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

June 10-12, 2008, W.A. Minkoff Senate Hall, BGU Marcus Family Campus, Beer-Sheva, Israel

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

Tuesday, June 10, 2008 Welcome dinner

18:00 **Dr. Eilat Almagor, Rubin Academy of Music and Dance**
Does Awareness Promote Learning Through Movement?

Wednesday, June 11, 2008

8:20-8:50 Registration, poster placement & coffee

8:50-9:00 Greetings – **Dr. Opher Donchin**,
Head of the organizing committee, Ben-Gurion University

9:00-9:10 Opening remarks – **Prof. Moti Herskowitz**,
Vice-President and Dean for Research and Development

Action and perception

Chairperson: Prof. Anatol Feldman, University of Montreal, Canada

9:10-9:40 **Prof. Paul Gribble,**University of Western Ontario, Canada
Motor Learning by Observing

9:40-10:10 **Dr. Pierre Baraduc,** Institute for Cognitive Science, France
Role of Visual Feedback in the Oculomotor State Estimate

10:10-10:40 **Prof. A. J. Van Opstal,** Institute for Neuroscience, Radboud University, The Netherlands
The Neural Encoding of Eye Movements in Primate Midbrain

10:40-10:50 Discussion

10:50-11:30 Posters & coffee

Adaptation

Chairperson: Dr. Rony Paz, Weizmann Institute of Science

11:30-12:00 **Dr. Amir Karniel,** Ben-Gurion University
Adaptation To and Perception of Delay During Motor Control

12:00-12:30 **Dr. Maurice Smith,** Harvard University, USA
Distinct Parallel Adaptive Processes in Motor Learning and What They Tell Us About Learning and Retention

12:30-13:00 **Prof. Eilon Vaadia,** Hebrew University
Brain and Machine Learning in Brain Machine Interface

13:00-13:10 Discussion

13:10-15:10 Posters and lunch

Optimality

Chairperson: Prof. Zev Rymer, Northwestern University, USA

15:10-15:40 **Dr. Jörn Diedrichsen,** University of Bangor, Wales
Bimanual Coordination: an Optimal Feedback Control Perspective

15:40-16:10 **Dr. Emanual Guigon,** Inserm, University Pierre et Marie Curie, France
Can Optimal Control Explain Adaptation to Force Fields?

16:10-16:40 **Prof. Ehud Ahissar,** Weizmann Institute of Science
Active sensing: Motor Strategies for Optimizing Sensory Acquisition

16:40-16:50 Discussion

16:50-17:00 The Alpha Omega Sensegraphics and NanInstuments Best poster Awards

17:00-17:20 Posters and coffee

Basic science and applications

Chairperson: Prof. Charles Capaday, Université Laval, Canada

17:20-17:50 **Dr. John Krakauer,** Columbia University, USA
Adaptation, Skill and Recovery

17:50-18:20 **Prof. Dagmar Timmann,** University of Duisburg-Essen, Germany
Lesion-Symptom Mapping of the Human Cerebellum

18:20-18:50 **Prof. Mindy Levin,** McGill University, Canada
Deficits in Threshold Control Related to Spasticity and Disordered Motor Function

18:50-19:00 Discussion

20:30 Dinner and discussion

Thursday, June 12, 2008

09:00-16:00 Desert hike

The desert hike

Dear friends:

On Thursday the 12th of June, we are going for a trip to the Dead Sea and the Ein Gedi springs of the Judean desert. Our hike will take us up the impressive 400 meter cliffs that drop from the floor of the Judean Desert straight down to the Dead Sea. From there we will appreciate the stark scenery into which the water carves its steep canyons. We will then drop into the canyon to see the oasis and waterfall from above and then wind down to the pool below and enjoy the water.

After the hike, we will have lunch at hot springs by the Dead Sea and then have a chance to actually float in its waters and feel their unusual buoyancy. Time permitting, we will also include a short, late afternoon hike to Mount Sedom where Lot's wife was famously turned into a pillar of salt.

Meeting time: 08:30 A.M.

Meeting place: The Golden Tulip Hotel

What to bring: Back pack, sunscreen, a hat, comfortable clothes and shoes.

Cost: 150 NIS per person

We will be back in Beer-Sheva approximately at 16:00 P.M. at the Golden Tulip Negev Hotel

See you then
Eitan (the tour guide)

Talks

Does Awareness Promote Learning Through Movement?

Dr. Eilat Almagor

A Feldenkrais Practitioner, The Rubin Academy of Music and Dance Jerusalem Israel

It is of great interest to movement control research to find out a useful analysis of an action. What are the ingredients of which a complex function is composed?
Bernstein describes the human brain as made up of several hierarchical levels which usually cooperate in performing an action. In Bernstein's model, the higher level, the one which organizes the movement, is the level of awareness and the lower levels serve as the suppliers of the components to be orchestrated by that higher level.
Bernstein also says that the attempt to bring the awareness to levels lower than the organizing one, will usually disturb the function or even cause a failure of the action.
By our experience in the Feldenkrais method, we find out that there are certain conditions and certain components (attributes) of an action to which bringing the awareness or attention creates a higher quality of performance. On the other hand there are other conditions and other components to which an attempt to bring awareness is fruitless.

The differentiation between those 2 groups of attributes, the one which by the aid of attention and awareness facilitate action, learning and dexterity and the other group of attributes which do not, might be useful in the research of motor control.

Motor Learning by Observing

Paul L. Gribble

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I will describe studies in which we explored the neural basis of motor learning by observing. We show that subjects can acquire information visually on the basis of observation that helps them later perform arm movements in novel force-fields. This process appears not to be dependent on the use of conscious strategies but instead is based on the implicit engagement of motor systems. A study using rTMS supports the idea that motor learning by observing is based on the activation of the motor system during observation, and provides direct evidence that neural representations of motor skills in M1, a cortical region whose role has been firmly established for active motor learning, are also involved in motor learning by observing.

Role of Visual Feeback in the Oculomotor State Estimate

Pierre Baraduc

Institute for Cognitive Science, Lyon, France

Combined use of actual sensory feedback and efference copy is thought to be a key feature of sensorimotor control systems. I'll review recent data that quantify the contribution of the visual input to the control of the eye movement. Vision-based corrections to the estimated position of the eye could arise by comparing the postsaccadic visual scene to the visual scene predicted through a remapping of the presaccadic visual input. We tested the contribution of retinal input by briskly shifting the visual stimuli in the middle of the saccade. The effect of this perturbation was evaluated using a double-step saccade task: the second saccade to a memorized target T2 was used as a probe to measure the effect of the perturbation introduced during the saccade to T1.

A first study tested whether an unconscious displacement of the target T1 can elicit changes in the execution of the second saccade. To minimize the likelihood of T2 being encoded relative to T1, the targets were shown separately in reverse order. Visual feedback was effective in biasing the second saccade only for T0-T1 saccades over 12°. For these large saccades, corrections increased with saccade size but never exceeded 30% of the introduced bias. Corrections were markedly covaried with the presence of a corrective saccade to T1.

In the second study, we manipulated the visual environment but not the target. A background consisting of a superimposition of randomly positioned Gabor patches at different scales appeared after presentation of T2 but before presentation of T1. T1 was extinguished at the go signal, and the whole background was rotated during the saccade to T1 to simulate a saccadic error. This time, there was no significant effect of background displacement on the endpoint of the second saccade. However, and surprisingly, the manipulation affected the gain of the second saccade. This gain modification was consistent with the visual perturbation: it was increased when the background was shifted along the direction of the first saccade, and reduced in the converse condition.

This apparent dissociation between target and background shift suggest that visual feedback is used at different levels of the oculomotor control system, either to adjust the target of the next eye movement or to adjust the motor command to reach it. The fit with optimal control models will be discussed.

How Linear Ensemble-Coding in Midbrain Superior Colliculus Specifies the Nonlinear Kinematics of Saccadic Eye Movements

John Van Opstal and Jeroen Goossens

Department of Biophysics, Donders Centre for Neuroscience, Radboud University Nijmegen, The Netherlands

Recently, we proposed an ensemble-coding scheme of the midbrain superior colliculus (SC) in which, during a saccadic eye movement, each spike emitted by each recruited SC neuron contributes a fixed minivector to the gaze-control motor output. The size and direction of this 'spike vector' depend exclusively on a cell's location within the SC motor map (Goossens and Van Opstal, 2006). According to this simple scheme, the planned saccade trajectory results from instantaneous linear summation of all spike vectors of the spatial-temporal distribution of neural activity across the motor map.

In our simulations with this model, the brainstem saccade generator was simplified by a linear feedback system, rendering the total model (which has only three free parameters) essentially linear. Interestingly, when this scheme was applied to actually recorded spike trains from 139 saccade-related SC neurons, measured during thousands of eye movements to single visual targets, straight saccades resulted with the correct velocity profiles and nonlinear kinematic relations ('main sequence properties' and 'component stretching'). Hence, we concluded that the kinematic nonlinearity of saccades resides in the spatial-temporal distribution of SC activity, rather than in the brainstem burst generator. The latter is generally assumed in models of the saccadic system.

Here we will demonstrate that this behaviour might actually emerge from this simple scheme by a precisely tuned spatial gradient in the peak firing rate and burst duration of collicular neurons in the motor map, such that neurons involved in small saccades have high peak firing rates and short saccade-related bursts, vs. neurons recruited for large saccades that have lower peaks and longer bursts. The total number of spikes in the burst, however, is fixed across the motor map (Van Opstal and Goossens, 2008). Thus, for each saccade, the population of neurons in the SC motor map sends a fixed number of spikes to the brainstem circuits. We will show that this mechanism fully explains how the motor SC can act as a nonlinear vectorial pulse generator, and we provide new experimental evidence in support of this mechanism.

Reference:

H.H.L.M. Goossens and A.J. Van Opstal (2006): Dynamic Ensemble Coding in the Monkey Superior Colliculus. Journal of Neurophysiology, 95: 2326-2341

A.J. van Opstal and H.H.L.M. Goossens (2008): Linear Ensemble Coding in Midbrain Superior Colliculus Specifies the Saccade Kinematics. Biological Cybernetics, 98: 561-577

Adaptation to and Perception of Delay during Motor Control

Amir Karniel

Department of Biomedical Engineering, Ben-Gurion University of the Negev, Beer-Sheva, Israel

Neural conduction of sensorymotor information involves significant time delay which should be addressed by the brain. In this talk I'll report a series of studies designed to unravel the mechanisms employed by the brain to handle delays and then discuss the potential applications of the derived insights to the design of transparent teleoperation.

In a forced choice paradigm subjects were presented with two surfaces and asked to identify the stiffer one. For one surface the force was proportional to the position but in the second the force was proportional to a prior position of the surface a few tens of milliseconds earlier. We found that subjects tend to overestimate delayed stiffness. Additionally, we found that shifting the boundary also modified stiffness perceptions. Interestingly as we observed the human performance in similar adaptation study we observed that the expected stiffness as measured by the motor behavior is not always similar to the expected stiffness as declared by the subject. Moreover, in another study we found that when subjects did not cross a boundary – i.e., when their hand remained inside an elastic field all the time – they tend to underestimate delayed stiffness. We proposed regression based computational models to account for these results, and discuss their possible interpretation for our understanding of the neural control of delayed environments.

In another study subjects performed reaching movements and experienced delayed viscous force perturbations. We found clear evidence for adaptation to delayed viscous force field. This trial to trial adaptation clearly involved a feedforward controller adaptation. In another study when applying delayed visual feedback during reaching movements, we observed feedback adaptation rather than feedforward adaptation.

Finally I'll discuss the possible value of these findings to the design of transparent teleoperation systems and close the talk by proposing a Turing like handshake test for motor intelligence.

Acknowledgements
Parts of the studies described in the talk have been conducted with Sandro Mussa-Ivaldi, Assaf Pressman, Noa Levy, Lior Botzer and Ilana Nisky and were supported by the United States-Israel Binational Science Foundation (BSF), Jerusalem, Israel; the National Institute for Psychobiology in Israel – Founded by The Charles E. Smith Family; as well as by a grant from the Ministry of Science, Culture & Sport, Israel, and by the Ministry of Research, France.

Distinct Parallel Adaptive Processes in Motor Learning and What They Tell Us About Learning and Retention

Maurice Smith

Department of Biomedical Engineering, Harvard University, USA

Using a combination of computational and experimental methods, we recently found that two distinct adaptive processes evolve in parallel to underlie motor adaptation – one process learns quickly but forgets rapidly while the other learns slowly but retains information well. We show that a simple computational model of the natural interactions between these two adaptive processes can provide a unifying explanation for several key properties of motor adaptation seen in arm and eye movements that were previously considered to be separate phenomena. These properties include savings, interference, spontaneous recovery, and rapid unlearning. Additionally, we show that the memory formed by one of these processes subsequently decays purely as a function of time while the other decays with experience, and only one of these processes provides a gateway to long-term memory formation. This work shows that understanding the interplay between the different processes involved in memory formation can give us fundamental insights into understanding how learning proceeds and decays.

Brain Control Using Adaptive Brain Machine Interface

Eilon Vaadia[1], Hagai Lalazar[2], Lavi Shpigelman[2]

Department of Physiology, Faculty of Medicine and the Interdisciplinary Center for Neural Computation (ICNC), The Hebrew University, Jerusalem, Israel

The talk describes our studies of neuronal activity in motor cortex during performance of reaching task and adaptation to a brain machine interface. We developed a modified adaptive version of the Kernel Auto-Regressive Moving-Average (KARMA) and interfaced it with neuronal activity in motor cortex to perform a sensorimotor task. In our framework, KARMA uses its previous prediction and the current neural activity to predict the next intended movement. Adaptivity is achieved by running a learning algorithm in parallel to real-time movement control, and updating the model as often as specified. We found that this mode of "co-adaptation" of brain and the algorithm, allows fast target acquisition good brain control and stable performance. The reconstruction precision (as can be quantified in experiments with real arm movements) significantly outperformed other algorithms used in BMI experiments. 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. Additionally, the model continues to adapt in the background adjusting to changing neural responses, in contrast with methods that freeze the model after an initial training session and require the subject to keep producing neural activity that is consistent with the frozen model.

Notes: 1 The Jack H. Skirball Chair & Research Fund in Brain Research
2 Equal contributions

Bimanual Coordination: An Optimal Feedback Control Perspective

Jörn Diedrichsen

Wolfson Centre for Cognitive and Clinical Neurosciences, School of Psychology, Bangor University, United Kingdom

Bimanual coordination provides a model system on how the brain solves the problem of redundancy in the motor system: We always have more joints, muscles, - or in this case hands - available than would be strictly necessary to solve a given motor task.
Three problems issues arise from such redundancy: the first is the question of how to share the work across different effectors. Our experiments suggest that signal-dependent noise plays a major role in determining these distributions, and that a new distribution can slowly be learned if noise properties are artificially altered. The second problem lies in feedback control: with multiple effectors involved in the action, how should feedback correction be distributed? Recent results indicate that the distribution of feedback correction across different effectors can flexibly change with changing task goals. The third problem, adaptation, is closely related to feedback control. We show that the way a redundant system adapts to perturbation on the next trial also depends strongly on the task goal and the controlled object. These results can be coherently explained in an optimal control theoretical model, in which coordination between the involved effectors is established through the high-level representation of task relevant variables.

Can Optimal Control Explain Adaptation to Force Fields?

Emmanuel Guigon

Inserm, University Pierre et Marie Curie

In everyday life, humans frequently encounter unknown environments which distord the normal relationship between motor commands and their perceived effects, e.g. when manipulating devices with unknown dynamics. When an individual first interacts with an unknown environment, its motor behavior is in general different from the behavior observed in its usual environment, revealing on-line feedback control processes. Furthermore, repeated exposure to the same perturbation generally induces long-lasting modifications in motor control which tend to reduce or cancel the influence of the perturbation. Accordingly, such situations have been customarily reproduced in laboratory experiments as a way to probe feedback control and adaptive characteristics in sensory-motor systems. A critical step before to address adaptation is to obtain a quantitative description of perturbation-induced error signals (e.g. modifications in movement trajectory, changes in movement time, patterns of final error, …). Only a few studies have addressed this issue. Shadmehr and Mussa-Ivaldi (1994) have shown that initial hand trajectory deviations in a velocity-dependent force field can be explained by the presence of an error-feedback system that steers the hand along a desired trajectory. In the same framework, Bhushan and Shadmehr (1999) have shown that feedback control in a force field involves the interaction between an inverse dynamics model and a state estimator. This latter study provided a quantitative account of movement characteristics (trajectory, velocity profile, …) during early force field exposure. Yet these studies rely on the questionable idea that motor commands are elaborated based on a desired movement trajectory (Todorov and Jordan 2002; Donchin and Shadmehr 2004; Guigon et al. 2007). Here we explore the issue of perturbation-induced modifications of movement trajectory in the framework of optimal feedback control, i.e. in the absence of desired trajectory.

Active Sensing: Crucial Roles of Motor Strategies in Sensory Acquisition and Coding

Ehud Ahissar

Department of Neurobiology, Weizmann Institute of Science, Israel

What initiates perception? Many text books refer to stimulations of sensory receptors by external events as the starting point. However, anatomy, physiology and behavior indicate that perception emerges from motor-sensory-motor loops with no clear initiation point. With such loops, sensory acquisition and coding depend crucially on motor strategies. I will show data from rats localizing objects in their environment using their whiskers, and from humans performing similar tasks, demonstrating this crucial dependency.

Acquisition and Consolidation of Motor Skills

John Krakauer

Deparment of Neurology Columbia University, USA

Adaptation paradigms have been studied extensively in recent years to gain insight into motor learning. It could be argued , however, that motor adaptation differs from skill acquisition. Here two skill learning experiments will be described. The first shows that different interference mechanims operate on the explicit and implicit components of sequence learning. The second shows that transcranial direct current stimulation over primary motor cortex has differential effects on skill acquisition over multiple days and retention over months. We propose that motor skill learning, in contrast to motor adaptation, be considered the time course over which improvements in explicit categorical components are combined with improvements in continuous implicit components.

Lesion-Symptom Mapping of the Human Cerebellum.

Dagmar Timmann

Department of Neurology, University of Duisburg-Essen

High-resolution structural magnetic resonance imaging (MRI) has become a powerful tool in human cerebellar lesion studies. Functionally meaningful correlations between a cerebellar lesion site and behavioural data can be obtained both in subjects with degenerative as well as focal cerebellar disorders.

One example are correlations with clinical data which are in good accordance with the known functional compartmentalization of the cerebellum in three sagittal zones: In patients with cerebellar cortical degeneration ataxia of stance and gait was correlated with atrophy of the medial (and intermediate) cerebellum, oculomotor disorders with the medial, dysarthria with the intermediate, and limb ataxia with atrophy of the intermediate and lateral cerebellum. Similar findings were obtained in patients with focal lesions. In addition, in patients with acute focal lesions a somatotopy in the superior cerebellar cortex was found which is in close relationship to animal data and functional MRI data in healthy control subjects. Finally, comparison of data in patients with acute and chronic focal lesions revealed that lesion site appears to be critical for motor recovery. Recovery after lesions to the nuclei of the cerebellum was less complete.

Another example with extended knowledge about functional localization within the cerebellum is classical conditioning of the eyeblink response, a simple form of motor learning. In healthy subjects learning rate was related to the volume of the cortex of the posterior cerebellar lobe. In patients with focal cerebellar lesions acquisition of eyeblink conditioning was significantly reduced in lesions including the cortex of the superior posterior lobe, but not the inferior posterior lobe. Disordered timing of conditioned eyeblink responses correlated with lesions of the anterior lobe. Findings are in good agreement with the animal literature. Different parts of the cerebellar cortex may be involved in acquisition and timing of conditioned eyeblink responses in humans.

Finally, correlations with cognitive data are of interest. In a group of patients with focal cerebellar lesions, mild abnormalities in a verbal fluency task were related to lesions affecting the right posterior cerebellar hemisphere.

These examples demonstrate that MRI-based lesion-symptom mapping is helpful to study the contribution of functionally relevant cerebellar compartments in motor control and recovery, and certain non-motor domains in patients with cerebellar disease. In addition, information about the function of cerebellar cortex and nuclei can be gained. Although the study of participants with focal lesions is preferable, studies in participants with degenerative disorders do also lead to meaningful results.

Deficits in Threshold Control Related to Spasticity and Disordered Motor Control

Mindy F. Levin, PhD, PT,

School of Physical and Occupational Therapy, McGill University

The λ model of motor control describes how central control of the tonic stretch reflex threshold results in different motor actions. Previous studies have shown how this regulation can account for muscle relaxation as well as the appearance of muscle activation patterns in different parts the angular range of a single-joint or multi-joint system. Research in animals and in healthy subjects suggests that the tonic stretch reflex threshold may be altered by descending systems mediating both direct and indirect influences on motoneurons. Our results show that deficits in agonist-antagonist muscle activation in the single-joint elbow system in patients with spastic hemiparesis are directly related to limitations in the range of regulation of the thresholds of muscle activation. We extended these findings to the double-joint, shoulder-elbow system in 10 non-disabled individuals and 11 stroke survivors with spasticity in upper limb muscles. Stroke survivors had sustained a single unilateral stroke 6-36 months previously, had full pain-free passive range of motion of the affected shoulder and elbow and had some voluntary control of the arm. EMG activity from 4 elbow and 2 shoulder muscles was recorded during quasi-static (<5°/s) stretching of elbow flexors/extensors and during slow voluntary elbow flexion/extension movement through full range. Stretches and active movements were initiated from full elbow flexion or extension with the shoulder in 3 different initial positions (60°; 90°; 145° horizontal abduction). SRT angles obtained by passive muscle stretch were compared with the angles at which the respective muscles became activated during voluntary elbow movements. Elbow flexors SRTs were correlated with clinical spasticity scores. In contrast to healthy subjects, in patients at rest, SRTs of both elbow flexors and extensors could lie within the biomechanical range of the joint. These SRTs varied with changes in the shoulder angle in all subjects with hemiparesis. In patients, limitations in the regulation of SRTs resulted in a subdivision of all-possible shoulder-elbow arm configurations into two areas, one in which spasticity was present (“spatial spasticity zone”) and another in which it was absent. Spatial spasticity zones varied for different muscles in different patients but, for all elbow muscles, the zones occupied a large part of elbow-shoulder joint space. The shape of the boundary between the spasticity and no-spasticity zones depended on the state of reflex inter-joint interaction. SRTs in single- and double-joint flexor muscles correlated with the positions at which muscles were activated during voluntary movements for all shoulder angles, and this effect was greater in elbow flexor muscles (brachioradialis, biceps brachii). These findings support the notion that motor impairments after CNS damage are related to deficits in the specification and regulation of SRTs,

Posters

Rectilinear Versus Curvilinear Trajectories During Adaptations to Force Fields and Visuomotor Rotations

Fritzie Arce1,4*, Itai Novick1,4, Maayan Shachar1,4, Claude Ghez3, Eilon Vaadia1,2,4

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When reaching to an object, estimating the hand position is not as certain when we cannot see the hand as when we can see it. This uncertainty can lead to errors in sensory estimates and consequently to movement variability. Optimal estimation of the state of the body and the environment is all the more critical when reaching in novel environments. In such conditions, humans may compensate for errors by combining sensory information with the knowledge gained from previous experience. Here we demonstrate that prior knowledge and state estimates based on vision and proprioception differentially influence the choice of a trajectory plan during adaptations to dynamic force fields and visuomotor rotations. Separate subjects (n=28) adapted to force fields with or without concurrent visual feedback of their hand trajectory and were retested after 24 hours. Additional groups learned visuomotor rotation immediately after force field to assess interactions between them. We found that comparable levels of endpoint accuracy were achieved in two ways: with visual feedback, the adapted trajectories in force fields were straight whereas without it, the trajectories remained curved. Further, the straight or curved trajectories were carried over to a subsequent adaptation to visuomotor rotation. The transfer of curved trajectories to a different task and feedback condition demonstrates that curved trajectories in force adaptation reflect a newly learned control policy with its new trajectory plan. Overall, we show that strategies selected during adaptation depend on subjects' prior experience and the calibration of sensory channels conveying state estimates for different control policies and tasks. Our finding that endpoint accuracy and precision can improve while trajectories remain curved does not support the notion that straight trajectories follow from minimizing endpoint variance (Harris and Wolpert, 1998). The curved trajectories seem to obey a minimum intervention principle in which deviations are not corrected unless they interfere with task performance (Todorov, 2004) and that newly acquired control policies are used in subsequent adaptations if they continue to produce successful performance. The dissociated effects on trajectory and endpoint support the notion of separate controllers governing them (Scheidt and Ghez, 2007).

Reference: Harris CM, Wolpert DM (1998) Signal-dependent noise determines motor planning. Nature 394:780-784.

Scheidt RA, Ghez C (2007) Separate adaptive mechanisms for controlling trajectory and final position in reaching. J Neurophysiol.

Todorov E (2004) Optimality principles in sensorimotor control. Nat Neurosci 7:907-915.

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Reaching Movements Under Visuomotor Delay are Driven by Feedback Adaptation

Lior Botzer and Amir Karniel

Department of Biomedical Engineering, Ben-Gurion University of the Negev, Israel

Humans tend to perform reaching movements in a straight, smooth, and accurate fashion. When forces or visuomotor perturbations are imposed, these features of the movement that were initially disturbed gradually return to baseline by means of adaptation. In this study we explored a new perturbation, a visuomotor time delay, and examined whether the observed adaptation process is feedforward driven or feedback driven.
Theoretically, the visuomotor time delay perturbation can be ignored, lead to feedforward adaptation, or lead to feedback adaptation; our results are consistent with the latter option.
Subjects held the handle of a desktop phantom in a virtual augmented system while performing out-and-back reaching movements towards a visual target. During the reach subjects observed a visual feedback of their hand in the form of a small virtual sphere.
The visual feedback was either non-delayed (N – Normal condition) or 70 mSec delayed (D –Delayed condition), relative to the true hand position. The N or D conditions were either constantly imposed (block trials) or entwined in the block (catch trials): delayed catch trials (Dc) during N block and non-delayed catch trials (Nc) during D block. We compared the movement kinematics of the various conditions in an attempt to discriminate between the different hypotheses. Normally, before comparing movement kinematics, it is required to detect the movement onset. This detection is often based on a conventional velocity threshold technique. In this study we used the velocity threshold technique as well as a new onset detection method which is based on a recent underlying principle for optimal trajectories: the minimum acceleration criterion with constraints (MACC). We show that although both methods yield similar results when comparing the initial parts of the movements, the new method is more accurate. All subjects were able to adapt to the visuomotor delay. However, during catch trials in the Dc/Nc condition they overshoot/undershoot the target, respectively. These results indicate that the subjects do not simply learn to ignore the delay perturbation, and also, that those subjects used continuous control rather than ballistic preplanned movements. In order to test for a possible feedforward adaptation, we compared the kinematics changes of the initial part of the movement during D block and N block conditions, as described previously, and concluded that these kinematic changes are not driven by feedforward adaptation to visuomotor time delay. Altogether, our findings suggest that visuomotor adaptation is a result of feedback adaptation rather than feedforward adaptation.

Acknowledgements: This research was supported by a grant from the National Institute for Psychobiology in Israel - Founded by The Charles E. Smith Family, and a grant from the Ministry of Science, Culture and
Sport, Israel, and by the Ministry of Research, France

Do Motor Invariants Constrain Motion Perception? An fMRI Study

Eran Dayan (Computer Science & Applied Mathematics; Neurobiology, Weizmann Institute of science, Israel), Antonino Casile* (Hertie Institute for Clinical brain Research,Tuebingen, Germany), Nava Levit-Binnun (Physics of Complex Systems, Weizmann Institute of Science, Israel), Martin A Giese (Hertie Institute for Clinical brain Research, Tuebingen, Germany), Talma Hendler (Tel-Aviv Sourasky Medical Center & Tel-Aviv University) & Tamar Flash (Computer Science & Applied Mathematics, Weizmann Institute of Science, Israel
*Equal contribution

Human movements are characterized by a relatively small set of invariants. One such invariant, the so called "two-thirds power law", dictates a strong coupling between movement curvature and velocity. Previous studies have established that the two-thirds power law characterizes curved human hand and drawing movements. More recently it has been shown that human motion perception also seems to reflect this constraint. The fMRI study reported here demonstrates that the brain's response to this law of motion is much stronger and more widespread than to other types of motion. Compliance with this law is reflected in the activation of a large network of motor and motor related brain areas. Our results strongly support the notion of similar neural coding for motion perception and production. These findings suggest that cortical motion representations are optimally tuned to the kinematic and geometrical invariants characterizing biological actions

Acknowledgements: This work was supported by the Human Frontier Science Program, by the European Commission, by the Volkswagenstiftung and by the Deutsche Forschungsgemeinschaft.

Functional Meaning of Cortico-Spanal Facilitation in the Control of Posture and Movement in Humans

H. Raptis, L. Burtet, R. Forget, A. G. Feldman

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We tested the hypothesis that descending cortical signals can influence mechanical variables and EMG signals while remaining virtually independent of them. Subjects specified two static positions (45 º wrist flexion or 25º extension). By applying small spring-like loads compensating passive muscle tensions, it was possible to equalize the EMG activity at these positions at near zero levels. The reflex excitability of motoneurons of wrist muscles was evaluated by applying brief pulses generated by a torque motor. EMG responses to these perturbations were not significantly different between the two positions. Transcranial magnetic stimulation (TMS, single pulses, 1.2-1.4 motor threshold) of the M1 wrist area was then used to evaluate the excitability of cortico-spinal pathways projecting to motoneurons of wrist muscles at the two wrist positions in 16 healthy subjects.

Extensor motor evoked potentials (MEPs) elicited by TMS in the extension position were substantially bigger whereas flexors MEPs were smaller than in the flexion position. In other words, active changes in wrist position were associated with reciprocal changes in cortical facilitation of flexors and extensors motoneurons, and these changes were independent of EMG levels. MEPs significantly decreased and became less correlated with position when subjects fully relaxed wrist muscles at the two positions established passively. We also analyzed the changes in the MEP signals resulting from unloading of pre-loaded wrist extensors elicited either involuntary (with the torque motor), or intentionally, by subjects themselves. In both cases, extensors MEPs decreased but the decrease was bigger in self-initiated unloading, even though the final EMG levels were the same. The dissociation between EMG levels and corticospinal excitability suggests that the motor cortex is not involved in the specification of EMG patterns and resulting mechanical variables. Rather, the primary effect of cortico-spinal facilitation is a change in the threshold position of body segments, i.e. the position at which muscles are silent but are ready to be activated in response to deviations from it. Thereby, to produce a motor action, descending systems reset the threshold position of appropriate body segments whereas the EMG patterns emerge following the difference between the actual and the threshold position of these segments.

Threshold position resetting allows the system to make movement without evoking resistance of posture-stabilizing mechanisms, which solves the classical posture-movement problem.

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Patterns of Finger Force-Sharing When Grasping a Handle With a Variable Load and Constant External Torque.

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When grasping an object, the grip force applied by the fingers increases linearly with an increase in the load force (Johansson & Westling, 1984). However, if a non-zero external moment is applied to the handle, simply scaling the grip forces to the changes in load force will not maintain rotational equilibrium of the handle because the grip (normal) digit forces contribute to the total moment of force produced by the hand on the object. Hence, the grip and load forces applied by the individual fingers must be coordinated to maintain this equilibrium.

The goal of this study has been to investigate the techniques used by the CNS to maintain equilibrium in such a situation. We have constructed a handle with five 6-DOF force sensors, which has a bar attached allowing application of different external torques. The handle is connected to a linear actuator via an extension spring, which allows the application of a vertical force downwards on the handle in a ramp-like manner. Using this apparatus, we apply forces starting at zero and up to a maximum magnitude equal to the gravitational force on the handle when it is unconnected to the motor.

We have analyzed the force sharing patterns of the fingers, and how they vary during changing load force in order to maintain torque and force equilibrium. We find that the force sharing of the fingers depends on the history of force production, and is not symmetrical for up and down force application. Additionally, the contribution of the tangential and normal forces to the total moment of force applied by the hand remains fairly constant despite the large changes in the load force. The results speak in favor of a hypothesis that the neural controller uses templates of sharing the hand action between the elements and scales the templates to changes in task parameters.

Reaction Time is Related to Inter-Trial Variability of Single Unit Activity in Motor Cortex

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How can we rely on variable neuronal activity to encode precise movement? Conventional approaches view trial-by-trial variable activity as signal with noise and try to eliminate the noise by either averaging it out or looking at population activity. In this study I explored the single trial reliability of neurons in reflecting a behavioral parameter (e.g. reaction time) that putatively represents the degree of readiness for an upcoming movement.

We simultaneously recorded single neuron activities using 32 independently moveable microelectrodes from primary motor and premotor areas of two monkeys during performance of a "center-out" reaching task.

My working hypotheses are: (1) The variability of neuronal activity is not merely noise and (2) the level of readiness for movement on a single trial basis is reflected in the variability of the movement. My goal is to quantify the relations of the neuronal variability and the behavioral variability.

My preliminary results suggest that movement parameters can be represented in pre-movement neuronal activity with single trial resolution – specifically I found examples demonstrating that single neurons can have single trial reliability in predicting reaction time during the preparatory activity epoch.

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A Detailed Model of the Cerebellar Contribution to Perturbed Arm Movements

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Theoretical and experimental considerations have led many researchers to believe that the cerebellum plays a central role in our ability to adapt to perturbing forces during movements. The same theoretical considerations, but a different set of experiments, have also led to the suggestion that the cerebellum plays a central role in our ability to compensate for interaction torques during multi-joint movements. There is an implicit understanding that a single cerebellar architecture should be able to accomplish both goals since both are amenable to error-driven force compensation. We built a model of neural control of arm movements -- including a detailed network model of the cerebellum -- to test whether it is indeed possible to solve both tasks using the same model. We based our work on that of Schweighofer et al., 1998. They embedded a neural network model of the cerebellum in a biologically motivated dynamic model of the motor control system, and showed that their model was capable of compensating for interaction torques during reaching movements. We reproduced their results for interaction torques, and then used the model mimic how humans adapt to a force field that perturbs their arm movements. With some changes in the error detection and transduction system, we were able to build a model that succeeded in both tasks. Our predictions regarding the physiology of cerebellar neurons will be discussed.
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Phase Resetting in Response to Perturbation of the Leg During Walking

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Reciprocal arm swinging during standing involves transitions between steady states of each arm (equilibrium points), coupled by a common timing mechanism such that both arms function as a single unit (Ustinova et al., 2006). During locomotion however, arm movements are also coordinated with the movements of the lower limbs. We hypothesized that during walking, mechanical, reflex and central interactions between muscles of different skeletal segments compel all four limbs to act as a coherent unit. This implies that perturbation of a single limb may have a global effect on the whole body in addition to the local influence on the perturbed limb. To test this hypothesis, we analyzed the effects of perturbation of a single leg on motion of both arms, both legs and the trunk during walking. Healthy young subjects walked on a self-paced treadmill at two different speeds (1 and 1.2 x comfortable speed) paced by a metronome. During 40-s long trials, brief mechanical perturbations at the ankle transiently (~200ms) blocked the movement of the leg at mid-swing. Subjects were instructed to continue walking while swinging their arms despite the perturbation. Movements of the arms, legs, trunk and head were recorded with a 3-dimensional motion analysis system at 120 Hz (Vicon-512, Oxford, UK). Results show that subjects adopted a consistent strategy in reaction to perturbation, regardless of the leg being perturbed. The perturbation elicited a rapid phase shift from swing to stance in the perturbed leg, and a shortened stance phase and faster transition to swing phase in the contralateral leg. Moreover, changes in movement amplitude and speed of both arms were observed following the leg perturbation. Arm swing amplitude and velocity were reduced for 1-2 cycles following the perturbation. During the transitional period, the non-perturbed limbs (contralateral leg and both arms) continued to move until they reached pre-perturbation extreme positions. This implies that, after the phase resetting, regular walking resumed only when the system reached its steady state. Arm swinging recovered pre-perturbed amplitude following heel strike of non-perturbed leg. The coordinated response of both arms and legs, and the regularity of this response within and between subjects suggest that the resetting is controlled by a central timing mechanism, which may involve modulation and gating of proprioceptive, cutaneous and vestibular reflexes, and allows efficient adaptation to an unexpected perturbation during locomotion.

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Does Adaptation Depend on a Single Cerebellar Mechanism?

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An important question about the motor system is its ability to adapt to new environments. Two common tasks to induce adaptation are the force field and visuomotor adaptation. In both tasks the subject is required to move a handle connected to a robotic arm, seeing his movement represented as a point on a screen while trying to reach to a target. In the force field the robotic arm exerts forces on the subject while moving. In the visuomotor task, the point representing the movement is moving in a different direction than expected. In order to achieve the goal of the movement one has to compensate for these perturbations. It is known that the cerebellum is an essential part of the adaption process in both these tasks. Here we ask whether the same cerebellar mechanism controls the adaptation process of the two different tasks. Healthy controls and people with general degeneration of the cerebellum performed both force field and visuomotor adaptation. We predicted that differences between subjects in the pattern of degradation would lead to dissociable differences in performance in the two tasks in different cerebellar subjects. Our results show that the two tasks are learnt by controls at the same rate and that controls reach the same plateau performance level. Cerebellar patients, as a whole, show the same decreased performance in both tasks compared to control subjects, confirming in one cohort of patients what has already been shown separately regarding the cerebellar role in these tasks. However, we found that some cerebellar subjects show a large difference in performance between the two tasks. The relevance of this to the clinical diagnosis will be discussed, and we are currently pursuing a similar project in patients with focal lesions, in hopes of determining which cerebellar areas are critical for success in each of the two tasks.

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Can Cats Learn to Perform an Accurate Reaching Movement in a New Force Field?

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We characterized cats' ability to adapt to perturbing force fields during reaching movements. This project is part of a larger project designed to explore the role of the cerebellum during adaptation using perturbed reaching movements in cats as the central behavioral paradigm.

Because adaptation to perturbations of reaching has not been demonstrated in cats, we set out to determine the appropriate forces to use and to demonstrate that adaptation in cats was similar to that found in humans. Our behavioral setup uses two separately programmed robots.

The 'target' robot is in front of the cat and supplies food during the training. The 'perturbing' robot is connected to the cat's right forelimb, measures the 3D position of the cat's limb and perturbs the forelimb while it makes reaching movements to the target robot. After training the cats to make reaching movements toward the target robot in response to an auditory cue, we used occasionally applied forces to determine the range of forces with which the cat could work comfortably.

Once an appropriate range of forces was determined, we then applied a standard force field perturbation paradigm where the cat needed to adapt to perturbing forces that were velocity dependent and perpendicular to the movement direction. The magnitude and direction of force application were changed on each day of data collection. On each day, cats performed 150-300 trials in the following sequence: null trials, erturbation trials, null trials, interference trials, and finally null trials.

During perturbation trials, forces were applied in one of 4 different possible directions and with a consistent magnitude. During interference trials, we applied forces with the same magnitude as in the perturbation trials but directed in the opposite direction. Our results show that cats do adapt to perturbing forces with a learning rate similar to humans (~15 trials) and ultimately perform accurate reaching movements in the force field.

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Patterns of Generalization While Locally Adapting to Force Field, a Behavioral and Electrophysiological Study.

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We present experiment and analyses designed to investigate generalization of a local adaptation to force field (FF), measured by behavioral performance and neuronal activity. To this end we recorded neuronal activity in M1 while a monkey performed a well known center-out reaching movements ("*standard*") to 7 out of 8 directions whereas introducing FF in the 8th direction ("*learnt direction*", LD).

Previous studies reported a bimodal narrow generalization function, which drops off towards 45 degrees but moderately rises back by 180 (Donchin 2003). Although our experiment's scheme encourages not generalizing, when checking movements in trials which immediately followed a FF trial, we found a similar generalization function around the LD.
Interestingly, we found that the decay in time of generalization is different across space and asymmetric. Generalization to 180 degrees away from the learnt direction decayed after two trials while generalization to 45 degrees contra to the applied FF direction remained highly significant for over than 7 trials.

We examined neuronal activity along the learning process by tracing cell's preferred direction (PD). Previous studies showed that introducing FF to all movement directions caused PD-shift in the direction of FF (Li 2001). In our case, apparently, the asymmetric generalization function governs neuronal changes giving rise to only subpopulations of cells that show significant PD shift, according to the distance between the cell's PD and the LD, and with respect to the force-field direction.

Further analyses will be done to explore the neuronal basis of a local FF adaptation; specifically, the relation between the neuronal and behavioral findings we reported above – how the PD shifts explain the different effect of FF on movements across space.

Optimal Control Predicts Human Performance on Objects With Internal Degrees of Freedom

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Humans regularly interact with objects with internal degrees of freedom from carrying a cup of coffee to folding a shirt. While objects with no internal degrees of freedom can be regarded as some kind of extension of our limbs, non-rigid objects pose a more complex control problem. In recent years stochastic optimal feedback control has emerged as a framework for human motor coordination. Optimal control has been used to explain average movement trajectories as well as trial-by-trial variability in a wide range of motor behaviours, such as obstacle avoidance and bimanual coordination. In this study, we investigated whether the optimal control framework can be extended to object manipulation with internal degrees of freedom and whether it can account for the complex behaviour necessary to control such objects. We used a virtual reality set-up together with a vBOT robotic interface to simulate the dynamics of a virtual object attached to the subject's hand (for details see Körding et al., 2004). Subjects started with both hand and object aligned in the starting position and were required to move both the hand and object to the target position within a certain time window that was reduced during training down to 1 ± 0.2 s. As a prototypical object with internal degrees of freedom, the object was simulated as a damped mass, attached to the hand by a spring. However, we created six different complex dynamic objects by introducing anisotropies for the mass, viscosity and spring constant matrices (such as x-y dependencies and a velocity-dependent rotational force field applied to the mass). Subjects (n = 6) learned to control the six different mass-spring objects until they achieved 25% correct trials. Positional data and forces were recorded at 1000 Hz and the last 25 successful trials were analysed. We used an optimal control model based on the model proposed by Todorov & Jordan (2002) and included the dynamics of the different mass-spring-damper systems. Our optimal control model predicted complex hand trajectories such as loops and s-shaped curves, which deviate substantially from the straight hand paths seen during normal reaching movements. Experimental performance of subjects was well predicted explaining 83 – 96% of the variance with the same parameter settings across all conditions. The results suggest that the framework of optimal control can be extended to manipulation of objects with internal degrees of freedom and underlines the generality of the optimal control framework as a theory of motor coordination.

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Is There a Proximo-Distal Gradient in the Perception of Stiffness of Virtual Delayed Elastic Force Fields, and is it Related to the Combination of Force and Position Control During Probing?

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While in robotics we find a clear distinction between force and position control, it is still unclear whether such a distinction exists in the human motor control system. We hypothesize that position and force control mechanisms operate concurrently, and combined by our system according to environmental conditions as well as according to the joint that is dominant during the movement. In addition, we hypothesize that there is a proximo-distal gradient in the combination of these control modes when probing virtual elastic force fields.

In our previous studies we explored perception of stiffness in delayed environment, and found that subjects interacting with delayed elastic force fields tend to underestimate the stiffness if they do not move across the field's boundary, and overestimate the stiffness when they move across the elastic field boundary. A model based on a convex linear combination between regression of force-over-position and position-over-force according to the relative fraction of probing movements completed outside and inside the field best predicted our behavioral results. Since relation between the force applied by the field and the penetration that caused it in delayed environments is nonlinear, exploring perception and action in these environments provides a fertile ground for exploring control policy through perception. We suggest that the estimation process is directly related to a combined force and position control policy that guides the hand.

There is evidence for discrepancy in the control and perception of proximal versus distal joints: there is a positive proximo-distal gradient in accuracy of endpoint position, but there is a negative gradient in resolution of force control; the cortico-spinal system exerts greater excitatory influence over distal than over proximal muscles. In order to explore the effect of delay on perception through proximal and distal joints we designed a set of experiments where probing of elastic force fields was constrained to isolated elbow and wrist movements. We observed difference in the effect of delay on the perception of stiffness; however, the direction of the difference was inconsistent between subjects. We will present a regression-based model that will account for the effect of boundary as well as the proximo-distal gradient in the perception of delayed stiffness.

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Artificial Tremor and Neuronal Activity of the Primary Motor Cortex (M1) and the Globus Pallidus (GP) in Primates

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Low-frequency tremor is one of the pivotal symptoms of Parkinson's disease (PD). In parallel, the firing pattern of the Basal Ganglia (BG) and cortical neurons becomes bursty and, at least in part, oscillatory and synchronized. The oscillatory activity has well-defined spectral characteristics and appears to be concentrated mainly around double tremor frequency, as well as to a lesser extent around the tremor frequency. Albeit the co-appearance of the tremor and the changes in discharge pattern suggests a connection between them, their interrelation remains illusive. Either one of the phenomena could cause the other, both could be caused by some unknown confounding factor and, finally, they could be completely unrelated and caused by different aspects of the disease.

In this study we examined the contribution of sensory feedback paths to the discharge patterns of GP and M1. We have recorded from the arm related area of M1 and the GP of two healthy African green monkeys (Cercopithecus aethiops), while applying forced oscillations (artificial tremor) to the contralateral arm at several discrete frequencies for duration of 90 seconds per frequency.

We report the following results:
267/669 (40%) of the M1 neurons displayed a discharge pattern that was phase locked and coherent with the movement induced by the experimental procedure.
45/226 (20%) of neurons in the GPe and 24/133 (18%) of neurons in the GPi showed a discharge pattern that was phase locked and coherent with the movement.
Both the GP and the M1 displayed low-pass filtering properties in their response in the sense that the coherent and phase-locked firing of the units was more pronounced in the low-frequency range of movement.
The M1, but not the GP activity showed a tendency towards increased coherence with the arm oscillations following an increase in movement amplitude, suggesting M1 reaction to acceleration rather than to movement frequency.

Our results imply that sensory feedback from PD tremor can not account for the all the changes in discharge patterns of M1 and GP neurons in MPTP-treated primates. Recordings in the MPTP-treated primate model of PD are being performed to validate this conclusion.

Studying the Information Content of Cortical and Spinal Neurons During Voluntary Wrist Movements

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Corticospinal (CS) pathways provide the structural foundation for executing voluntary movements. Although the anatomy of these pathways is well explored, little is known about the information processing taking place along this route during voluntary movements. This question was addressed by simultaneously recording single-unit cortical and spinal activity in primates performing an isometric wrist task with multiple targets and two hand postures (pronation and supination).

To quantify and compare the coding of directional torque by motor cortical neurons against that exhibited by spinal interneurons (INs), the information theoretical measure of mutual information (*MI)* was used. *MI* was calculated between direction of wrist torque and the cells' firing rate during different task epochs. *MI* was calculated using an adaptive "greedy" algorithm introduced by Nelken & Chechik (2005).

The results indicate that on average, cortical cells are most informative about movement direction around the time of torque onset. During this period cortical cells are significantly more informative than spinal cells. This is true even though the cortical cells' firing rate is lower than that of the spinal cells. By contrast the spinal cells were still informative about torque direction during the sustained hold period, whereas cortical cells were considerably less informative at this time. Cortical cells also exhibited significantly higher *MI* than spinal cells during the epoch following the presentation of a visual target cue, with cortical *MI* rising earlier than spinal *MI*. In addition, taking hand posture into account significantly increased the mutual information between cell response and torque direction.

These results suggest that around the onset of motor action both spinal and cortical neurons contain substantial torque-related information. However, the time-dependent dynamic of this information greatly differs between these structures. It is suggested that spinal circuitry translates the cortical transient command into sustained activity suitable for muscle activation.

Model of control of speed of point-to-point voluntary movement

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Voluntary movements can be made with different speeds chosen by the subject. It has been shown that movements made with "the same speed" instruction over a range of distances exhibited similar initial slopes in the movement kinematics and agonist muscle electromyogram (EMG) while the peak velocity increased with distance. Movement speed can be thought of as a control parameter related to an intuitive notion of movement "urgency" or "effort". Here, we present a model of control of single joint point-to-point movement in which movement speed is determined by a constant rate of change of the neural control. The complete control trajectory is found using optimal control theory. The model was used to simulate experimentally recorded data in "fast" and "moderate speed" movements made over a 50° distance to a wide 6° target on the screen (Experiment 1) or over self-chosen distances between 30°-70° with no target (Experiment 2). The model reproduced the movement kinematics, linear relations between the peak velocity and movement distance, and experimentally observed tri-phasic and bi-phasic muscle EMG patterns. In contrast to other models of optimal control where movement time is chosen either heuristically or based on the explicit or implied accuracy requirements for every movement, the control solution in the speed control model presented here is determined by the explicit task parameters such as load, distance, and a chosen speed that may remain the same in movements made over different distances against different loads.

Directional Selectivity in the Motor Cortex

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Neurons in the motor cortex are typically tuned to the direction of limb movements. There is also evidence for similar tuning of the local field potential (LFP), representing the pooled neural activity (at roughly 1 mm). But it is currently unclear if the different directions of movement are represented in clusters within the limb areas of the human brain.

To that end, we conducted an event-related fMRI study in which subjects performed a reaching task towards 5 targets using an MRI-compatible joystick. The targets were between 0 and 180 degrees, separated by 45 degrees. Regions of interest (ROIs) were selected in the visual, motor and intermediate areas on the basis of their activation during the reaching task. In each ROI, we studied the degree to which the spatial patterns of the fMRI activation (across all voxels within each ROI) were correlated across runs. Spatial correlations of the fMRI patterns allows tracing weak but consistent trends that stem from an inhomogeneous distribution of the preferred directions in the 3*3*3 mm scanned voxels.

First, we compared the correlation coefficients computed for trials with movements in the same direction (“same” condition) and for trials with movements in different directions (“different” condition). We found that in the primary motor cortex (M1), SMA, the cerebellum, MT, and the calcarine sulcus, the spatial pattern of fMRI activation was positively correlated across trials in the “same” condition. These correlations were found to be significantly higher than the correlation between trials in different directions.

Next, we wanted to find which reference frame (visual or motor) dominates the correlation in the different ROIs. Thus, we ran the same reaching experiment, this time under a 45 degrees visuomotor rotation, and conducted correlation analysis between the rotation and the standard (no rotation) runs. The trials were aligned either according to the location of the targets in the visual field or according to the direction of movement. Interestingly, while the correlations in M1 and the cerebellum were significant under the 'movement direction' alignment, the correlation in the calcarine sulcus and MT were significant only under the 'visual field' alignment.

These results indicate that while the visual and intermediate areas such as MT represent primarily the visual elements of the movement, M1 and the cerebellum represent the direction of movement. Furthermore, the directional selectivity that was found in M1 and the cerebellum, using 3*3*3 mm voxels, suggests an inhomogeneous clustered representation of movement directions in these areas.