct sensory feedback. However, whisking may be modulated by sensory feedback: upon whisker-object contacts, neural signals evoked by contacts often modulate whisking timing in a way that adds a "touch-induced pump" (TIP) and extends object palpation. While the kinematics of TIPs have been characterized in detail, the control mechanism that generates them is still not known. By using a dynamic, bottom-up computerized model built using the statecharts language, several possible sensorimotor control mechanisms were inspected. Testing various wirings between different types of neurons and muscles ruled out all hypothesized control mechanisms but one, which adequately simulated the corresponding motion observed in the rat. Results of the simulations suggested that TIPs were generated via sensory feedback that activated extrinsic retractor muscles in the mystacial pad. Furthermore, the model provided several predictions that further characterized this motion. One prediction anticipated that in addition to the touching whisker, all whiskers found on the same side of the snout would exhibit a TIP. We present results that approve the predicted movements in the behaving rat, establishing the validity of the proposed control mechanism for the generation of TIPs.

Comparing non-human primate vermal and lateral cerebellar saccade related activity while performing a pro- and antisaccade task.

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Anatomical and functional evidence suggests that the cerebellum processes motor and non-motor information as its inputs and outputs form part of a closed loop with cortical structures. At the time there is no consensus and experiments lack to show how the cerebellum might be processing cortical information as part of this loop. The cerebellum builds up internal models that manage motor activities that code for prediction of sensory consequences of movements. A correct prediction develops as a result of learning from a past experience. Given its highly similar topography throughout its regions, the same algorithm may be applied to all its inputs. Is this cerebellar output effecting motor commands only or is involved in more complex and abstract information processing such as decision-making (executive functions)? Our aim is to contribute our understanding of how the cerebellum may be participating in these complex cognitive processes. We used a pro- and antisaccade task that requires a monkey to suppress a reflex saccade to a shown target and direct its gaze to a mirror position. This type of inhibition is known to engage prefrontal regions (goal-oriented behavior). We trained two non-human primates (macaca mulatta) to perform interleaving pro and anti saccadic eye movements while recording saccade related activity in Purkinje cells in Lobules Vic and VII in vermis and lateral hemisphere (Crus I and II). We present preliminary results obtained of one non-human primate.

Enhanced neural modulations during BMI experiments: optimal control approach

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During the execution of reaching movements the neural activity is modulated by several motor parameters (i.e., hand position, velocity, speed and gripping force). BMI are designed to decode the neural activity from an ensemble of neurons and control general reaching movements.

It has been shown that the overall modulations of the firing rate of cortical neurons (POM) increase after monkeys stated operating the BMI. On the other hand the neural modulations that are correlated with the profile of the trajectory (PKM) remain relatively unchanged.

We modeled both the hand and the cursor using linear-quadratic-Gaussian (LQG) control method. The model variables – i.e., the internally estimated state and the control signal are encoded into neural activity under the assumption that the spike trains are realizations of *inhomogeneous* Poisson processes.

Switching our model from pole control to brain control results in the same phenomenon observed in the BMI experiments: The POM increased while the PKM remained unchanged. In order to investigate the source of this phenomenon, we increased the actual and/or the internal process noise in pole control and demonstrate that there is dramatic increase of the POM while minor changes in the PKM. Furthermore, we trace this phenomenon to increasing variance of the encoded motor variables.

Thus, we conclude that the increase in POM reflects changes in the variance of the encoded variables that are due to changes in the process noise and not coding additional variables or increasing variance of the executed movement, which would have affected PKM too.