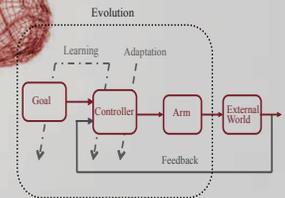
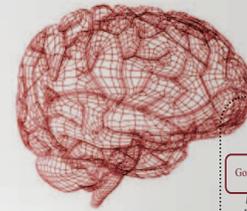


Joint Research Workshop of the
Institute for Advanced Studies & the
Israel Science Foundation



June 7 - 10, 2009

Israel Motor Days in Jerusalem

Abstracts

Organizers

Opher Donchin, Amir Karniel, Eilon Vaadia

The Workshop will take place at the Institute for Advanced Studies,
at the Hebrew University of Jerusalem, Edmond J. Safra Capus
at Givat Ram, Jerusalem

האוניברסיטה העברית בירושלים
The Hebrew University of Jerusalem

Joint Research Conference of the Institute for Advanced
Studies and the Israel Science Foundation



ISRAEL MOTOR DAYS IN JERUSALEM June 7-10, 2009

All lectures will take place at the Feldman Building,
on the Givat Ram Campus

Organizers: Opher Donchin, Amir Karniel (Ben-Gurion University),
Eilon Vaadia (The Hebrew University)

PROGRAM

Sunday, June 7

9:00-10:00 Registration

MODELS AND MEANING IN MOTOR EXPERIMENTS AND COMPUTATION

Chairperson: Kurt Thoroughman (Washington University, St. Louis)

10:00-10:10 Greetings: **Eliezer Rabinovici** (IAS Director)
Opening statements: **Kurt Thoroughman**

10:10-10:50 **Paul Cisek** (University of Montréal)
The Blurry Borders between Deciding and Doing

10:50-11:30 **Stephen Scott** (Queen's University, Kingston)
Interpreting Primary Motor Cortex Based on Optimal Feedback Control

11:30-12:00 Coffee break

- 12:00-12:40 **Ron Meir** (The Technion)
On the Existence of a Forward Model in Motor Control
- 12:40-13:10 Panel
Chair: **Kurt Thoroughman**
Participants: **Kenji Doya** (Okinawa Institute of Science and
Technology), **Paul Cisek**, **Stephen Scott**, **Ron Meir**
- 13:20 Lunch and organized tour in the old city of Jerusalem
- 19:00 Dinner at the Terasa Restaurant

Monday, June 8

- 9:30-11:00 Tutorial: **Olivier Sigaud** (Université Pierre et Marie Curie)
Supervised and Reinforcement Learning Tools for Motor Learning Models
- 11:00-11:30 Coffee break
- FORCES, ERRORS AND ADAPTATION**
Chairperson: **Jeroen Smeets** (VU University)
- 11:30-12:10 **Sandro Mussa-Ivaldi** (Northwestern University)
Force-Motion Duality and its Relevance to Control
- 12:10-12:50 **Pietro Mazzoni** (Columbia University)
How not to Generalize in Sensorimotor Adaptation
- 12:50-13:30 **Konrad Kording** (Northwestern University)
Causes of Motor Errors: Why We Adapt the Way We Do
- 13:30-15:00 Lunch at Beit Belgia
- REPRESENTATION OF MOVEMENT IN THE MOTOR CORTEX**
Chairperson: **Moshe Abeles** (Bar-Ilan University)

- 15:00-15:10 **Moshe Abeles:** Opening statements
- 15:10-15:50 **Ariel Tankus** (UC Los Angeles)
Speed and Direction of Movement are Encoded by the Human
Supplementary Motor Area
- 15:50-16:20 Coffee break
- 16:20-17:00 **Felix Polyakov** (Weizmann Institute)
Geometric Invariance, Cortical States and Decision Making:
Evidence for Parabolic Primitives
- 17:00-17:30 Discussion
Chair: **Moshe Abeles**
Participants: Tamar Flash (Weizmann Institute), Sandro Mussa-Ivaldi

Tuesday, June 9

- 9:30-11:00 Tutorial: **Amir Karniel** (Ben-Gurion University)
The Spatiotemporal Hierarchy of Feedback Adaptation Learning
and Evolution
- 11:00-11:30 Coffee break
- MATHEMATICAL TOOLS FOR MOTOR BEHAVIOR ANALYSIS**
Chairperson: **Opher Donchin** (Ben-Gurion University)
- 11:30-12:10 **Reza Shadmehr** (Johns Hopkins University)
Mathematical Motor Control as a Window to Neurological
Disorders of the Brain
- 12:10-12:50 **Esther Adi-Japha** (Bar-Ilan University)
Group Data may Mask Critical Phases in the Individuals'
Acquisition of Skilled Performance

- 12:50-14:20 Lunch at Beit Belgia
- EQUILIBRIUM POINT HYPOTHESIS**
Chairperson: **Tamar Flash**
- 14:20-14:30 Opening statements: **Tamar Flash**
14:30-15:10 **Anatol Feldman** (University of Montréal)
Common Spatial Frames of Reference for Action and Perception
- 15:10-15:50 **Mark Shapiro** (Northwestern University)
A Model of Control of Speed of Reaching Movement
- 15:50-16:20 Coffee break
- 16:20-17:00 **Mark Latash** (Pennsylvania State University)
Equilibrium-Point Control and Prehension Synergies
- 17:00-17:30 Discussion
Chair: **Tamar Flash**
Participants: **Randy Flanagan** (Queen's University),
Anatol Feldman, Jeroen Smeets, Mark Latash, Mark Shapiro

Wednesday, June 10

- INTERFACING THE BRAIN (BMI/BCI)**
Chairperson: **Sandro Mussa-Ivaldi**
- 10:00-10:10 Opening statements: **Sandro Mussa-Ivaldi**
- 10:10-10:50 **Eilon Vaadia** (The Hebrew University)
Neuronal Basis of Sensorimotor Learning and its Implications
for Brain Machine Interface
- 10:50-11:30 Coffee break

- 11:30-12:10 **Miriam Zacksenhouse** (The Technion)
Neural Modulations and Computational Motor Control
- 12:10-12:50 **Sandro Mussa-Ivaldi**
Dual Learning in Human/ Machine Interfaces
- 12:50-13:30 Buffet lunch at the IAS lobby
- 13:30-14:00 Panel
Chair: **Sandro Mussa-Ivaldi**
Participants: **Emanuel Donchin, Miriam Zacksenhouse,**
Eilon Vaadia, Tim Ebner (University of Minnesota),
Pieter Medendorp (Radboud University Nijmegen),
Kenji Doya
- 14:00-14:40 **Ilan Golani** (Tel Aviv University)
The Inverse Bernstein Problem in Ethological Descriptions of
Whole Animal Free Movement
- 15:00 Travel to Beer-Sheva, dinner

Check www.bgu.ac.il/cmaw for the fifth annual computational motor control workshop on Thursday, June 11 and the tour of the Negev on Friday, June 12

The Blurry Borders Between Deciding and Doing”

Paul Cisek, Université de Montréal

The motor system is often seen as the output end of a long sequence of information processing stages which include perceptual analysis and cognitive decision-making. Framed in this way, the problem of motor control is defined as the problem of how to turn a plan, descending from higher centers, into the pattern of muscular contractions that produce movement. Different models propose different concepts of a plan, sometimes as a more-or-less detailed desired trajectory, and sometimes as an abstract goal (e.g. acquiring a target while minimizing some cost). Nevertheless, most theories imply that by the time the problem of motor control begins, “cognitive” problems such as decision-making have already been completed.

In my talk, I will present several experimental results which support an alternative view, in which the borders between cognition and motor control are not so crisp and clear. First, I will show how the process of deciding between two motor acts can “spill into” activity in primary motor cortex. Using transcranial magnetic stimulation, we found that corticospinal activity during the reaction time period of an Eriksen flanker task reflects the replacement of an incorrect prepotent response with a correct one, and that this process determines reaction time. Second, I will show how choices between different paths around obstacles can be influenced by the biomechanical costs of the potential movements. This suggests that parts of the motor system sensitive to biomechanics, such as the primary motor cortex and cerebellum, may influence decisions prior to movement onset. Third, I will suggest that the timing of decisions is not determined solely at the central level, but may be directly influenced by motor preparation processes. In particular,

I will show behavioral data suggesting that the build-up of neural activity to a threshold, often assumed to reflect a process of sensory integration, may in fact be due to motor initiation-related build-up processes. In other words, perhaps it is not the case that we move after we’ve decided, but that we commit to a decision when we move.

Interpreting Primary Motor Cortex Based on Optimal Feedback Control

Stephen Scott, Queen's University, Kingston Dept. of Anatomy and Cell Biology,
Centre for Neuroscience Studies, Queen's University, Kingston, Canada

Primary motor cortex (MI) is a key component of the volitional motor system providing the largest contribution to the corticospinal tract and receiving input from many cortical and subcortical structures. The most common approach for interpreting MI function has been based on the notion of sensory motor transformations, focusing attention on experiments that identify which coordinate frames best describe neural activity in MI. However, myriad coordinate frames or neural representations have been observed illustrating correlations with spatial goals, hand motion, joint motion, muscular torque, muscular power and EMG activity. How do all these 'representations' contribute to or create coordinated motor behavior?

The focus of my talk will be to provide an alternate approach for interpreting MI function based on optimal feedback control. I will show how this conceptual framework is consistent with many aspects of neural processing in MI including the importance of sensory feedback, dramatic shifts in neural coding across behaviors and the intimate link between MI activity and the properties of the musculoskeletal system.

On the Existence of a Forward Model in Motor Control

Ron Meir, Department of Electrical Engineering, Technion

Biological motor control provides highly effective solutions to difficult control problems in spite of the complexity of the plant and the significant delays in sensory feedback. Such delays are expected to lead to non trivial stability issues and lack of robustness of control solutions. However, such difficulties are not observed in biological systems under normal operating conditions. Based on early suggestions in the control literature, specifically the so-called Smith predictor, a possible solution to this conundrum has been the suggestion that the motor system contains within itself a forward model of the plant (e.g., the arm), which allows the system to 'simulate' and predict the effect of applying a control signal. In this work we formally define the notion of a forward model, and provide simple conditions that imply its existence for tasks involving delayed feedback control. As opposed to the bulk of previous work in the control literature, which dealt mostly with linear plants and quadratic cost functions, our results apply to rather generic control systems, showing that any controller (biological or otherwise) which solves a set of tasks, must contain within itself a forward plant model. We suggest that the generality of our results provides strong theoretical support for the necessity of forward models in most delayed control problems, implying that they are not only useful, but rather, mandatory, under general conditions. We present precise conditions for their necessity, and provide examples where they are not needed.

Models and Meaning in Motor Experiments and Computation

Panel chaired by Kurt Thoroughman, Washington University, St. Louis

Participants: Kenji Doya , Okinawa Institute of Science and Technology, Paul Cisek, Stephen Scott, Ron Meir

I will ask our speakers and panelists to specify the motivation and meaning of the models they create to pose their most central research questions. Our models can be explicit and mathematical, or implicit and conceptual. Across our formalisms we will aim to illuminate the foundations, consensuses, and open questions within 21st century approaches to motor behavior and neuroscience.

Supervised and Reinforcement Learning Tools for Motor Learning Models

Olivier Sigaud , Université Pierre et Marie Curie

Reinforcement Learning (RL) is a mathematical framework initially meant to give account of trial-and-error learning in psychology. Recently, neuro-physiologists found counterparts of RL mechanisms in dopamine neurons of the striatum and suggested that the basal ganglia may implement an Actor-Critic architecture.

The tutorial will be intended to a life sciences audience, it will present the basics of the mathematical RL framework and cover the domain so as to explain very recent progress in Actor-Critic algorithms.

Force-Motion Duality and its Relevance to Control

Sandro Mussa-Ivaldi, Northwestern University

To manipulate an object, we must simultaneously control the contact forces exerted on the object and the movements of our hand. I will review recent experimental evidence suggesting the existence of distinct neural mechanism to control hand motions and contact forces. I will then discuss the theoretical basis for the modular separation of motion and force control. This analysis shows that by combining controllers that are independently competent to operate at the singular extremes of an impedance range one achieves the ability to produce desired force or motion trajectories over the entire range of environment impedance. I will discuss the relevance to motor learning of this theoretical framework and experimental results.

How not to Generalize in Sensorimotor Adaptation

Pietro Mazzoni, Motor Performance Laboratory; Department of Neurology, Columbia University

When a new sensorimotor mapping is learned through practice, learning commonly transfers to unpracticed regions of the mapping, that is, generalization ensues. A critical question about generalization is whether it reflects fixed properties of how the nervous system represents a mapping, or whether it is simply a passive consequence of learning and may therefore arbitrarily change depending on details of the learned mapping. We investigated how generalization patterns change with learning by studying visuomotor adaptation in human subjects making reaching movements. Subjects adapted to a change in gain between the amplitude of a reaching movement and the displacement, on a computer screen, of a cursor indicating hand position. This type of adaptation is known to generalize broadly across directions. By training subjects on two different gains in two directions, we set up a potential conflict between overlapping generalization functions. We found that subjects were able to successfully learn two gains in two directions, though more slowly than when they adapted to a single gain. We then investigated the pattern of generalization in the two-gain condition, and compared it to generalization after adaptation to a single gain in one direction.

We considered five different mechanisms through which the generalization pattern observed after learning two gains could arise. The data was best explained by a weighted combination of single-gain generalization functions, in which the weighting takes into account the relative angular separation between training directions. These results support the modular decomposition approach to visuomotor adaptation suggested by Ghahramani and Wolpert (Nature 386:392, 1997), in which a complex mapping is generated through combination of simpler mappings in a "mixture-of-experts" architecture. Fixed generalization functions can thus give rise, through their combination, to patterns that are compatible with learning a complex mapping. This supports the hypothesis that generalization patterns reflect stable structures from which sensorimotor mappings are constructed.

Causes of Motor Errors: Why We Adapt the Way We Do

Konrad Kording , Northwestern University

Motor adaptation is usually defined as the process by which our nervous system produces accurate movements while the properties of our bodies and our environment continuously change. Many experimental and theoretical studies have characterized this process by assuming that the nervous system uses internal models to compensate for motor errors. Here we extend these approaches and construct a probabilistic model that not only compensates for motor errors but estimates the sources of these errors. These estimates dictate how the nervous system should generalize. For example, estimated changes of limb properties will affect movements across the workspace but not movements with the other limb.

We provide evidence that many movement generalization phenomena emerge from a strategy by which the nervous system estimates the sources of our motor errors.

Encoding of Speed and Direction of Movement in the Human Supplementary Motor Area

Ariel Tankus, UC Los Angeles

The supplementary motor area (SMA) plays an important role in planning, initiation and execution of motor actions. These actions are impaired in patients with SMA lesions, which can be quantified as a change of various kinematic parameters, such as velocity and duration of movement. However, the relationships between neuronal activity and these parameters in the human brain have not been fully characterized. This is a study of single-neuron activity during a continuous volitional motor task, with the goal of clarifying these relations for SMA neurons and other frontal lobe regions in humans.

Subjects were seven patients undergoing evaluation for epilepsy surgery requiring implantation of intracranial depth electrodes. Single-unit recordings were conducted while subjects played a computer game involving movement of a cursor in a simple maze.

In the SMA proper, most of the recorded units exhibited a monotonic relation between the unit firing rate and hand motion speed. The vast majority of SMA proper units with this property showed an inverse relation, i.e., the firing rate decreased when speed increased. In addition, most of the SMA proper units were selective to the direction of hand motion. These relations were far less frequent in the pre-SMA, anterior cingulate gyrus and orbitofrontal cortex.

Our findings suggest that the SMA proper takes part in the control of kinematic parameters of end-effector motion, and thus lend support to the idea of connecting neuroprosthetic devices to the human SMA.

Joint work with Yehezkel Yeshurun (Tel-Aviv University), Tamar Flash (Weizmann Institute of Science) and Itzhak Fried (University of California, Los Angeles, Tel-Aviv Medical Center and Tel-Aviv university).

Geometric Invariance, Cortical States and Decision Making: Evidence for Parabolic Primitives

Felix Polyakov, Eran Stark, Rotem Drori, Moshe Abeles, and Tamar Flash, Weizmann Institute

Flash & Handzel (1996; 2007) and Pollick & Sapiro (1997) proposed a geometric approach to the investigation of movement segmentation and compositionality which is motivated by the equivalence of the 2/3 power-law to moving at a constant equi-affine speed. We have derived a mathematical equation whose solutions reconcile the 2/3 power law and the criterion for smoothness maximization (Polyakov et al. 2001; Polyakov et al. 2009): $(\mathbf{r}' \cdot \mathbf{r}^{(6)})=0$, where prime denotes a derivative with respect to the equi-affine arc-length. Parabolic shapes constitute the only equi-affine invariant solution of this equation. We have fitted free monkey scribbling movements with basic parabolic strokes and found that following practice, these drawing movements could be decomposed into only 3-4 well separated clusters of parabolic segments with respect to their orientation. Our results demonstrate that through practice and learning the motor system seeks to achieve a greater parsimony of motor representations. Of 72 movement-related motor cortical neurons recorded during scribbling 16 (22%) were tuned to either equi-affine or Euclidian speed. Of them 6 (38%) were tuned mostly to equi-affine speed, only 3 (19%) were tuned mostly to Euclidian speed, and 7 (44%) to both. Unsupervised segmentation of simultaneously recorded multiple neuron activities by means of hidden Markov modeling (HMM) yielded states related to distinct parabolic elements. We thus suggest that the cortical representation of movements is state-dependent and that parabolic elements are building blocks used by the motor system to generate complex movements (Polyakov et al. 2009). Defining a movement primitive as an elementary stroke that cannot be intentionally stopped unaccomplished after its initiation, we have also found that when the monkey's motor performance was altered by giving a reward at certain locations: the monkey indeed tended to decelerate and stop its movements but not before the completion of parabolic-like path segments. This indicates that receiving a reward affects the monkey's decision strategies regarding initiating a new movement component and composing it with the ongoing movement, and suggests that decision-making needs to be accounted for in the studies of movement primitives and their compositionality rules (Polyakov et al. accepted). In summary, our mathematical, behavioral, and neurophysiological studies have characterized candidate geometric movement primitives from which well-practiced complex movements are composed in a parsimonious way and indicate that non-Euclidian metrics may be relevant for the neural representation of motor actions. Supported in part by DIP.

Representation of Movement in the Motor Cortex

Chairperson: Moshe Abeles, Bar-Ilan University

Discussion chaired by Moshe Abeles

Participants: Tamar Flash, Sandro Mussa-Ivaldi

It stands to reason that complex arm movements are compositional much like language (phones-phonemes-words-phrases-sentences). Similarly, hand motions may be generated by a small set of elementary motions which are then composed (in a hierarchical manner) into more and more complex ones. Such basic elements will be called here "primitives". Primitives may be concatenated serially, in a partially overlapping way or in parallel.

The discussion is aimed at clarifying some of the pros and cons for this compositional hypothesis. As well as discussing whether synergies, velocity profiles, pieces of trajectories or other aspects of motion may be regarded as such primitives.

The Spatiotemporal Hierarchy of Feedback Adaptation Learning and Evolution

Amir Karniel, Ben-Gurion University The Computational Motor Control Laboratory Department of Biomedical Engineering, Ben-Gurion University of the Negev

Motor control is the primary task of the nervous system; adaptation is one of the defining features of biological systems in general and of biological control systems in particular. The interplay between artificial control theory and the theory of biological motor control has been a useful tool to boost both scientific and technological breakthroughs from the dawn of cybernetics long before this term was coined by Norbert Wiener.

In this tutorial I will present a new perspective that put together all types of adaptation in a single structural-temporal hierarchy that includes feedback control, adaptive control, skill learning and evolution. I review the study of biological motor control and the parallel artificial motor control theory from the viewpoint of this hierarchy.

Following the theory of control engineering adaptive control is defined as control strategy that allows plastic changes in the parameters of the control function this is in contrast to feedback control that contains a fix controller that changes the control signal based on the desired and measured output. At the top of the hierarchy, optimal control can be viewed as the parallel to biological evolution, employing feedback, adaptation, and learning for the ultimate goal of survival. Some well-known controversies such as the equilibrium point hypothesis versus internal models for control as well as the question of learning time representation are presented in a new light.

The proposed hierarchy provides alternative definitions to the terms evolution, learning, adaptation and feedback from an engineering perspective and call for further experiments to discover the borders and generate finer definitions to various aspects of this important phenomenon that virtually defines living creatures namely adaptation.

Due to my limited knowledge, the tutorial is biased towards my studies, and therefore I urge the audience to interrupt during the tutorial and introduce additional relevant examples from their studies or other relevant studies which I failed to mention.

The tutorial follows the essay titled "Computational Motor Control" in the Encyclopedia of Neuroscience (Springer, 2009). The essays as well as the slides are going to be available in my homepage www.bgu.ac.il/~akarniel.

Mathematical Motor Control as a Window to Neurological Disorders of the Brain

Reza Shadmehr , Johns Hopkins University

When the brain generates a motor command, it also predicts the sensory consequences of that command via an “internal model”. The reliance on a model appears to make the brain able to sense the world better than is possible from the sensors alone. However, this happens only when the models are accurate. To keep the models accurate, the brain must constantly learn from prediction errors. Here I use examples from saccade and reach adaptation to demonstrate that learning is guided by multiple timescales: a fast system that strongly responds to error but rapidly forgets, and a slow system that weakly responds to error but has good retention. Cortical cerebellar damage impairs the fast timescales of adaptation, but not the slow timescales, whereas motor cortical inhibition appears to impair the slower timescales. Analysis of movements suggests that the function of the cerebellum is monitoring of ongoing motor commands and compensation for their variability. Next, I focus on the role of reward in motor control and show that learning from reward prediction errors has a fundamentally different characteristic than learning from sensory prediction errors (i.e., the visual and proprioceptive consequences of motor commands). I consider the role of dopamine in motor control in an optimal control framework and show that reduced availability of dopamine appears to increase the estimated costs of a movement in people with Parkinson’s disease. The presentation will attempt to speculate with regard to the role of the basal ganglia, the cerebellum, and the motor cortex within a single computational framework for control and learning of movements.

Group Data may Mask Critical Phases in the Individuals' Acquisition of Skilled Performance

Esther Adi-Japha , Bar-Ilan University

I will describe a transient phase during training on a movement sequence wherein, following an initial improvement in speed and decrease in variability, individual participants' performance showed a significant increase in variability without change in mean performance speed. Subsequent to this phase, as practice continued, variability re-decreased, performance significantly exceeded the gains predicted by extrapolation of the initial learning curve, the type of errors committed changed and performance became more coherent. The transient phase of increased variability may reflect a mixture of two (or more) performance routines before the more effective one is set and mastered; presumably, the setting-up of a sequence-specific representation. Both group and individual analyses indicated a departure from the single process (e.g., power-law) model of learning. However, although similar phases appeared in the mean group data, there was little correspondence to individual participants' time-courses, and the individuals' gains in the second low-variability phase were masked.

Common Spatial Frames of Reference for Action and Perception

Anatol Feldman , Department of Physiology, University of Montreal

According to a view that has dominated the field for over a century, the brain programs muscle commands and uses a copy of these commands (efference copy) to adjust not only resulting motor action but also ongoing perception. This view was helpful in formulating several classical problems of action and perception: (1) the posture-movement problem of how movements away from a stable posture can be made without evoking resistance of posture-stabilizing mechanisms; (2) the problem of kinesthesia or why our sense of limb position is quite adequate despite typically ambiguous positional information delivered by proprioceptive and cutaneous signals; (3) the problem of visual space constancy or why the world is perceived as stable while its retinal image shifts following changes in gaze. On closer inspection, the efference copy theory actually does not solve these problems in a physiologically feasible way. Solutions to these problems are offered in the advanced formulation of the equilibrium-point hypothesis that suggests that action and perception are accomplished in a common spatial frame of reference selected by the brain from a set of available frames. Experimental data suggest that the brain is also able to translate or/and rotate the selected frame of reference by modifying its origin and orientation and thus substantially influence action and perception. Because of this ability, such frames are called physical to distinguish them from mathematical frames that are used to describe system behavior without influencing this behavior. Experimental data also imply that once selected, each physical frame can be modified in a feedforward way, thus enabling the brain to act in an anticipatory and predictive manner.

These notions will be illustrated by demonstrating that the motor cortex in humans is directly involved in the specification and resetting of spatial frames of reference, thus guiding motor actions without evoking resistance of posture-stabilizing mechanisms.

A Model of Control of Speed of Reaching Movement

Mark Shapiro, Northwestern University

Voluntary reaching movements are often described as slow or fast. When understood in this general sense, movement speed is related but not equivalent to parameters of kinematics of movement such as peak velocity or movement time. For example, in movements made under the “same speed” instruction over various distances the peak velocity and movement time increase with distance. We present a model of the control of single joint point-to-point elbow movements in which movement speed is determined by a rate of change of the neural control. The neural control sets the equilibrium angle of the joint which shifts alternatively into flexion and extension. The control problem is reduced to finding three switch times of a piece-wise linear control sequence. The switch times depend on the dynamical properties of the limb and load, so the control trajectory is the solution to the problem of inverse dynamics although the joint torque is never calculated explicitly. The model was used to simulate the experimental data in movements made over a fixed distance to a target (experiment 1) or over self-chosen distances with no target (experiment 2). Both experiments included “fast” and “moderate speed” movements. The speed control model reproduced the movement kinematics and tri-phasic and bi-phasic muscle EMG patterns observed in movements over a fixed distance to a target. The speed control model also reproduced experimentally observed slopes of the linear fit of the peak velocity vs. movement distance. These slopes were higher than that predicted by the constrained minimum-time model of Tanaka et al. (2006).

The simulations indicate that in the absence of explicit accuracy requirements, the CNS does not adjust the movement time to satisfy an implicit accuracy criterion as suggested by the constrained minimum-time model. Instead, the CNS may control the movement speed directly by choosing a rate of change of the neural control and then finding the time parameters of the control sequence that will move a given load over a desired distance with a preferred speed, either fast or slow. A decision to move fast or slow may depend upon the accuracy requirements, metabolic energy demands, dopamine deficiency, social context, and others factors.

Equilibrium-Point Control and Prehension Synergies

Mark Latash , Pennsylvania State University

Recent studies of human prehension have used the notion of a prehension synergy as a co-varied (across trials) adjustment of elemental variables that stabilizes their combined mechanical output. Prehension synergies were studied at two levels of a hypothetical control hierarchy. At the upper level, the thumb and the virtual finger (an imagined digit with the mechanical action equal to the sum of the actions of the four fingers) generate elemental variables (forces and moments of force) that co-vary to stabilize the total force and moment of force exerted on the hand-held object. At the lower level, the forces and moments of force produced by the fingers co-vary to stabilize the action of the virtual finger. Recent studies have demonstrated a trade-off between synergies at the two hierarchical levels. Prior to a quick lifting action of a hand-held object, there were strong synergies at the lower level of the hierarchy and modest synergies at the upper level stabilizing the normal force and the moment of force. As soon as the lifting action started, the synergies at the lower level disappeared while the synergies at the upper level became stronger. Prehension synergies may be viewed as consequences of control with excitation thresholds for neuronal pools that lead to changes in referent configurations for salient geometric variables. Such control can naturally lead to co-varied adjustments in elemental variables stabilizing their combined output. In experiments with unexpected disappearance of the hand-held object (unloading) during very fast movement of the object, motion of the digits and the whole hand was observed towards the referent configuration. In particular, there were non-monotonic changes in the hand aperture during the unloaded trials.

These results may be interpreted as resulting from a control scheme involving a hierarchy of neuronal circuits, with each circuit involving an input signal that defines excitation threshold of a neuronal pool and a feedback loop on the output of the pool.

Equilibrium Control Hypothesis

Discussion chaired by Tamar Flash

Participants: Randy Flanagan, Jeroen Smeets, Anatol Feldman, Mark Latash, Mark Shapiro

In two of the talks by Feldman and Latash the speakers discuss a variety of notions concerning the importance of coordinate frames. Latash suggests that "Prehension synergies can be viewed as consequences of control with excitation thresholds for neuronal pools that lead to changes in referent configurations for salient geometric variables", while Feldman discusses the idea concerning the existence of "physical coordinate frames common to both perception and action". Feldman talks also about dynamic modifications of the origins and orientations of such coordinate frames while Shapiro talks about direct control of the speed of shifting the underlying equilibrium point. The discussion will deal with the importance of coordinate frames in motor control, to what extent the notions used by models based on the equilibrium-point hypothesis differ from those of other models and also how do the accounts given by the equilibrium point hypothesis for action-perception coupling and for sensorimotor integration differ from those of other models especially in the context of motor tasks such as reaching and grasping and when switching between posture and movement.

Another point to be discussed is the issue of the control variables used by other models versus those used by the equilibrium point hypothesis. How do such differences between the assumed control variables (position and force versus equilibrium position and impedance) affect the definitions and approaches to the notion of muscle synergies?

The third point to be discussed is whether the models and approaches, based on the equilibrium point hypothesis, are opposed to or orthogonal to models based on the concept of the optimality of desired trajectories and or optimal feedback based control schemes.

Finally the discussion will deal with the existence of tension/contrast and/or agreement between equilibrium point hypothesis models and the idea of the existence of internal models for grasping and other motor tasks.

Mutual learning of machine and brain in BMI

Eilon Vaadia, The Hebrew University, Hagai Lalazar, Lavi Shpigelman

Department of Physiology, Faculty of Medicine and the Interdisciplinary center for neural computation (ICNC) The Hebrew university, Jerusalem

Brain machine interface requires learning – in most cases of the algorithms (the machine) and the brain (the subject). We developed an adaptive version of the Kernel Auto-Regressive Moving-Average (KARMA) and interfaced it with neuronal activity in motor cortex. In our framework, the KARMA Adaptivity is achieved by running a learning algorithm in parallel to real-time movement control. We found that this mode of “co-adaptation” of brain and the algorithm, allows fast target acquisition good brain control and stable performance. The algorithm learns practically instantly; the subject can achieve the first successful trial within seconds (even though a new model is learned each day from scratch). The model’s learning is completely automatic and does not involve any explicit training by the subject or a technician.

This model continues to adapt to changing neural responses, it also allows learning new tasks in BMI without pre-training of the animal.

Neural Modulations and Computational Motor Control

Miriam Zacksenhouse, Faculty of mechanical Engineering, Technion

Recent experiments with brain-machine-interfaces (BMIs) indicate that the extent of neural modulations increases abruptly upon starting to operate the interface. In contrast, neural modulations that are correlated with the profile of the trajectory remain decline or remain relatively the same. Furthermore, the enhanced modulations subside with further training, mirroring the trend in task performance, which degraded when starting to operate the interface and improved gradually with training. The interpretation of the enhanced modulations and the characterization of the signals that they may encode are of major interest for understanding human motor learning and control, the improvement of future BMIs and the development of effective rehabilitation programs.

The observed enhancement in neural modulations may be interpreted in the context of three computational motor control models: (i) hybrid control, (ii) optimal control, and (iii) dual control. Here we concentrate mainly on the framework of optimal control, and how the different components of this system may be affected by the transition from pole to brain control. Within this framework, the neural activity is assumed to encode both the estimated state and the control signals. State estimation is derived using a Kalman filter, which optimally combines sensory measurements with predictions based on an internal model. During pole control both proprioceptive and visual feedback are available, and the first is most heavily combined given its reliability and short delay. However, when the hand stops moving, visual feedback from the cursor remains the only measurements contributing to state estimation. Since under BMI control the cursor exhibits a much more erratic behavior than exhibited by the actual hand, our model predicts a major increase in neural activity during brain control, as demonstrated by simulations.

The observed decline in the correlation between neural activity and the cursor trajectory requires special considerations. Initial investigations demonstrate that this does not emerge solely from the inability of the BMI filter to decode the enhanced activity in the neural activity. Instead we demonstrate that it may result from decoupling the hand and cursor state estimation during brain control. Possible experiments to verify these conclusions are discussed.

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The Remapping of Motor Space in Human-Machine Interfaces

Sandro Mussa-Ivaldi

Studies of motor adaptation to patterns of deterministic forces have revealed the ability of the motor control system to form and use predictive representations of the environment. One of the most fundamental elements of our environment is space itself. Starting from the assumption that we interact with the world through a system of neural signals, we observe that these signals are not inherently endowed with metric properties of the ordinary space. The ability of the nervous system to represent these properties depends on adaptive mechanisms that reconstruct the Euclidean metric from signals that are not Euclidean. Gaining access to these mechanisms will reveal the process by which the nervous system handles novel sophisticated coordinate transformation tasks, thus highlighting possible avenues to create functional human-machine interfaces that can make that task much easier.

A set of experiments is presented that demonstrate the ability of the sensory-motor system to reorganize control signals in novel geometrical environments. In these environments multiple degrees of freedom of body motions are used to control the coordinates of a point in a two-dimensional Euclidean space.

I will discuss the relevance of these studies to some of the same challenges encountered in Brain-Machine Interfaces. Furthermore, I will present evidence suggesting that practice leads to the acquisition of the metric properties of the controlled space. Methods of machine learning based on the reduction of reaching errors are tested as a means to facilitate learning by adaptively changing the map from body motions to controlled device.

I will discuss the relevance of the results to the development of adaptive human machine interfaces and optimal control.

Interfacing the Brain (BMI/BCI)

Panel chaired by Sandro Mussa-Ivaldi

Participants: Emanuel Donchin, Miriam Zacksenhouse, Eilon Vaadia, Tim Ebner, University of Minnesota, Pieter Medendorp (Radboud University Nijmegen), Kenji Doya

The last decade has seen a vigorous research aimed at establishing functional interactions between the nervous system and external devices. This is an area of study driven by the clinical objective to reconnect paralyzed people with the sensory-motor world. At the same time, however, as researchers are attempting to apply what is known about how the brain works, the very same difficulty of this task is highlighting important limits in our fundamental understanding and may be guiding toward new insight. What is really encoded in signals recorded from neuronal populations? How are the mechanisms of learning affected by changes in the operating environment, induced by other learning systems.

How is the dimensionality of sensory-motor tasks related to the dimensionality of control signals? How can plasticity be guided toward desired goals? These are just some of the questions that the panel will be addressing with the goal of shedding some light on the role of BMI research at the boundary between clinical application, neurobiology and computational neuroscience.

The Inverse Bernstein Problem in Ethological Descriptions of Whole Animal Free Movement

Ilan Golani ,Tel Aviv University

In Motor Control, the problem of coordination of many kinematic degrees of freedom (KDFs) is known as the Bernstein Problem, and is the celebrated goal of the Coordination Dynamics paradigm. In our opinion, however, not enough attention is devoted to the problem we will call here the inverse Bernstein Problem. That is, how can an observing scientist, in a natural environment and context, define behavior patterns by their component KDFs, and recognize them in an objective and reliable manner? Practical solutions for this problem are crucial for all the fields in the behavioral neurosciences that have to measure whole animal unrestrained behavior. While the two problems are closely related theoretically, in practice they demand different paradigms. Since there are no known algorithmic ways or common procedures for defining natural coordination patterns, I will present several examples that illustrate how, by using Movement Notation Analysis and various graphical representations, we visualize the same complex behavior in several coordinate systems, thereby highlighting both the invariant features of synergies and their underlying kinematics. I will present examples at three scales: gait, locomotor behavior, and (cognition-related) exploration.

Check www.bgu.ac.il/cmaw for the fifth annual computational motor control workshop on Thursday, June 11 and the tour of the Negev on Friday, June 12