



## **4<sup>th</sup> Joint Spring School**

### **Multisensory Perception for Action**

**Wildbad Kreuth, June 3 – 6, 2014**

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The Organizers

Marburg/Gießen	IRTG 1901 – “The Brain in Action”
London, Toronto, Kingston	IRTG 1901 – CREATE
München	GRK 1091 – “Orientation and Motion in Space”
Tübingen	Graduate School of Neural & Behavioural Sciences

## Program of the Spring School „Multisensory Perception for Action”

**Venue:** Educational Center Wildbad Kreuth, 83708 Wildbad Kreuth, Phone: +49 8029-170

03. June: until 14.00h: Arrival
03. June: 14.00h – 16.00h: Poster session (Doctoral candidates (DCs))  
16.00h – 16.30h: Coffee break  
16.30h – 18.00h: Introduction of the RTG-1091 Munich (by DCs)  
18.00h – 19.30h: Dinner  
19.30h – 21.00h: **Keynote lecture (Doug Crawford, Toronto)**
04. June: 8.30h – 10.15h: **Session I (Alessandro Farnè, Lyon; Andreas Bartels, Tübingen)**  
10.15h – 10.45h: Coffee break  
10.45h – 12.30h: **Session II (Martin Giese, Tübingen; Daniel Braun, Tübingen)**  
12.30h – 14.30h: Lunch and German-Canadian project meeting  
14.30h – 16.00h: Introduction of the GC Tübingen (by DCs)  
16.00h – 16.30h: Coffee break  
16.30h – 18.15h: **Session III (Patrizia Fattori, Bologna; Uwe Ilg, Tübingen)**  
18.15h – 19.30h: Dinner  
19.30h – 21.00h: Poster session  
19:30h – 21:00h: meeting of the *IRTG-1901-CREATE Joint Directorate*
05. June: 8.30h – 10.15h: **Session IV (Paul MacNeilage, Munich; Zhuanghua Shi, Munich)**  
10.15h – 10.45h: Coffee break  
10.45h – 12.30h: **Session V (H. Deubel, S. Glasauer & A. Straube, Munich)**  
12.30h – 14.30h: Lunch and German-Canadian project meeting  
14.30h – 16.00h: Introduction of the IRTG-1901-Marburg/Giessen (by DCs)  
16.00h – 16.30h: Coffee break  
16.30h – 18.15h: **Session VI (Laurence Harris, Toronto; David Burr, Pisa)**  
18.15h – 19.30h: Dinner  
19.30h – 21.00h: **Ethics in the Neurosciences (Jens Clausen, Tübingen)**
06. June: 8.30h – 10.15h: **Session VII: (M. Concetta Morrone, Pisa; Marc Ernst, Bielefeld)**  
10.15h – 10.45h: Coffee break  
10.45h – 12.15h: Introduction of the IRTG-CREATE Queens/Toronto/Western  
(by DCs)  
12:15h – 13:00h: General discussion and future planning (German-Canadian lab  
visits, workshops, retreat 2015, etc.)  
13.00h – 14.30h: Lunch and departure

**Abstracts**

**Presenting authors (underlined) are listed in alphabetical order**

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**Multimodal Perception of Action**

*Belkis Ezqi Arikan*, Benjamin Straube, Jens Sommer, Bianca von Kemenade and Tilo Kircher

During the execution of a movement, motor commands and their efference copies are sent to a forward model which will predict the outcome of the self-generated action. The predicted outcome is then compared to the actual sensory feedback, potentially leading to adjustments of the sensory system or of future predictions of the forward model. Thus, such predictive mechanisms from one modality may affect judgments and perception of a property from another modality. In addition, a number of neural structures are found to be related to multisensory action. However, the effect of different motor commands on the perception of related multisensory feedback and its neural correlates are still unclear. Furthermore, the role that feedback from one's own versus other's action plays in multisensory perception needs to be clarified. The aim of my PhD thesis is to investigate the effects of predictive mechanisms in the action-perception cycle on the perception of visual and auditory consequences of one's own actions. Through three main studies involving behavioral methods and fMRI, we aim to assess supramodal versus unimodal effects of action-sensory feedback matching processing, and the neural correlates of supramodal predictive mechanisms and their consequences. Accordingly, we will test different hand movements, which will be coupled with a tone. The movements will be both actively and passively executed, and visual feedback of the movements will be fed-back online to the participant. Delays between the executed action and feedback of varying duration will be induced for each modality. Participants will be asked to detect these delays, or to judge whether the auditory and visual information were congruent, which would allow us to assess the behavioral and neural effects of predictive mechanisms on multisensory consequences of one's own actions.

**Dual adaptation to opposing visuomotor rotations is facilitated by intrinsic contextual cues and saturates upon extended training**

*Maria N. Ayala & Denise Y. P. Henriques*

When reaching towards objects, the human central nervous system (CNS) can actively compensate and adapt to two different perturbations simultaneously, though this does not simply occur upon presentation. In fact, the CNS requires distinctive contextual cues to differentiate between adaptive states. Furthermore, not all contextual cues are effective in facilitating dual adaptation. In two experiments we investigated the efficacy of contextual cues which are intrinsic to the CNS including hand and body posture, as well as the role of extended training in adapting to two opposing visuomotor rotations concurrently. Using a virtual reality paradigm, participants manipulated a projected hand-cursor using a digitizing tablet. A 30° CW and CCW rotation were each associated with 2 distinct hand postures (i.e. precision and power grips) respectively in the first experiment and 2 distinct body rotations (i.e. leftward and rightward turn of the seat, while fixating straight) respectively in the second experiment. Also, because the learning rate in dual adaptation is not as steep as that of single adaptation, we implemented an extended training set in the first experiment to examine the effect of greater practice. We found that how people held the tool or oriented their body while reaching is sufficient for recalling an adaptive state such that over time, reach errors decrease despite being presented both perturbations in a randomized and concurrent manner. Extended practice did not provide additional benefits suggesting that dual adaptation training reaches a saturation point. Our results suggest that intrinsic cues which produce distinct muscle synergies are effective at facilitating dual adaptation while extended training provides no additional benefits.

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**Title: Identifying spatiotopic and retinotopic mechanisms of trans-saccadic object feature integration: an fMRIa study**

*B.-R. Baltaretu, B. T. Dunkley, S. Monaco & J. D. Crawford*

The human visual system is able to retain and integrate a limited amount of visual feature information across saccades, but the neural mechanisms for this are little understood. A recent fMRIa study (Dunkley & Crawford SFN Abstracts 2013) found adaptation effects to stimulus orientation in a spatiotopic frame in bilateral parietal cortices. Here, we used a similar fMRIa paradigm, but further investigated which cortical areas are involved in feature integration. Similar to Dunkley & Crawford (2013), 13 participants took part in an orientation-discrimination task that was six blocks long, with 24 trials in each block. Therein, participants maintained fixation on one of two possible fixation crosses. Within each trial, two circular stimuli comprised of obliquely oriented lines were presented sequentially one after the other. The lines were presented in the same orientation (45° or 135°) in both stimulus presentations within each trial, or in different orientations (45° firstly and 135° secondly, or vice versa). Participants were instructed to indicate via a button press whether the orientations of the stimuli within each trial two were the same (Repeated) or different (Novel). In our analysis, we investigated adaptation effects to stimulus orientation in spatiotopic, retinotopic and frame-independent spatial conditions. This analysis

revealed significant adaptation effects to the orientation of the stimulus in the retinotopic condition in bilateral supplementary eye fields (SEF), left supramarginal (SMG) and left intraparietal sulcus. In the spatiotopic condition, we found significant adaptation within the left primary motor area (M1), left inferior parietal lobe (IPL) and left SMG. In the frame-independent condition, we found significant adaptation in right pre-SEF, left SPL and left IPL. Similar to Dunkley & Crawford (2013), these results indicate that parietal cortex plays a role in low-level object feature processing, such as of object orientation. Most importantly, we find here that this occurs in a manner independent of the frame of reference.

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### **Locomotion-related corollary activity in mechanoreceptor efferent neurons modulates peripheral sensory processing**

*Roberto Banchi, Boris P. Chagnaud and Hans Straka*  
*Division of Neurobiology, Ludwig-Maximilians-Universität München*

Major consequences of animal locomotion are undesired reafferent signals related to self-motion in space. In order to limit the deteriorating impact of the latter signals on sensory perception while retaining adequate sensitivity, an adaptation of the respective sensory encoding system is necessary. Spinal locomotor pattern generator-derived corollary discharge is a feed-forward mechanism that informs sensory systems about impending reafferent activity. Here, we show in an isolated in vitro preparation of *Xenopus* tadpoles that locomotor efference copies modulate the sensitivity of lateral line and vestibular afferents via mechanoreceptor-related efferent neurons that project to the respective sensory epithelia. Multi- and single unit activity, recorded from the proximal end of mechanoreceptor (vestibular, lateral line) nerves along with spinal ventral root activity during spontaneous swimming revealed a rhythmic modulation of efferent neurons that is timed to the locomotor behavior, in phase with the spinal discharge on the ipsilateral side. Calcium imaging of hindbrain efferent neurons during fictive swimming confirmed the coupling of the respective nerve activity with the spinal locomotor commands. With respect to signal content, the major parameters of locomotion such as frequency, duration and amplitude are represented in the corollary discharge in the mechanoreceptor-related efferent neurons. As a functional consequence, the gain of the modulated spike activity of vestibular and lateral line nerve afferents during natural stimulation is considerably reduced in the presence of fictive locomotion. This reafferent signal suppression thus eliminates undesired sensory perturbations during active motor behavior.

Combes D, Le Ray D, Lambert F, Simmers J, Straka H (2008) An intrinsic feed-forward mechanism for vertebrate gaze stabilization. *Curr Biol* 18: R241–R243.

Lambert FM, Combes D, Simmers J, Straka H (2012) Gaze stabilization by efference copy signaling without sensory feedback during vertebrate locomotion. *Curr Biol* 22:1649–1658.

Von Uckermann G, Le Ray D, Combes D, Straka H, Simmers J (2013) Spinal efference copy signaling and gaze stabilization during locomotion in juvenile *Xenopus* frogs. *J. Neurosci* 33(10):4253-64

### **Parietal function in ego-motion**

Andreas Bartels

*Vision and Cognition Lab, Centre for Integrative Neuroscience, University of Tübingen*

Human parietal cortex consists of a number of distinct regions that can be delineated from each other using retinotopic mapping. However, very little is known about their function. I will present a series of fMRI studies (some combined with transcranial magnetic stimulation (TMS)) that each sheds light onto distinct regions within parietal cortex, demonstrating that parietal subdivisions have drastically distinct functional preferences. Most likely I will have time to present four studies: on high-level visual ego-motion cues as induced when humans freely view a movie, on the integration of visual motion with self-induced motion through eye-movements, on the representation of ego-centric space beyond the field of view, and on seeing the wood for the trees (i.e. global vs. local Gestalt perception). If time permits, I may additionally present a new study on cortical colour coding that emphasizes a concept introduced also in the motion studies, namely the influence of feedback on early visual cortex that is consistent with predictive coding.

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### **Sensorimotor learning and decision-making in complex environments**

Daniel Braun

*Max-Planck-Institut für biologische Kybernetik, Tübingen*

Recent advances in movement neuroscience suggest that sensorimotor control can be considered as a continuous decision-making process in complex environments in which uncertainty and task variability play a key role. Leading theories of motor control assume that the motor system learns probabilistic models and that motor behavior can be explained as the optimization of payoff or cost criteria under the expectation of these models. Here we discuss first how the motor system exploits task variability to build up efficient models and then discuss evidence that humans deviate from Bayes optimal behavior in their movements, because they exhibit effects of model uncertainty. Furthermore, we discuss in how far model uncertainty can be considered as a special case of a general decision-making framework inspired by statistical physics and thermodynamics.

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### **Cross-sensory integration and calibration during development**

David Burr

*Department of Psychology, University of Florence, Italy*

Much evidence suggests that humans integrate information between senses in a statistically optimal manner, maximizing the *precision* of performance. We have recently shown that reliability-based integration of vision and touch develops only after about 8 years of age. In younger children one sense dominates the other: for size discrimination touch dominates vision but for orientation discrimination visual dominates. We suggest that the dominance of one or other sense reflects *cross-modal calibration* of developing systems: one sense *calibrates* the other, rather than fusing with it to improve precision. But unlike sensory fusion, it is the more *robust* and

*accurate* sense that dominates the calibration, even if it is the less *precise*. Several lines of evidence support this idea: congenitally blind children show a selective deficit in haptic orientation-discrimination, and dyskinetic children (with highly impaired movement control) show a selective deficit in visual size judgments. Both these impairments could result from a lack of cross-sensory calibration in early development.

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### **The “toolish” hand illusion: when tools become hand in the brain**

L. Cardinali, A. C. Roy, J. C. Culham, A. Farné

Almost 15 years ago, Botvinik and Cohen discovered that when subjects watched their hand being brushed synchronously with a fake hand, they felt like the fake hand was their real hand. This illusion, called the Rubber Hand Illusion (RHI), has since been studied by many researchers who found that a key aspect is the *visual similarity* between the fake hand and the subjects’ hand. Here we tested whether *functional similarity* (instead of anatomical similarity) is sufficient for the illusion of ownership to extend to non-hand-shaped tools. We hypothesized that motor experience with the tool would be necessary to induce the illusion.

We tested subjects in a modified version of the classical RHI paradigm. Subjects were asked to observe a grabber being stroked synchronously (test condition) or asynchronously (control condition) with their own (hidden) right hand. This procedure was applied twice, before and after a short tool-use period consisting in grasping and lifting objects with the grabber. Crucially, subjects had no previous experience with the tool prior to the experiment. We used three different measures to quantify and describe the illusion: a finger localization task, a questionnaire and skin conductance response (SCR) changes during threat to the tool.

We found that participants experienced the illusion of the tool being their own hand as they localized their real hand as shifted toward the tool and showed higher SCR in the synchronous compared to the asynchronous brushing condition. Moreover, both measures were also modulated by the short period of tool use. The results of the questionnaire supported the presence of the illusion although did not seem to be influenced by tool use.

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### **Neural Correlates of Spatially and Temporally Predictive Saccades**

Benedict J. Chang, Donald C. Brien, Brian C. Coe, Douglas P. Munoz

Prediction is the process of using information from either the past or present to guide future behaviour. It is needed to compensate for neural delays between a sensory input and an appropriate motor output. We designed an eye movement task to clarify the behavioural control and neural correlates that are involved in both temporal and spatial prediction. A task involving temporally and spatially predictive and non-predictive saccades was employed in an MRI in which four conditions were tested: spatially/temporally predictive (STP), temporally predictive/spatially non-predictive (TP), spatially predictive/ temporally non-predictive (SP), and spatially/temporally non-predictive (NON). Data from 24 normal human subjects (mean age =



22.4 yrs) showed distinct behavioural differences between conditions. All subjects elicited primarily predictive saccades (saccadic reaction time: SRT < 100ms) in the STP condition. The NON condition elicited primarily reactive saccades (SRT > 100ms). The average SRT of the SP condition fell between the average of the STP and NON conditions, and no significant differences in SRT were observed between the TP and the NON conditions. Analysis of the functional imaging data identified regions of interest with activations that correlated to the predictive conditions. Contrasts of predictive conditions isolating both spatially and temporally predictive areas showed activation of the parietal eye fields (PEF), insular cortex, and medial prefrontal cortex (MPFC) which may play a role in the control of predictive saccades. Contrasts that isolated spatially predictive areas also showed activation of the PEF, insular cortex, and MPFC while contrasts that isolated temporally predictive areas showed select activation of the cerebellum which may serve as the internal clock that drives the regular rhythmic behaviour observed for the temporal aspect of predictive saccades. Surprisingly, activation of frontal areas responsible for saccadic control such as the Frontal and Supplementary Eye fields were equal among all conditions. The behavioural differences validated the activity of the contrasts to isolate brain areas that are correlated with both spatial and temporal prediction. The results from these contrasts indicated that brain activation in the STP/SP and TP conditions reflect predictive responses to visual stimuli and motor-timed responses, respectively. This suggests that utilizing a predictive saccade task is a valuable tool for simultaneously testing both spatial and temporal prediction that involves fast internally-guided responses.

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### **Seeing through the tectal eye: spatial frequency tuning & temporal responses of superior colliculus**

*Chih-Yang Chen<sup>1,2</sup> & Ziad M. Hafed<sup>2</sup>*

- 1. Graduate School of Neural and Behavioural Sciences, International Max Planck Research School, Oesterbergstrasse 3, Tuebingen, 72074, Germany*
- 2. Werner Reichardt Centre for Integrative Neuroscience, Otfried-Mueller Strasse 25, Tuebingen, 72076, Germany*

Superior colliculus (SC) receives various visual inputs including from retina, LGN, and V1. Each of these areas has different spatial frequency (SF) tuning characteristics: retinal output and LGN neurons are predominantly low-pass and tuned for low SF's, whereas V1 neurons can be band-pass. However, collicular SF tuning properties in primates are unknown. Here, we characterized these properties.

We recorded activity from 87 neurons of two monkeys fixating a white spot over a gray background. Inside a neuron's response field (RF), a high-contrast, vertical Gabor grating having one of five SF's (0.56, 1.11, 2.22, 4.44, 11.11 cpd) appeared. We measured peak neuronal activity 30-150 ms after stimulus onset and divided neurons based on their preferred retinotopic eccentricity. We characterized visual (V) and visual-motor (VM) SC neurons, and we excluded trials in which stimulus onset occurred <100 ms from microsaccades, to avoid peri-microsaccadic modulations in activity. In separate behavioural sessions, we measured saccade reaction time

(SRT) when monkeys made visually-guided saccades towards the same stimuli from our recording sessions. For these behavioural sessions, we fixed the stimulus at 2.5 deg either on the left or right horizontally.

All neurons (32 V; 55 VM) showed low-pass characteristics, but foveal neurons also had peaked tuning curves. Neurons with RF centers between 1 and 3 deg preferred SF's up to 4.44 cpd. Slightly more eccentric neurons (<8 deg) were most responsive for up to 1.11 cpd. The remaining neurons (<24 deg in our population) only preferred 0.56 cpd and sharply reduced their activity for all other SF's. We also analyzed visual burst latency. Interestingly, this latency increased progressively with SF even for neurons that preferred higher than the lowest SF. This effect was mirrored very closely in SRT, such that SRT's were shortest for the lowest SF and gradually increased for higher SF's.

Thus, SC shows clear SF tuning correlated with visually-guided SRT, but this tuning appears different from V1. Besides clarifying SC visual properties, this observation is interesting because it could potentially explain visual performance changes in V1-lesioned 'blindsight' patients, for whom the collicular visual pathway is presumably important.

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### **Ethics and the Neurosciences**

*Jens Clausen*

*Universität Tübingen, Germany*

Progress in neurosciences, increasing computational power, and ongoing miniaturisation of micro-technological components enable both, a better understanding of human brain functions and development of new diagnostic and therapeutic tools. Research and development as well as clinical application of devices designed for recording neural signals from the brain raise several social and ethical questions. This talk will focus on question of responsibility and autonomous decision making in the context of brain interventions as well as the widespread fear for changing personality / personal identity through brain interventions.

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### **Delayed reaching in a pure case of ventral pathway damage**

*Sonja Cornelsen<sup>1</sup>, Marc Himmelbach<sup>1,2</sup>*

*<sup>1</sup>Division of Neuropsychology, Center of Neurology, Hertie-Institute for Clinical Brain Research, University of Tübingen, Tübingen, Germany*

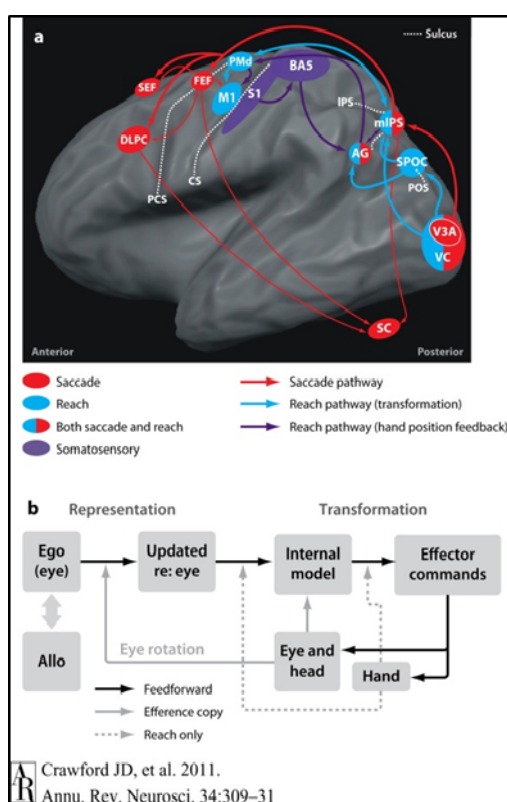
*<sup>2</sup>Centre for Integrative Neuroscience, University of Tübingen, Tübingen, Germany*

The so-called perception-action model (PAM) postulates two visual systems. A dorsal pathway from early visual areas to posterior parietal cortex processes information for the control of action whereas a ventral pathway from early visual areas to inferotemporal cortex serves the transformation of visual information for perception. One postulation of the PAM was that the ventral pathway plays an essential role for the guidance of delayed movements to memorized targets. This assertion was only tested in patient DF who not only suffered damage to the ventral

pathways but also damage to the dorsal system bilaterally. We examined a stroke patient (HWS) with a unilateral lesion in the ventral pathway who showed lateralized symptoms of visual agnosia. HWS showed accurate immediate reaching towards a visible peripheral target. However, introducing a delay between stimulus presentation and motor response, HWS was less accurate in his contralesional hemisphere compared to age-matched healthy controls. This observation not only confirms previous findings but also allows for a clear attribution of a deficit in delayed reaching to the ventral stream since HWS suffered from a first-time unilateral stroke resulting in a circumscribed lesion to the occipital-temporal cortex in the right hemisphere.

### Spatial Transformations for Gaze and Reach

*J. Douglas Crawford, Centre for Vision Research, York University, Toronto, Canada.*



Our knowledge of the brain has now advanced to the point where one can both identify functional regions for gaze control and reach, and link them together within functional circuits (e.g., **Figure a**). To understand what these circuits do (from a *spatial* perspective), we recently proposed an overarching model for the visual guidance of both gaze and hand motion (**Figure b**). Here, I will trace through these circuits from the perspective of our model, including 1) early egocentric and allocentric representations of target location, 2) the updating of eye-centered target representations during eye motion, and 3) the transformation of these eye-centered signals into effector (eye/head, hand) specific commands. To illustrate each point I will cite primate electrophysiology, human

fMRI & TMS, and saccades and / or reach. The result, we believe, provides a comprehensive description of the early neural transformations for eye-hand coordination.

## **Investigating hippocampal and cortical activations elicited by watching indistinct motion stimuli**

*Nisha Dalal* <sup>1, 2</sup>, *Virginia Flanagin* <sup>1, 3</sup>, *Stefan Glasauer* <sup>1, 2, 3</sup>

<sup>1</sup>*Graduate School of Systemic Neurosciences,*

<sup>2</sup>*Institute of Clinical Neuroscience,*

<sup>3</sup>*German Centre of Vertigo and Balance Disorders*

Our previous study (Fraedrich et al, 2012) show that the meaningless phase scrambled videos activate hippocampus bilaterally compared to the corresponding virtual tunnel videos. But hippocampus, not being activated in response to the static phase scrambled images, indicates some interesting aspects about the dynamic nature of the visual input. Not only hippocampus, even the early visual cortex activity is increased in response to the spatiotemporal phase scrambled videos compared to the tunnel videos (Fraedrich et al, 2010). In the present work, we introduced a third type of videos as well, which are created by pixel scrambling the previous tunnel videos spatiotemporally. These videos are also meaningless like the phase scrambled videos but they lack any kind of spatial or temporal structure as well.

We conducted an fMRI experiment with 120 (12 seconds each) videos of three different types: virtual tunnel videos, corresponding phase scrambled videos and pixel scrambled videos (noise). Videos were presented to 25 young subjects in a pseudorandom order divided in two runs.

The hippocampal and visual cortex activations were found strongest for pixel scrambled videos compared to tunnel videos and phase scrambled videos ( $p < 0.001$ , uncorrected). As shown by the PPI analysis (Fraedrich et al, 2012), cortical hippocampal networks are recruited when noisy and indistinct visual inputs are presented. Not only hippocampal involvement, but also hippocampal connectivity with different cortical areas is dependent on the driving visual input. By further investigating the temporal characteristics of the visual stimulus we can further characterize the concrete role of hippocampus in visual processing.

Acknowledgement: DFG (GRK 1091 and GSN) and BMBF.

Fraedrich EM, Glasauer S, Flanagin VL (2010) Spatio-temporal phase-scrambling increases visual cortex activity, *NeuroReport* 2010, 21:596–600.

Fraedrich EM, Flanagin VL, Duann JR, Brandt T, Glasauer S (2012) Hippocampal involvement in processing of indistinct visual motion stimuli, *J Cogn Neurosci* 2012, 24:1344-57.

Ratliff CP, Borghuis BG, Kao YH, Sterling P and Balasubramanian V (2010) Retina is structured to process an excess of darkness in natural scenes, *Proc Natl Acad Sci USA* 2010, 107:17368-73

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## **Spatial Attention and Action Planning**

*Heiner Deubel*

*Department Psychologie, Ludwig-Maximilians-Universität München*

It is now well established that goal-directed movements are preceded by covert shifts of visual attention to the movement target. I will first review recent evidence from our lab in favour of this claim for manual reaching movements, demonstrating that the planning of some of these actions establishes multiple foci of attention which reflect the spatial-temporal requirements of the intended motor task.

Recently our studies have focused on how finger contact points are chosen in grasp planning and how this selection is related to the spatial deployment of attention. Subjects grasped objects with thumb and index finger. A perceptual discrimination task was used to assess the distribution of visual attention prior to the execution of the grasp. Results showed enhanced discrimination for those locations where index finger and thumb would touch the object, as compared to the action-irrelevant locations.

These results highlight the important role of attention also in grasp planning. Our findings are consistent with the conjecture that the planning of complex movements enacts the formation of a flexible “attentional landscape” which tags all those locations in the visual lay-out that are relevant for the impending action. They have implications also for the understanding of some deficits of patients with attentional disorders.

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### **Eye movements of patients with schizophrenia in a natural environment**

*Stefan Dowiasch, Bianca Backasch, Wolfgang Einhäuser, Dirk Leube,  
Tilo Kircher & Frank Bremmer  
Philipps-Universität Marburg, Germany*

Alternations of eye movements in schizophrenia patients have been widely described for laboratory settings. For example, gain during smooth tracking is reduced and fixation patterns differ between patients and healthy controls. The question remains, if such results are related to the specifics of the experimental environment, or whether they transfer to natural settings. Here, we used a mobile light weight eye tracker (EyeSeeCam) to study eye movements of patients and healthy controls during natural behavior in an indoor environment. Overall 20 ICD 10 diagnosed patients with Schizophrenia and 20 healthy age-matched controls participated in the study, each performing four different everyday oculomotor tasks: (I) fixating stationary targets, (II) sitting in a hallway with free gaze, (III) walking down the hallway, and (IV) visually tracking a target on the floor while walking straight-ahead.

When looking at predefined targets, patients showed more fixations with reduced durations as compared to controls. The opposite was true when participants were sitting in a hallway with free gaze. During visual tracking, patients showed a significantly greater root-mean-square error (representing the mean deviation from optimal) of retinal target velocity. Surprisingly and different from previous results obtained in laboratory settings no such difference was found for velocity gain.

Taken together, we have identified significant differences in fundamental oculomotor parameters between schizophrenia patients and healthy controls in a natural environment. However, our data also provides evidence that in natural settings patients overcome some impairments, which are present only in laboratory studies, by as yet unknown compensatory mechanisms or strategies.

## **Multisensory Perception and Sensorimotor Behaviour: A Probabilistic Approach.**

Marc Ernst

*Bielefeld University, Bielefeld, Germany*

The human brain uses multiple sources of sensory information together with prior knowledge about the statistical regularities of the world in order to generate the most appropriate action. However, there is uncertainty due to noise and ambiguity in the sensory information. Furthermore, sensory information as well as prior knowledge may be imprecise and possibly inaccurate for the current action context. Therefore, a decision for choosing some action can only be taken probabilistically. Bayesian Decision Theory, which I will review here in this talk, provides a suitable probabilistic framework to come up with ideal observer models, against which human perception and performance can be compared. Besides an introduction to this general framework, I will talk about two of our recent studies in more detail, which are examples of the application of this framework to multisensory perception and action. The first study deals with the decision process, which signals to combine. Sometimes there are seemingly arbitrary association between multisensory signals such as, for example, sound frequency and spatial elevation. This goes so far that even in most natural languages the spatial labels “high” and “low” are used for particular sound frequencies. We recently showed (Parise et al., PNAS, 2014) the reason for this association to be found in the statistics of the natural environment where high frequency sounds are more likely to originate from a higher spatial elevation and vice versa. The second study (van Dam, Ernst, PloS One, 2013) investigates the knowledge we have about the errors we make when executing actions. This is important because it is the knowledge about such errors that shapes sensorimotor learning. We show that we have a surprisingly detailed understanding of even the random errors we make and that we can use this knowledge in a statistically optimal way for the correction of the errors. I will end my talk with a discussion about the benefits and the limits of this framework.

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## **Sensorimotor and social features of peripersonal space**

Alessandro Farnè

*Lyon Neuroscience Research Centre, ImpAct Team, France*

The binding of visual information available outside the body with tactile information arising, by definition, on the body, allows for the representation of the space lying in between, which is often the theatre of our interactions with objects. The definition of what has become known as “peripersonal space”, originates from single-unit electrophysiological studies in monkeys, based on a class of multisensory, predominantly visual–tactile neurons. Such neurons, identified in several parietal and premotor regions of the monkey brain, respond both to visual and tactile stimuli, their visually evoked responses being stronger when objects are closer to the tactile receptive field. These functional properties allow for the coding of visual information in advance to the contact with the body (e.g., with hands), in a body-part centred reference frame.

Today, I will first review the behavioural and functional neuroimaging evidence that suggested the existence of a similar representation of the peripersonal space in humans, which is similarly based

upon a network of posterior parietal and premotor areas. I'll present results indicating that, similar to non-human primates, the peri-hand space in humans is represented in hand-centred coordinates. My focus will be the following question: what is the function of such multisensory systems? I will provide behavioural and electrophysiological evidence for their implication in the planning and execution of both defensive (avoidance) and appetitive (reach-to-grasp) actions on nearby objects. This evidence demonstrates how multi-sensory-motor systems may process hand-related visual inputs within just 70 ms following a sudden event, and before the execution of a grasping action. I'll then present data showing that other people's actions can induce in the observer not only a motor resonance, but also a resonance of the multisensory perceptual consequences of the observed action. Intriguingly, this effect appears dependent on the observer's prior actual experience, suggesting a differential role for enacted vs. merely potential actions in the subject's sensorimotor repertoire.

Overall, previous and on-going work in our laboratory indicate that performing actions induce a fast remapping of the multisensory peripersonal space, as a function of on-line sensorimotor requirements, thus supporting the hypothesis of a role for peripersonal space in the generation and control of rapid hand-centred avoidance and acquisitive actions.

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### **Multisensory perception for action: the monkey medial parietal cortex**

*Patrizia Fattori*

*Universita di Bologna, Italy*

In the posterior parietal cortex (PPC) different sensory signals converge and coexist with motor-related signals to accomplish several functions, one of which is the control of prehension. The medial PPC is composed by a constellation of areas collectively involved in the visuo-somato-motor transformations necessary for controlling goal-directed actions.

Visual information is processed for the purpose of reconstructing space, so to correctly guide reaching movements. Also visual information related to graspable objects is processed in medial PPC, so to correctly shape the hand when grasping different objects, or objects differently oriented in the peripersonal space: object encoding reflects representations for action, useful for motor control in reach-to-grasp actions.

Somatosensory information, such as tactile and proprioceptive signals from the upper limbs, is encoded in medial PPC for monitoring arm actions. Vergence and version signals are encoded too, and are integrated with corollary discharge signals coming from premotor structures, so to control movement online when it unfolds.

The presence of multisensory inputs and action-related signals in medial PPC allows the gradual coordinate transformations necessary to transform retinocentric visual information about target locations in body-centred coordinates necessary to correctly perform prehension.

In summary, medial PPC is involved in the visuo-oculo-somato-motor transformations useful for arm and hand actions in 3D space.

**Degraded coupling between head and body reference frames optimizes integration between subjective visual and haptic verticals**

*Lindsey E. Fraser, & Laurence R. Harris*

Clemens and colleagues (2011) proposed a model where the head and the body form two separate references for the direction of gravity. Information is shared between these two references by converting gravity estimates in one into the coordinates of the other via perceived head-on-body position. The authors show the subjective visual vertical (SVV, determined by aligning a visual probe to gravity vertical) accesses the head-based gravity estimate. Here and elsewhere we argue that the subjective haptic vertical (SHV, aligning a tactile probe) accesses the body-based estimate. We hypothesize that shared information between head and body may prevent optimal integration of SVV and SHV. Sixteen participants lay on their left side at 45° and judged the SHV, the SVV using a sharp or blurry rod, and two bimodal conditions (SHV + sharp or blurry). A maximum likelihood estimate function well predicted within-subject accuracy but not within-subject precision in the bimodal conditions. Curiously, blurring the visual stimulus reversed the bias in SVV from an A-effect (in the direction of tilt) to an E-effect (away from tilt). A subset of participants returned at least a month later and performed the SHV, SVV (blurry) and bimodal (SHV + blurry) tasks with vibration applied to the upper dorsal neck. Applying vibration in this way disrupts the head-on-body estimate, thus decoupling head and body and facilitating optimal integration. A maximum likelihood estimate function predicted both within subject accuracy and, now, within-subject precision in the bimodal condition, providing supporting evidence for Clemens’ two-frame model and differential access of sight and touch to gravity estimates. Results for the SHV + vibration also provide additional support for a “head-body-aligned” prior.

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**Defining Gravity: Differences in judging verticality by sight or touch**

*Lindsey E. Fraser, Bobbak Makooie & Laurence R. Harris*

There are many scenarios in which we need to be able to tell how gravity acts on objects in the world. We can measure this ability by asking participants to judge if a stimulus rod is tilted left or right of gravity, and defining perceived gravity vertical as the angle at which participants respond “left” and “right” equally. During whole body roll of 45°, participants’ visually perceived vertical (a.k.a. subjective visual vertical) tilts in the direction of roll; perceived tactile vertical (subjective haptic vertical) may be either accurate, or tilted slightly opposite to the roll. Why might these two estimates of the same thing be different? Clemens and colleagues (2011) proposed a model for gravity perception where both the head and the body form separate internal references for the direction of gravity, and information is shared between references via a head-on-body estimate. While sight-based verticality estimates have been shown to rely primarily on the head, we argue touch-based verticality estimates rely primarily on the body. Thirty-two participants were randomly assigned to either a group where vestibular noise was created via galvanic vestibular stimulation (GVS) or a control group. All participants made orientation judgments of a test rod by sight or touch. Judgments were made in with either the head upright and body tilted leftward 45°, or body upright with head tilted 45°. Results show a differential effect of posture on sight versus touch. Data are largely consistent with our hypothesis that touch uses the body as a primary



reference for the direction of gravity, but necessitate the addition of a “head-body-aligned” prior to explain why touch estimates are skewed when only the head is tilted, and skew further when GVS is applied.

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**Infants’ visual discrimination of objects in two and three dimensions.**

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One important ability for acting successfully upon the visual world around us is the ability to visually discriminate between real 3D objects and 2D photographs of those objects. For an adult, this discrimination seems to be rather easy as we would, for example, never try to drink out of a depicted coffee cup. Furthermore, Snow et al. (2011) showed that even within the human brain 3D objects and 2D photographs may be processed differently.

As considerably less is known about when and how infants acquire an understanding of the difference between real 3D objects and 2D photographs of those objects, this study aims to investigate whether this differentiation already exists at the second half of the first year when infants’ 3D vision is developed.

Using the Habituation-Dishabituation Paradigm and measuring infants’ looking times, we first habituated 7- and 9-month-old infants to a three-dimensional object or the corresponding photograph of that object. At test, we presented the 3D and corresponding 2D stimuli as pairs. We predict that infants show early indicators of understanding relevant differences between 3D and 2D objects. More specifically, we expect that infants’ habituation to 2D objects differs from the habituation to the corresponding 3D objects and that infants prefer to look at 3D objects. In addition, we hypothesize that infants grasp more precisely for the 3D objects than for the 2D objects. We assume that young children will make more reaching attempts to real objects than 2D objects especially when placed within reach compared to beyond. All in all, the results of these studies will allow us insight into the developmental origin of the understanding on the difference of 3D and 2D objects.

Snow JC, Pettypiece C, McAdam TD, McLean AD, Stroman PW, Goodale MA, Culham JC (2011) Bringing the real world into the fMRI scanner: Repetition effects for pictures versus real objects. *Scientific Reports* 1:130.

## **Neural theory for the visual processing of goal-directed actions**

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The visual recognition of biological movements and actions is a centrally important visual function, involving complex computational processes that link neural representations for action perception and execution. This fact has made this topic highly attractive for researchers in cognitive neuroscience, and a broad spectrum of partially highly speculative theories have been proposed about the computational processes that might underlie action vision in primate cortex. Additional work has associated underlying principles with a wide range of other brain functions, such as social cognition, emotions, or the interpretation of causal events. In spite of this very active discussion about hypothetical computational and conceptual theories, our detailed knowledge about the underlying neural processes is quite limited, and a broad spectrum of critical experiments that narrow down the relevant computational key steps remain yet to be done.

I will present a physiologically-inspired neural theory for the processing of goal-directed actions, which provides a unifying account for existing neurophysiological results on the visual recognition of hand actions in monkey cortex. At the same time, the model accounts for several new experimental results, where a part of these experiments were motivated by testing aspects of the proposed neural theory. Importantly, the present model accounts for many basic properties of cortical action-selective neurons by simple physiologically plausible mechanisms that are known from visual shape and motion processing, without necessitating a central computational role of motor representations. We demonstrate that the same model also provides an account for experiments on the visual perception of causality, suggesting that simple forms of causality perception might be a side effect of computational processes that mainly subserve the recognition of goal-directed actions. Finally we also will point to possible extensions of the model that might provide a useful theory to address the neurodynamics of the representation of body actions, and associated perceptual organization phenomena.

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## **Goal-directed action: combining eye and head movements for gaze shifts**

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When we look from one visual target to the next, we rapidly shift our gaze by performing a highly coordinated turning movement of the eyes, the head, and often also the body. Here we will use eye-head gaze shifts as example to show how the brain controls goal-directed multi-segment action. We argue that the highly stereotyped nature of eye-head gaze shifts is a result of minimizing the combined impact of signal-dependent and constant noise on the between-trial post movement variability (Saglam et al. 2011). The properties of the movement depend strongly depend on limb dynamics, which rules out some of the previously proposed optimization criteria.

We further show that not only gaze shifts of healthy subjects can be conceived as resulting from solving an optimization problem, but that patient data can as well be seen as optimizing costs under specific constraints dictated by the condition. This view allows evaluating the role of sensory vestibular information and of the cerebellum for movement planning and control (Saglam et al. 2014). Finally we propose how sensory feedback, efference copy, and feed-forward control might interact to allow efficient gaze control.

Supported by the German Federal Ministry of Education and Research (Grant 01 EO 0901)

Saglam M, Lehen N, Glasauer S. Optimal control of natural eye-head movements minimizes the impact of noise. *J Neurosci* 31: 16185-16193, 2011

Saglam M, Glasauer S, Lehen N. Vestibular and Cerebellar Contribution to Gaze Optimality. *Brain* 137:1080-1094, 2014

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### **Development of cerebellar function in *Xenopus laevis***

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The cerebellum plays an important role in assisting gaze stabilization and in the adaptive plasticity of eye movements during visuo-vestibular mismatch. To test this connectivity the dynamics and properties of eye movements of *Xenopus laevis* in semi-intact preparation were studied. The functionality of this circuitry was tested using optokinetic, pharma-physiological and removal (cerebellectomy) experiments. The optokinetic experiments show a decrease in gain during shunting-off of the *an*el<sub>e</sub>-ocular reflex (VOR), due to a mismatch with retinal image slip signals. During electrophysiological recordings, an increase in the firing rate of the trochlear nerve was observed after cerebellectomy and drug injection of *w*-agatoxin, indicating the presence of functional connections within the VOR circuitry. Ongoing physiological experiments will test the functional role of the cerebellum for the spatio-temporal precision of reflexive and voluntary eye movements.

The relatively simple structure of the cerebellum in amphibians facilitates morpho-physiological analyses of the developmental events that control the formation of afferent connections from the sensory periphery and the establishment of Purkinje cell projections to brainstem gaze control networks. Here, we studied the progression of cerebellar circuit formation during the ontogeny in *Xenopus laevis*. The immunoreactivity for the calcium-binding protein Calbindin-D28k, which specifically identifies cerebellar Purkinje cells, was examined at different larval stages and in adults in combination with labeled VIIIth nerve terminations in the cerebellum. Between stage 47 and stage 55 a considerable augmentation of Purkinje cells in the corpus cerebelli was observed with a further increase after metamorphosis. In addition, the layering of the cerebellum matures during the early larval period to reach adult appearance between stage 52 and 55. Simultaneously, the projection density of vestibular nerve afferents increased continuously during larval development. Further experiments will reveal potential regional differences in terminal distributions of afferent fibers in the cerebellum with respect to their peripheral labyrinthine origin. These results suggest that the cerebellar influence on eye movements might occur early during ontogeny.

### **Multisensory Integration and Action**

*Laurence Harris, Adria Hoover, Michael Carnevale, Vanessa Harrar, Michael Jenkin*

I will review some of the reasons that multisensory integration is important for survival by ensuring that redundant cues such as to location or object properties are used optimally. Multisensory integration can also make up for the inadequacies of some senses such as the inability of the vestibular system to convey velocity or position information or vision to convey accurate timing. I will give examples of multisensory interactions in motion perception (e.g., visual-tactile apparent motion andvection) and in movement control. Movement control requires knowing about yourself – identifying that it is your hand and body, your orientation and the arrangement of your body parts. One cue to ownership is the correspondence between making and seeing a movement. I will show how ownership can be quantified and how it can be affected by an unexpected source. I will describe how one’s perception of orientation depends on integrating visual, body, and gravity cues and how this can be affected by exposure to microgravity. Lastly, I will address cross-modal correspondences between apparently unrelated stimuli received by different modalities at least some of which may be related to natural statistics in the world. I will address the question of the frames of reference in which they may be coded.

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### **Expect to be distracted: Motor predictability attenuates irrelevant singleton interference in visual search**

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Irrelevant singleton items are known to be able to negatively affect performance in a parallel visual search (e.g., Theeuwes, 1992). One possible reason for that is that the shifts of attention are purely bottom-up driven so that attention goes first to the most salient item (Theeuwes, 2010). Another possibility is the influence of various top-down influences, one of them being that attention is more likely to be shifted to unexpected items in our visual world than to the expected ones. According to recent theories of motor cognition, the motor system routinely predicts the sensory effects of our actions (Jeannerod, 2006). To further investigate action-effect processing in the visual modality, we used an additional singleton task with only briefly presented displays and accuracy as the sole measure. In the baseline condition, we found an interfering effect of the distractor which was largest if both the target and distractor occupied the same visual hemi-field. When the distractor’s presence and location was endogenously cued its influence was reduced, although not significantly. The effect was similar regardless of laterality. The last blocked condition was preceded by a phase in which the associations between an action and a distractor location and presence were learned. The motor predictability of the distractor resulted in a reversed pattern of accuracy compared to the baseline: when occupying the same hemi-field as the target the distractor did not produce any interference as opposed to it being in the opposite hemi-field. These results suggest that previously learned sensorimotor contingencies can influence visual perception already in the short time window of 205 ms of stimulus presentation on average.

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Theeuwes, J. (1992). Perceptual selectivity for color and form. *Perception & Psychophysics*, 51(6), 599–606. doi:10.3758/BF03211656

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## Action prediction of deceptive and non-deceptive \_aniel\_e\_ in sports-related environments

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The ability to judge a movement as deceptive or not plays a crucial role in high-skilled sports performance where motor expertise allows to deceive in an accurate manner. Thus, it is important to recognize the outcomes of an opponent's movement at an early stage, in particular for deception. To our today's knowledge we know that among others the expertise advantage in general anticipation tasks is determined by the ability to pick up relative motion information such as kinematics (Williams et al., 2011). However, there are no conclusive evidences which identify the critical movement features for decision-making in predicting movements either as deceptive or as non-deceptive. This identification seems to be important for team ball games where 1 vs. 1 situations and deceptive \_aniel\_e\_ are ever-present.

On this background, we plan to investigate which are critical movement features for the prediction of deceptive and non-deceptive 7-meter throws in team handball by manipulating the kinematics of 3D-video stimuli produced by motion capture techniques. Because of the importance of a perception-action-coupled response, goalkeepers should give there judgement in form of a "whole body movement". Our stimuli manipulation will be based on a biomechanical analysis of captured 7-meter throws in a realistic situation during a first experiment (Troje, 2008). As we additionally capture the goalkeeper reaction in this experiment we expect new findings by relating the goalkeeper's reactions to the time sequence of the fieldplayer's throws. With these kinds of natural movement settings we expect new insights into the effects of action prediction in sports.

Troje N (2008) Retrieving information from human movement patterns. In: *Understanding events: How humans see, represent and act on events* (Shipley TF, Zacks JM, eds), pp308-334. New York: Oxford UP.

Williams MA, Ford PR, Eccles DW, Ward P (2011) Perceptual-cognitive expertise in sport and its acquisition: Implications for applied cognitive psychology. *Appl Cognitive Psych* 25:432–442.

## **Internal attention and the maintenance of information in visual working memory**

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It has recently been shown that visual working memory can be dynamically modulated according to changes in the relevance of maintained items. This is achieved by internally orienting attention towards specific representations. The present study used behavioural measures and event-related potentials (ERPs) to investigate the mechanisms underlying this modulation of the maintenance of information. Participants performed a visual working memory task, in which attentional orienting during maintenance was manipulated by presenting two successive retrocues. These retrocues provided spatial information as to which items were most likely to be probed, leading to a cueing benefit. Results confirm that representations can be flexibly adjusted according to changing task goals, and strongly support the idea that no longer attended items are not discarded, but that internal attention serves to protect focused items from decay. Analysis of ERPs revealed that the benefit for focused items increases with higher individual efficiency of attentional selection. The present findings provide new insights into the way in which attention and working memory interact in order to cope with a constantly changing environment and into how an update of representations is obtained.

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## **Multimodal representation of target trajectory in space**

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During the execution of smooth pursuit eye movements, the retinal image of the tracked target remains stationary near the fovea whereas the image of a structured background moves at eye speed in the opposite direction. Nevertheless, motion perception of the subject is just opposite to the retinal motion signals: the target is moving whereas the background is stationary. The reference principle is able to explain this perception by the presence of an efference copy or corollary discharge signal (Sperry, 1950; von Holst and Mittelstaedt, 1950).

We recorded single-unit activity recorded from the middle temporal (MT) and medial superior temporal area (MST) of macaque monkeys performing various pursuit tasks and vestibular-ocular reflex. A distinct group of neurons located in the lateral part of area MST showed pursuit-related activities which reflected extra-retinal signals related to the executed eye movement as well as head velocity signals. So rather than signaling object image motion on the retina, these neurons represent object motion in world-centered coordinates based on the combination of the retinal slip, eye and head velocity (Ilg et al., 2004).

In addition, area MST is not only involved in the generation of smooth pursuit eye movements. The results of microstimulation experiments and inactivation studies reveal that area MST is also involved in the generation of visually guided hand movements (Ilg and Schumann, 2007). The representation of object motion in world-centered coordinates may simplify the coordination of various object-directed actions and ego motion-invariant visual perception.

Ilg UJ, Schumann S (2007) Primate area MST-I is involved in the generation of goal-directed eye and hand movements. *J Neurophysiol* 97:761-771.

Ilg UJ, Schumann S, I P (2004) Posterior parietal cortex neurons encode target motion in world centered coordinates. *Neuron* 43:145-151.

Sperry RW (1950) Neural basis of the sponateous optokinetic response produced by visual inversion. *Jcomp Physiol* 43 483-489.

Von Holst E, Mittelstaedt H (1950) Das Reafferenzprinzip. *Naturwissenschaften* 37:464-476.

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**Changes in camera elevation dictate perceived facing direction of depth-ambiguous biological motion stimuli**

*Kenny, S. & Troje, N. F.*

The degree of perspective distortion of an object depends on the ratio of its size to its distance from the rendering camera (the field-of-view, FOV). Previously, researchers have reported that sufficient amounts of linear perspective can disambiguate the direction of an otherwise depth-ambiguous point-light display (e.g., Schouten & Verfaillie, 2010). We hypothesized that this finding is not based on linear perspective per se, but on an a priori bias to see the walker’s feet from above rather than below. We first found evidence that the effect of FOV on the FTV bias is modulated by the height of the camera above ground (Troje, Kenny, and Weech, 2013). We demonstrated that the effect of FOV on perceived facing direction is modulated by camera height, which incidentally affects camera elevation at threshold, as estimated by staircase procedures. Here, we test explicitly if the previously reported effects of linear perspective are caused by camera elevation changes that pit a facing the viewer bias (FTV) against a very strong viewing from above bias. We asked participants to indicate the perceived facing direction of point-light displays, and modified the camera elevation according to a staircase procedure targeting the 25%, 50% and 75% FTV thresholds. Camera elevation caused large changes in perceived facing direction at the three FTV bias thresholds. Increasing amounts of negative elevation, below the horizontal plane, led to the perception of point-light displays as facing away from the viewer. Most importantly, the resulting psychometric function is identical to those obtained with linear perspective methods that incidentally modify camera elevation (Troje, Weech, & Kenny, 2013). We argue that camera elevation, not linear perspective, produces the previously observed modifications of the facing-the-viewer bias of depth ambiguous point-light walkers.

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## Reaching for eggs and butter – Integrating spatial reference frames in natural scenes

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When interacting with objects in daily life situations, our brain can rely on information represented in two main classes of reference frames; an egocentric (relative to the observer) and an allocentric (relative to objects or the environment) reference frame. So far, most studies investigating how different reference frames are used to guide actions rely on simple and abstract stimuli lacking of ecological relevance.

We conducted two studies which aimed to examine the use of reference frames for reaching in naturalistic visual scenes. Subjects freely viewed a breakfast scene containing 6 objects on a table (local objects) and 3 or 5 objects in the environment (global objects) on a computer screen. After a 2s delay (grey screen) the same scene reappeared for 1s (test scene) but with one local object missing (target). Then the test scene vanished and a grey screen was shown again prompting the subject to perform a reaching movement towards the remembered location of the target. To manipulate the allocentric information derived from the objects in the scenes, 1, 3 or 5 local objects or 1, 3 or 5 global objects in the test scene were shifted horizontally either to the left or to the right. In one study, the global object shifts were combined with a shift of all local objects either in the same or in the opposite direction.

We found that reach endpoints deviated from the actual target location in the direction of the object shifts and varied as a function of the number of local objects shifted. Small effects of global object shifts occurred only when they were paired with local objects shifted in the same direction. Effects of global object shifts without a shift of local objects or with a shift of local objects in the opposite direction were negligible. Our results suggest that beyond egocentric information allocentric cues substantially contribute to reaching movements, but only if they are task-relevant, i.e. (local) objects in the scene which function as potential reach targets.

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## Learned control over spinal nociception in chronic back pain patients

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The descending pain inhibition is a top-down system exerting powerful endogenous pain inhibition. It originates in the brainstem and sends serotonergic and noradrenergic descending pathways to the spinal dorsal horn, where they inhibit spinal nociceptive transmission and therefore reduce the amount of nociceptive information ascending to the brain. The brainstem centers that are at the origin of descending inhibition are targeted by cortical regions like the



prefrontal cortex and the anterior cingulate cortex, and are susceptible to modulation by cognitive and emotional processes.

A method to measure spinal nociceptive transmission in humans and quantify the effects of the descending pain inhibition is the spinal withdrawal (RIII) reflex, which can be recorded in the thigh after painful electrical stimulation of the sural nerve at the ankle. In previous studies, we showed that young healthy subjects could learn to use cognitive-emotional processes to suppress their spinal nociception to 65,9% when receiving feedback on the size of their RIII reflex, likely by learning to deliberately activate their descending pain inhibition. Subjects that did not receive feedback could suppress their reflex to 88,3%, and subjects that received sham feedback were able to decrease it to 96,6% (n = 15; Ruscheweyh R, Weinges F, Schiffer M, Bäuml M, Feller M, Krafft S, Straube A, Sommer J, Marziniak M; Learned control over spinal nociception as quantified by the nociceptive flexor reflex [RIII reflex], submitted to the European Journal of Pain, in revision). Chronic pain patients exhibit an impaired descending pain inhibition, which is thought to be an important factor in maintenance of the chronic pain state.

In the present study, we therefore investigated if chronic back pain patients are also able to learn using cognitive-emotional strategies to suppress their spinal nociception under feedback of the RIII reflex. If yes, this approach may be used to improve descending pain inhibition in chronic pain patients.

Patients were trained in three sessions. The RIII reflex was recorded every 8-12 s, and patients received immediate feedback on their RIII reflex size on a separate monitor. During a defined time window, patients had the task to use cognitive-emotional strategies of their choice to reduce the RIII reflex size. Additionally, we recorded somatosensory evoked potentials (SEP) and documented the subjective pain sensation. Currently, seven patients have been trained to reduce their RIII reflex. In session 1, the patients achieved an average RIII-suppression to  $94,4 \pm 2,8\%$  (n = 7). In session 2, they could already further decrease it to  $84,7 \pm 1,8\%$  (n = 7). Finally, in session 3, the patients were able to suppress their RIII-reflex to  $81,9 \pm 2,2\%$  (n = 6). Hence, these preliminary data suggest that chronic pain patients are able to learn control over their spinal nociception when they receive feedback about it, but the extent of reflex reduction achieved seems to be smaller than in young healthy subjects. It remains to be determined if the feedback training has an effect on the patients' experimental and clinical pain and on SEP.

Consequently, this feedback training might be useful to enhance endogenous pain inhibition in chronic pain patients.

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### **Unequal but fair? Weights in the serial integration of haptic texture information**

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The sense of touch is characterized by its sequential nature. In texture perception, enhanced spatio-temporal extension of exploration leads to better discrimination performance due to combination of repetitive information. We have previously shown that the gains from additional exploration are smaller than the Maximum Likelihood Estimation (MLE) model of an ideal observer would assume. Here we test if this suboptimal integration can be explained by unequal weighting of information. Participants stroke 2 to 5 times across a virtual grating and judged the ridge period

in a 2IFC task. We presented slightly discrepant period information in one of the strokes in the standard grating. Results show linearly decreasing weights of this information with spatio-temporal distance (number of intervening strokes) to the comparison grating. For each exploration extension (number of strokes) the stroke with the highest number of intervening strokes to the comparison was completely disregarded. The results are consistent with the notion that memory limitations are responsible for the unequal weights. This study raises the question if models of optimal integration should include memory decay as an additional source of variance and thus not expect equal weights.

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### **Adaptation behavior during skill acquisition and the influence of the training schedule on intermanual transfer in the cart-pole balancing task**

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A current topic in motor learning is how multiple learning and control mechanisms interact to produce overall improvement. In this study, we examined the influence of different training schedules on reward based motor learning and the intermanual transfer subsequent one-handed training for the acquisition of the cart-pole balancing skill.

We examined 30 right-handed subjects in the computer-simulated cart-pole balancing task. Continuous lateral forces were applied by the subjects to the cart using a joystick-like device in order to balance a pole which is attached to the cart. Using this setup we can not only measure improvements in task performance but also changes in the timing of subjects' actions. In the presented experiment subjects trained for 90 minutes using their right hand and switched afterwards for 30 minutes to the left hand. We tested two training schedules for right-handed training: (i) gravity was gradually ( $g_{inc}=0.1$ ) increased after every successful trial, starting on  $g_0=1.0m/s^2$  up to a maximum level of  $g_{max}=3.5m/s^2$ ; (ii) subjects started directly on the maximum gravity level ( $g_{max}$ ). Trials were counted as successful, if the pole angle and cart position remained within the valid ranges for 30 seconds. In addition to trial success or failure, subjects received up to 10 points per second depending on the system state and applied force. During the post-training phase gravity was constant ( $g_{max}$ ). We analyzed subjects' performances during right-handed training and the timing of their actions as function of the system state and time. Subjects' left-handed performance has been analyzed as function of time and compared between groups.

The analysis revealed typical adaptation behavior in group (i) during right-handed skill acquisition. Hence, we observed a gradual increase in performance during phases of constant gravity but an instantaneous drop in performance after every change in gravity. Accordingly, we found that the timing of subjects' actions got worse (less predictive) after every gravity increment and recovered

during phases of constant gravity. Preliminary analysis of intermanual transfer shows that subjects in the constant gravity condition (group ii) transfer the balancing skill immediately and do not further improve during the 30 minutes of left-handed examination. Subjects in the gradual gravity condition (group i), however, improve significantly during this phase. This might be a sign for different learning mechanisms and representations being activated by the two training schedules which are distinguishable by the extent of intermanual transfer they allow.

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### **Shifts of attention in video game players and non-players**

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Video games are a widespread leisure activity but their behavioral effects are still heavily debated. Negative outcomes like increased aggressive behavior (Anderson et al., 2010) have been shown as well as beneficial effects like faster reaction times (Hubertus-Wallander et al., 2010).

Previously, we found shorter saccadic reaction times in video game players (VGPs) in an oculomotor task. In a follow-up study we used a cued visual attention task (Nakayama and Mackeben, 1989) with varying cue lead times (CLTs) to monitor the time course and benefit of shifting attention towards a cued location. We hypothesized that VGPs shift their attention faster than non-VGPs, which should lead to a superior performance and an earlier CLT of peak performance in these subjects. As expected, VGPs performed better. However, they did not differ from non-VGPs in their CLT of peak performance. Our results suggest that VGPs do not shift their spotlight of attention faster but that they assess stimulus properties more efficiently. Therefore, they acquire more information in the same amount of time than non-VGPs, which in turn leads to a more informed decision, and thus, a superior performance.

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Hubertus-Wallander B, Green CS, Bavelier D (2010) Stretching the limits of visual attention: the case of action video games. *WIREs Cogn Sci*.

Nakayama K, Mackeben M (1989) Sustained and transient components of focal visual attention. *Vision Res* 29:1631-1647.

**Vestibular-motor integration during self-motion perception. In two recent studies we explore the idea that motor signals may be used alongside vestibular sensory signals to estimate self-motion**

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The first study looks at the contribution of eye movements. As we move through the world we usually move our eyes to maintain fixation on objects of interest. However the consequences of these fixation eye movements for self-motion perception remain unclear. To investigate this question, we compared perceived displacement across world-fixed, body-fixed and free fixation conditions. Displacement was underestimated in the body-fixed condition, in which the eyes remain stationary, compared to the world-fixed condition, in which the observer must move the eyes to maintain fixation. Both eye movements and perception were intermediate during free fixation. Furthermore, perceived displacement was greater with near (50 cm) than with far (2m) world-fixed targets, consistent with the increased version eyemovement required to maintain near versus far fixation. Overall, larger eye movements were associated with larger perceived displacements.

The second study examines the possible role of locomotor signals. There is accumulating evidence that vestibular afferent signals are partially or fully suppressed during locomotion and that the suppressed signals are supplemented or even replaced by predictive signals based on efference copies of motor commands for locomotion. The value of this periodic and presumably deterministic efference copy for estimating head motion should depend critically on the stereotypy or predictability of the resulting head motion. Here we express this intuition quantitatively in the form of a statistically optimal model in which relative weight given to efference copy and sensory signals depends on motor predictability. We empirically quantify this predictability during human locomotion (running, walking, and walking stairs) by measuring head motion with an inertial measurement unit (IMU), and calculating the variance explained by the stride-cycle attractor (i.e. the mean stride-cycle). Head motion predictability is greater during running than during walking, such that efference copy signals should be upweighted and vestibular signals downweighted during running compared to walking. This coincides with reports that impairment of patients with vestibular dysfunction and of normal subjects with vestibular perturbations is less during running than walking. The model is general and applies to any situation in which achieved movement is estimated from both efference copy and a zero-mean sensory signal with signal-dependent noise.

## **Reward directly modulates perception in binocular rivalry**

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Binocular rivalry is a situation in which distinct stimuli presented to both eyes evoke alternating perceptual interpretations. Since value can have a direct impact on perception, we here investigated the effect of reward and penalty on the dynamics of binocular rivalry. Therefore we tested whether associating one stimulus with reward or penalty while keeping the other neutral modulates dominance durations.

We used gratings of different color (red/green) drifting in opposing directions to induce binocular rivalry. To ensure a veridical measure of observers' perceptual experience, we monitored their eye movements and used the direction of the slow phase of the optokinetic nystagmus (OKN) as objective measure of the currently dominant percept. Reward was \_aniel\_e\_ by a blue annulus encircling the grating that grew wider when the rewarded stimulus was perceived.

We found that if a percept is rewarded, dominance increases relative to the other percept. Since effects of reward were comparable to asking observers to attend one stimulus, we performed a second experiment aimed at dissociating effects of attention and value. Again we associated one percept with reward and, additionally, in half of the trials one percept was associated with penalty. At the same time observers were asked to perform an attentional demanding task either on the rewarded stimulus, the other stimulus or both. Participants had to detect changes in the duty-cycle of the respective grating, sufficiently subtle to not by itself cause a switch in dominance. We find that for constant attentional load (e.g., percept attended) reward still modulates perception, such that it is unlikely that the effect of reward is mediated by attention alone.

This demonstrates that associating a perceptual interpretation with value has a direct impact on perceptual representations even if the stimulus itself is constant.

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## **Effects of visual attention on perceptual and movement performance during saccade preparation**

*Tobias Moehler & Katja Fiehler*

*Experimental Psychology, Justus-Liebig-University, Giessen, Germany*

The present study investigated the coupling of selection-for-perception and selection-for-action during saccade preparation. Previous work yielded conflicting results if visual attention is locked at the saccade target during saccade preparation. Furthermore, studies on the effects of visual attention on movement performance are rather scarce when compared to the amount of studies on the effects of visual attention on perception. We employed dual-task experiments in which participants performed a visual discrimination task while they prepared a saccade. In order to investigate the effects of spatial congruency and movement preparation time on perceptual and movement performance, we varied the spatial congruency between saccade target location and discrimination target location and the time between saccade target cue and Go-signal. Spatial congruency of saccade target location and discrimination target location resulted in enhanced perceptual performance; however, perceptual performance in the incongruent condition was

clearly above chance level. Movement preparation time did not influence perceptual performance. Accuracy and precision of saccades were also affected by spatial congruency but not by movement preparation time. Saccade latency declined with increasing movement preparation time. Saccade curvature, a measure sensitive to attentional allocation in space, systematically varied for each saccade target location with the location of the discrimination target. We found that saccades curved away from the incongruent discrimination target location relative to saccades in the congruent condition. Our findings suggest that attention can be distributed upon saccade target location and discrimination target location in incongruent trials and thereby affects perceptual and movement performance in dual-task situations. Saccade curvature away from attended locations can be explained by the suppression hypothesis, derived from the premotor theory of attention, and by population coding accounts assuming that a prepared but unexecuted saccade plan to the discrimination target location influences the actual saccade plan to the saccade target location via inhibitory mechanisms.

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### **Cortical substrates for the integration of object properties and intended actions**

*Simona Monaco, Ying Chen, J. Douglas Crawford*

Object directed actions require the integration of object properties into the action to be planned. Although the parieto-frontal network has been shown to be involved in both the processing of visual object information and effector-specific actions, it is not known which of the components of this network are involved in the integration of these two processes. We used a slow event-related fMRI design to investigate the neural circuits involved in the integration of object properties and hand actions. In particular, we exploited a cue-separation task based on a neurophysiology study by Baumann and colleagues (2009). Fourteen participants received a visual cue (VC: a 3D wooden rod presented for 250ms in two possible orientations) and an action cue (AC: an auditory instruction to either ‘grasp’ or ‘align’ the hand with the rod) in two successive phases. Each cue was followed by an 8 second delay, with the second delay followed by a go cue to execute the instructed movement toward the rod in complete darkness. We manipulated the order of cue presentation (VC:AC and AC:VC) to test the areas involved in integrating these two processes would show greater activation after the 2<sup>nd</sup> cue presentation, regardless of the order of presentation. In addition, to test the visual field specificity of these processes, we asked subjects to fixate (either to the left or right) during the entire trial; Eye movements and hand motion were monitored and recorded using infrared cameras. We found that supplementary motor area (SMA), dorsal premotor cortex (dPM) and posterior intraparietal sulcus (pIPS) in the left hemisphere showed higher activation during the 2<sup>nd</sup> vs. 1<sup>st</sup> delay phase following the visual cue. Of these areas, pIPS also showed higher activation in the 2<sup>nd</sup> vs. 1<sup>st</sup> delay phase following the action cue. No visual field specificity was observed in any of these areas. These results suggest that SMA and dPM process visual information about object properties when an action type has already been specified. In addition, pIPS plays a role in the integration of object properties and action type regardless of the order of their presentation.

## **Visual and tactile clocks are synchronized by the motor system?**

Maria Concetta Morrone

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The perception of space and time are generally studied separately and thought of as separate and independent dimensions. However, recent research suggests that these attributes are tightly interlinked: event timing may be modality-specific and tightly linked with space and to the intention to perform an action. In this talk I will review the evidence that supports the idea that time mechanisms are closely related to coordinate frames of reference of the motor, visual and haptic systems.

During saccadic eye movements, time becomes severely compressed, and can even appear to run backwards. Adaptation experiments further suggest that visual events of sub-second durations are timed by neural visual mechanisms with spatially circumscribed receptive fields, anchored in real-world rather than retinal coordinates. Interestingly similar phenomena take place for tactile time intervals. Perceived duration of haptic stimuli is prone to compression after adaptation. Interestingly the compression is not specific to the sensor position, nor to the object position in space, but the effect is annulled by performing a voluntary action. As for vision, tactile time intervals are strongly compressed around the time of hand movements. The time compression began approximately 200 ms before movement onset, it increased up to 30 % until just before the hand started moving and continued until the end of the movement. As for vision the mislocalization of time and space of touch stimuli may be consequences of a mechanism attempting to achieve perceptual stability.

These results show that the motor signals has a leading role in the brain time-keeping mechanism. But how can the motor system govern the time synchrony?

I will show that performing an action can generate rhythmic oscillations of visual contrast sensitivity, a property that is determined at very early levels of cortical visual analysis, probably V1. Interestingly, the synchronized oscillations in visual sensitivity began before movement onset, suggesting that a motor preparatory signal might be responsible for synchronizing activity in primary visual areas. The results suggest that sensory-motor integration might be, at least partly, mediated by phase modulations of brain rhythmic activity. We postulate that the synchronized oscillatory performance may be instrumental in temporally aligning the many sensory inputs that reach perception, with multiple and varying delays due to the property of the various sensory receptors and pathways, and hence synchronizing the various sensory clocks.

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**Generalization of Reach Adaptation and Proprioceptive Recalibration at Different Distances in the Workspace**

*Ahmed A. Mostafa, Rozbeh Kamran-Disfani, Golsa Bahari-Kashani,  
Erin K. Cressman, Denise Y. P. Henriques*

Studies have shown that adapting one’s reaches in one location in the workspace can generalize to other novel locations. Generalization of this visuomotor adaptation is influenced by the location of novel targets relative to the trained location, such that reaches made to novel targets that are located far from the trained target direction (i.e.  $\sim 22.5^\circ$ ; Krakauer et al.(2000)) show very little generalization compared to those that are closer to the trained direction. However, generalization is much broader when reaching to novel targets in the same direction but at different distances from the trained target. In this study, we investigated whether changes in hand proprioception (proprioceptive recalibration), like motor adaptation, generalizes to different distances of the work space. Subjects adapted their reaches with a rotated cursor to two target locations at a distance of 13 cm from the home position. We then compared changes in open-loop reaches and felt hand position at these trained locations to novel targets located in the same direction as the trained targets but either at a closer (10 cm) or farther distance (15 cm) from the home position. We found reach adaptation generalized to novel, closer and farther targets to the same extent as observed at the trained target distance. In contrast, while changes in felt hand position were significant across the two novel distances, this recalibration was smaller for the novel-far locations compared to the trained location. Given that reach adaptation completely generalizes across the novel distances, but proprioceptive recalibration generalizes to a lesser extent for farther distances, we suggest that proprioceptive recalibration may arise independently of motor adaptation and vice versa.

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**Stochastic reference frame transformations add noise to decision making**

*T. Scott Murdison, Hannah Li and Gunnar Blohm*

It is known that reference frame transformations (RFT) induce variability in *perception* and perception in sensorimotor tasks (Schlicht and Schrater 2007; McGuire and Sabes 2009; Burns and Blohm 2010; Burns et al. 2011). Thus RFTs must be regarded as being stochastic in nature. It is unclear whether RFTs also affect decision making, presumably though adding noise/variability to sensory evidence undergoing RFTs. Here, we investigated this effect using a 2-AFC random dot motion direction discrimination reaction time task with the head either straight or rolled to the left or right shoulder. Human participants were asked to detect the direction (left or right) of a randomly selected subset of coherently moving dots, responding either with a left/right saccade or a button press. We created different RFT requirements by either (1) rotating only the on-screen stimulus, (2) rotating only the head, (3) rotating both the head and stimulus together or (4) rotating neither the head nor the stimulus. Compared to no rotations (4), we found that head/target rotations prolonged response latencies by different magnitudes between participants and response types. These variations lay along a continuum of reference frame predictions



between eye- head- and shoulder-centered. Therefore, our findings suggest that the sensory evidence used for the decision is first transformed in a stochastic way, degrading decision making. These data show for the first time that reference frame transformations impact decision making.

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**Direct evidence that spike timing correlations between neurons in lateral prefrontal and anterior cingulate cortex reflect control of attention**

*Mariann Oemisch, Stephanie Westendorff, Stefan Everling, Thilo Womelsdorf*

The neural basis of attentional control encompasses processes that determine which neurons become simultaneously activated in a selective neuronal network to support the processing of relevant stimuli as opposed to those deemed irrelevant. Among others, this flexible control of attention is achieved by functional interactions of cells within segregated areas in the prefrontal cortex (PFC). Previous studies suggest that neuronal circuits within the lateral PFC (areas 46, 8, 9) are responsible for the actual shifting of attention, as well as the implementation of task rules and generation of current goals that guide attention. Circuits within the medial PFC, mainly including the anterior cingulate cortex (ACC, area 24, 32), have been suggested to encode value information of possible attentional targets and may play a role in adjusting activity when task demands or rewards change. It is not yet understood how these diverse and interconnected brain areas integrate and coordinate their attention information. We therefore recorded the spiking activity of >3500 pairs of cells from medial and lateral PFC subdivisions in two macaque monkeys performing a demanding value-based attention task. To investigate functional connectivity between single cells, we implemented a shift predictor-corrected joint peristimulus time histogram (JPSTH) analysis. We show that cell pairs across the PFC significantly increase their correlated spiking activity about 250-550ms after the onset of a symbolic cue that triggers a shift of attention. This increase in correlated spiking activity was independent of the average firing rate of both neurons in a pair, and showed inter- and intra-areal specificity. Significantly increased correlated intra-areal spiking was found for cell pairs from within area 32 and within areas 8/9. Inter-areal correlated spiking was observed for pairs in which one cell was located in areas 8/9 and the second in either ACC or area 32. Increased non-correlated spiking activity was found for cell pairs from within area 46. These results provide the first empirical evidence suggesting that functional interactions of spiking activity in medial and lateral PFC subdivisions supports the flexible control of attention at a time when attention needs to be covertly shifted.

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## High-resolution fMRI phase-mapping of azimuth space in rhesus monkey auditory cortex

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Sound localization is one of the most fundamental tasks performed by the auditory system. In mammals, the location of a sound source in azimuth is mainly determined by interaural time and intensity differences between sounds reaching the two ears. Although binaural sound processing in subcortical structures is well understood, much less is known about the representation of space at the cortical level. In humans, the left auditory cortex (AC) shows a predominant response to sounds in the right hemifield, while the right AC responds to sounds in both hemifields (Krumbholz et al., 2007), with contrast between the two hemifields revealing activation along the dorsal stream into parietal cortex. In the monkey, selectivity of neurons in primary AC for positions in contralateral space has been observed, albeit with broad spatial tuning (Middlebrooks et al., 1994). Spatial tuning sharpens significantly in the caudal belt regions (Tian et al., 2001; Recanzone & Beckerman, 2004), but it is not known whether the preferred azimuth positions form a map of auditory space. Here we attempt to bridge studies across human and nonhuman primates by obtaining a comprehensive overview of the cortical representation of azimuth space in the monkey for the first time using phase-mapping functional magnetic resonance imaging (fMRI).

Sounds were generated in virtual acoustic space and played back via headphones during fMRI. Stimuli consisted of broad-band noise bursts (0.2-16 kHz, 100 ms duration) moving through azimuth in steps of 30° at a rate of 5° per second. They were presented in a sparse-sampling design as a moving wave analogous to methods used in visual field mapping (Wandell & Winawer, 2011). We acquired high-resolution images oriented along the superior temporal plane in two anesthetized monkeys. We then analyzed the BOLD signal amplitude modulation at the frequency of stimulus presentation (12 cycles per scan) to determine voxel coherence and phase values corresponding to the stimulus cycle.

In accordance with prior single-unit studies, a robust contralateral response to azimuth position was observed. The left AC represented mainly the anterior contralateral quadrant, including straight-ahead positions, while the right AC represented both ipsilateral and contralateral space. This hemispheric bias supports previous neuroimaging studies in humans. In addition, it may elucidate the hierarchical processing of space from AC into posterior parietal cortex and the sound localization deficits observed in humans with damage to the right temporo-parietal cortex (Spierer et al., 2009, Rauschecker & Tian, 2000).

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### **A core brain network for strategic decisions**

Parr, A.C., Coe, B.C., Dorris, M.C., & Munoz, D.P.

During competitive social interactions, one's actions and their associated outcomes change dynamically based on the actions of other agents. This often requires that one adopt mixed-strategies to avoid exploitation from opponents; that is, choosing among available actions unpredictably and stochastically. We have previously shown that strategic decision-making is associated with activation of a distributed corticostriatal network in humans; however, the contribution of motor structures to strategic action selection remains unknown. The current study used functional magnetic resonance imaging (fMRI) to dissociate the core regions of a strategic brain network from those involved in controlling specific motor effectors. A colour-based version of the strategic game, Matching Pennies, was played against a dynamic computer opponent that exploited biases in player's response patterns. Participants selected one of two different coloured visual targets, and were rewarded if their selection matched the opponent's. We used a block design, wherein participants indicated their choices with either the eye (saccade) or the hand (button-press). Brain activation during the saccade condition was contrasted with activation during the button-press condition; any difference in response patterns should highlight processes related to controlling individual motor effectors.

Strategic decision-making, *regardless of the effector used*, was associated with activation of a highly distributed network including the head of the caudate nucleus, dorsolateral prefrontal, anterior cingulate, parietal, insular and orbitofrontal cortices. We propose that this network represents the key elements of a functional network underlying strategic decisions. Conversely, we observed activation of cortical motor structures, *depending on the particular effector used* to make choices. Activation of the supplementary motor area (SMA) and the pre-SMA was associated with choices made using a button press, while activation of the frontal eye fields was associated with choices made using a saccade. These results suggest that strategic forms of decisions activate a common brain network, distinct from brain regions involved in controlling specific motor effectors.

### **Getting a grip on different materials**

*Vivian C. Paulun, Karl R. Gegenfurtner, Melvyn A. Goodale, Roland W. Fleming*

A precision grip of index finger and thumb is often used to interact with objects in our environment. To successfully accomplish this everyday task we adapt our grip depending on various extrinsic and intrinsic properties of the object to be grasped. For example, the grasping movement needs to be adjusted if we want to grasp a wooden spoon or a wet bar of soap to provide a stable grip without the object rotating or falling. This adjustment not only depends on object features like shape or size, but presumably also on the visually perceived material the object is made of. We let our participants grasp cylinders of the same size (height: 10 cm, diameter: 2.5 cm) but different materials, i.e. foam, wood and brass as well as an additional brass cylinder covered with \_aniel\_e to make it slippery. These stimuli laid on their long side at six different angles with respect to the participants (0°, i.e. horizontally, 30°, 60°, 90°, 120°, 150° rotated counterclockwise). The task was to grasp, lift and carry the target objects to a goal position and place them there. We found that timing of the movement towards and while holding the cylinders was influenced by its material properties. Reaction time, movement duration to the object, handling and transport duration were on average longer for the slippery cylinder covered with \_aniel\_e. Object orientation appeared to primarily affect spatial characteristics of the movement like position and orientation of the grasp axis. However, these spatial effects were modulated by the material of the target object. Taken together our results imply that the timing and positioning of the precision grip depends on the object’s visually perceived material properties.

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### **Sensory to motor transformation of the spatial codes in the frontal eye field and superior colliculus during the delay period in a memory-guided gaze task**

*Amirsaman Sajad, Morteza Sadeh, Xiaogang Yan, Hongying Wang,  
and John Douglas Crawford*

During the temporal gap (delay period) between target presentation and gaze movement in a memory-guided gaze task, neurons in the primate frontal eye field (FEF) and superior colliculus (SC) often exhibit activity with spatial tuning. Previously, we showed that when macaques perform this task in head-unrestrained conditions, in both structures, the visually-evoked responses encode the location of the visual stimulus and the motor-related responses encode final gaze position (both in eye-centered coordinates). However, it is not well understood what spatial information is encoded during the delay period. To address this question we analyzed the spatiotemporal evolution of the response fields using a method described previously (Keith et al. J. Neurosci. Meth. 2009). Analysis of 48 FEF neurons and 39 SC neurons revealed that, at the population level, as the activity progressed from stimulus- to movement-related response during the delay period, the spatial code in visuomovement neurons (FEF, n =23; SC, n =17) gradually drifted from a target code to a gaze code. A similar trend was also seen in FEF and SC visual neurons (FEF, n =8; SC, n =14) and FEF movement neurons (n =17). However, the SC motor population (n =8) exhibited a stable gaze code even during early delay period. Our results suggest that during the delay period the sensory spatial code gradually converges toward a motor code in

both SC and FEF. These findings reconcile sensory and motor theories of short term spatial memory and point toward specific roles for different cell types in the gaze control system.

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### **Parietal Representations of Egocentric Space include unseen Locations**

*Andreas Schindler & Andreas Bartels*

*Centre for Integrative Neuroscience, Vision and Cognition Group*

Our subjective experience links covert visual and egocentric spatial attention seamlessly. However, the latter can extend beyond the visual field, covering all directions relative to our body. Even with closed eyes we can rotate from the computer screen to face the window with little loss of accuracy, and once rotated we are aware of the computer’s updated egocentric position. It appears thus that our egocentric model includes seen and unseen locations. In contrast to visual representations, little is known about unseen egocentric representations in the healthy brain. Parietal cortex appears to be involved in both, because its lesions can lead to deficits in visual attention, but also to a disorder of egocentric spatial awareness, known as hemispacial neglect. In this study, our participants performed a novel egocentric orientation task inside an octagonal room. Once they were familiar with this setup, we exposed our participants to a virtual version of the same paradigm during fMRI recordings. We found egocentric unseen space represented by patterns of voxel activity in parietal cortex, independent of visual information. Intriguingly, the best decoding performances corresponded to brain areas associated with visual covert attention and reaching, as well as to lesion sites associated with spatial neglect.

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### **Delay-dependent egocentric and allocentric coding in a sequential reaching task?**

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The brain utilizes both egocentric and allocentric information to code target locations for reaching, such as target location relative to current gaze direction and target location relative to external landmarks, respectively (Byrne et al., 2010; Schütz et al., 2013). The use of egocentric and allocentric information in action guidance supposedly also depends on the temporal properties of the task, leading to a switch from an egocentric to an allocentric reference frame for delayed actions (Westwood & Goodale, 2003). While we could not find an effect of delay on reach errors in our previous single-target reaching paradigm (Schütz et al., 2013), the landmarks in this study were task-irrelevant. The goal of the presented study was to extend a sequential reaching task first used by Thompson et al. (2010) by including a delay of 5 or 12 seconds between target presentation and reaching. Since the first target is highly relevant for task execution, we expected a stronger allocentric contribution of the first target to subsequent reaches when movements are delayed.

Subjects reached to two targets in sequence, which were always separated by a constant distance. Before each reach, they performed a gaze shift of 10 or 15 degrees relative to the respective target. We found gaze-dependent reach errors that fell between those predicted by either purely egocentric or allocentric coding, with a stronger contribution of allocentric information. Preliminary results also suggest a stronger influence of allocentric information with longer delays.

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### **Differential organization of extraocular motoneurons for slow and fast phase components of the horizontal optokinetic reflex in *Xenopus laevis***

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During vertebrate locomotion, retinal image displacements are minimized by compensatory eye movements resulting from the activation of visuo-vestibular reflexes. Here, we studied the performance of the optokinetic reflex in *Xenopus laevis* tadpoles. Velocity step and sinusoidal optokinetic stimulation (0.2-50°/s; 0.032-1 Hz) by rotation of a vertically striped drum evoked eye movements in semi-intact preparations with a functional visual system. Eye movements, captured with a camera at 50 Hz, were quantified by computerized video analysis. The optokinetic response of larval *Xenopus* consisted of slow phases with a horizontal ocular motor range of ~50° and a maximal gain of 0.64 at 2°/s constant stimulus velocity. In contrast to the small eye movements in adult frogs, resetting fast phases with a velocity of up to 350°/s regularly interrupted the slow phases. Simultaneous motion recordings of one eye and extracellular multiple-unit recordings of the contralateral extraocular nerves during optokinetic stimulation facilitated direct comparison of motoneuronal commands and effective behavioral output. As the horizontal optokinetic reflex (OKR) with its two phases offers an ideal motor behavior to study the recruitment of different neuronal subunits, we revealed task specific contributions of individual motor units during the different movement components. Single spike analysis, along with the determination of activation thresholds, response properties and discharge regularity, confirmed a differential recruitment of motor units with different discharge behavior and suggests the presence of distinct subgroups

with specific contributions during motor behavior. Accordingly, the analyses revealed a specific extraocular motoneuronal subgroup that was only active during fast phases but not during slow following phases, while other motoneurons fired only during the latter OKR component, although at different thresholds. This presence of differentially operating motoneuronal subgroups provides the essential condition to generate the variety of eye movements elicited by the activation of visuo-vestibular reflexes.

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### **The role of motor timing in the temporal reproduction**

*Zhuanghua Shi*

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The ability of producing temporal patterns is important for our daily activities, such as speech and dancing. An accurate reproduction requires the brain to combine multiple timing sources, including sensory inputs, own active motoric commands, and prior knowledge of related event timing. Considering multiple sources of timing are often perturbed by noise from external environment and internal processing, motor reproduction could be biased and inaccurate. To maximize the reliability of temporal reproduction, the brain must optimally integrate multiple timing signals or calibrate certain timing sources (Shi, Church, & Meck, 2013). This hypothesis is supported by recent several behavioral findings. For example, using explicit sensorimotor duration reproduction we have found the reproduction bias is reduced with an additional auditory feedback signal (Shi, Ganzenmüller, & Müller, 2013). Importantly, the reproduction bias is an optimal weighted integration of biases of the perceptual and motor timing according to the associated precision of the source signals. Moreover, the brain also takes the prior knowledge of motor timing in the temporal reproduction. This has been shown in another recent study, in which we have investigated the influence of the prior on temporal reproduction by training participants to reproduce a given duration and then introducing a delay perturbation in the auditory reproduction. The prior information is dynamically updated with the perturbed delays and integrated in the temporal reproduction, which lends support to Bayesian inference of temporal reproduction.

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**The influence of meaningful hand and arm movements on the neural processing of figurative language – an fMRI study on continuous multimodal perception**

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In addition to speech, meaningful hand and arm movements (gestures) form an integral part of everyday communication. Figurative speech and corresponding gestures are usually understood without any difficulties (e.g. “He eats like a bird”; gesture illustrates pecking). While the processing of either figurative speech or gestures has mostly been studied in isolation, fewer studies have investigated the effect of gestures on the neural processing of abstract, figurative language or the processing of gestures in a naturally evolving language context. To date, no imaging study directly investigated the influence of gesture on the neural processing of figurative speech in continuous story comprehension.

Thus, we conducted an experiment in which 20 healthy subjects watched a video of an actor narrating a short story while performing natural meaningful hand and arm movements (gestures). During the presentation of the video (30 minutes), the participants’ BOLD response was measured with fMRI. Subjects were not asked to perform any specific task aside from listening and watching carefully. The unknown text contained 34 passages with figurative speech represented by an abstract comparison (so-called simile; e.g., “He climbed the tree like a monkey”), half of which were presented with meaningful gestures.

The main effect (Speech+Gesture > Speech Only) as well as the contrast (Simile+Gesture > Simile Only) revealed clusters of increased activation in bilateral temporo-occipital cortices and the right temporo-parietal junction (TPJ).

While the temporo-occipital region is part of a network well-known for its involvement in gesture processing, right TPJ was found to be selectively stronger activated for the Simile+Gesture condition. This result indicates a specific relevance of the right TPJ for the multimodal neural integration of figurative speech and meaningful corresponding gestures in a natural language context. It is speculated that the reported effect is due to higher processing costs for the speech-gesture integration in a simile context, as this requires a transfer of presented visual (action) and auditory (speech) information to the actual person or action referred to in the story. This process is further believed to draw upon different sensory cortices and result in the integration of the gathered information in the temporal lobe, which accords with functions associated with TPJ.



### **Cerebellum and frontal cortex: a relationship?**

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In general most scientists associate the cerebellum with motor functions and motor learning. Beside these functions the cerebellum might have also some non-motor functions.

One argument for linking the cerebellum to cognitive non-motoric functions is based on the observation that the hemispheres of the cerebellum showed an enlargement parallel to the enlargement of the frontal cortex during the evolution. Thus, there is evidence that acute lesions of the vermis can cause an autistic syndrome which can persist for weeks. Otherwise there also now some observations which link the cerebellum to age dependent decline in cognitive as well motor functions. Furthermore, most of the neo-cerebellar projections are organized in recurrent loops across thalamic relay nuclei to the frontal cortex and back.

What can be the general functions of these loops cerebellar frontal loops? In order to elucidate these questions we performed two sets of experiments.

1) Saccadic eye movements, quick conjugated ballistic movements, can be distinguished in reflexive external triggered goal directed and in internal triggered voluntary goal directed saccades. An example for such an internal guided and triggered saccade, which is thought to be mainly under control of the frontal cortex, is a saccade to a memorized target. Patients with focal cerebellar lesions due to an infarction shows abnormalities exact in these internal saccades (memory guided saccades, sequential memory guided and anti-saccades) as well as a general longer reaction time. All together we would interpret this as a sign of a reduced cortical frontal activation by loss of the connections from the cerebellum towards the frontal cortex.

2) Pain perception is classical not devoted to cerebellar function. Interestingly most of the imaging studies in pain perception show a strong and lasting activation of cerebellar structures. Therefore we studied the quantitative sensory thresholds (QST) in patients with cerebellar lesions due to ischemic infarctions as well the reaction towards a placebo intervention. Interestingly, compared to age matched controls, patients after cerebellar infarction exhibited a significantly increased pain perception (hyperalgesia) in response to acute 44-48 °C heat stimuli and to repeated 256 mN pinprick stimuli. In addition, patients showed reduced offset analgesia (change of pain intensity rating:  $0.0 \pm 15.8\%$  vs.  $-16.9 \pm 36.3\%$ ,  $p < 0.05$ ) and reduced placebo analgesia (change of pain intensity rating:  $-1.1 \pm 1.2$  vs.  $-1.7 \pm 1.3$  [0-10],  $p < 0.05$ ). Heat hyperalgesia in patients was more pronounced on the body side ipsilateral to the infarction. These results show that patients after a cerebellar infarction have deficient activation of endogenous pain inhibitory mechanisms. The anterior cingulate cortex in the frontal cortex is one of the main areas involved in the endogenous pain control system, which shows also a decreased activation after cerebellar lesions.

All together we suggest that the neocerebellar lesions cause a reduced activation of frontal cortical areas.

Ruschewyh R, Kühnel M, Filippopolus F, Blum B, Eggert T, Straube A. Altered experimental pain perception after cerebellar infarction.

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### **Effects of action on bistable perception: Re-learning contingencies**

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While our knowledge of the effects of perception on action is relatively deep, the conditions under which action alters perception are less clear. Our experiment investigates how learnt action-perception contingencies affect bistable perception.

From the work of Beets et al. (2010) we know that perception of an ambiguous stimulus can be modified by concurrent manual action, but only when the action is relevant to the perceptual task. Similar to their methods, we use an ambiguous rotating cylinder as visual stimulus. Participants use button presses or manual turntable rotation for reporting the perceived direction of rotation. We introduce ‘*induction*’ sessions between tests, where the rotation of a disambiguated version of the test-stimulus is controlled by manual rotation in a congruent or incongruent manner.

We hypothesize that the perceptual bias caused by manual rotation is a consequence of fixed congruent contingencies between hand movement and viewed rotation. We thus predict that motor learning through training of an incongruent coupling will manifest itself in a change of the perceptual bias.

Beets IA, ‘t Hart BM, Rösler F, Henriques DY, Einhäuser W, Fiehler K (2010) Online action-to-perception transfer: only percept-dependent action affects perception. *Vision Res*, 50(24):2633-2641

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### **Stick figures and point-light displays: Effects of inversion on the facing-the-viewer bias**

*Séamas Weech and Nikolaus F. Troje*

Depth-ambiguous point-light walkers are most frequently seen as facing-the-viewer (FTV). Inverting the figures considerably reduces this FTV bias (Vanrie et al., 2004). The finding has been used to argue that the FTV bias depends on recognizing the stimulus as a person – which is more difficult when the stimulus is inverted. Recent experiments indicate that the FTV bias is largely caused by a bias to perceive depth-ambiguous surfaces as convex (Weech and Troje, 2013). Based on this research, we hypothesized that the effect of inversion on FTV bias arises due to the difficulty with which coherent 3D shape is resolved from inverted point-light walkers. Without this shape, the stimulus appears ‘flat’ and the convexity bias does not play out. If explicit, coherent shape is provided (as in stick figures) we would expect no effect of inversion on FTV bias. We measured the FTV bias in 30 participants for upright and inverted point-light walkers and stick figures. We depicted stimuli at frontal and three-quarter views and recorded observers’ perceived facing directions. We defined the FTV bias as the percentage of responses signaling a facing-towards interpretation. Participants accurately chose one of the two veridical interpretations at a rate of over 95% for both stimulus types. We found an interaction between stimulus representation and orientation: The inversion effect for stick figures (44%) was smaller than that for point-light walkers (55%). This result supports our hypothesis to a limited degree.

Unexpectedly, both stimulus types generated reliable facing-away bias when inverted. Results are consistent with the hypothesis that the lower part of the stimulus takes precedence when subjects are making judgments of facing directions, given that the knees and elbows are opposing in terms of the facing direction implied when assumed to be convex.

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**Modulation of torque response to perturbations by changing feedback gains during arm reaching movements**

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Short latency torque response in arm joints can help minimizing the kinematic consequences of external force perturbations (Zhang et al. 2014) indicating efficient proprioceptive feedback. In the current study, we investigate whether such feedback mechanisms are systematically modulated across the time course of the movement. We measure responses to force perturbations applied at different times during the movement.

We established an experimental apparatus for constraining arm movements on pure elbow flexion-extension around an earth vertical rotation axis. Visual feedback was excluded. During elbow extension (Amplitude: 50 degrees, Peak velocity: 150 deg/s), an impulse-like force perturbation was induced through a rope which was attached to the forearm and briefly blocked by a magnetic brake. The onset time as well as the size of the perturbation can be adjusted by the onset and duration of the motor brake. For the first pilot experiments perturbations were applied after a rotation angle of 20 deg. Movements were recorded by an ultrasound system (sampling rate 200Hz). Small perturbations were compensated with only little effect on end position. This setup is demonstrated being suitable for evaluating the initial torque response to force perturbations.

Zhang L, Straube A, Eggert T (2014) Torque response to external perturbation during unconstrained goal-directed arm movements. *Exp Brain Res* 232 (4):1173-1184

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