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7th Tübingen Perception Conference

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Preface

Last year we started to make English the primary TWK language in recognition of the fact that perceptual scientists from all over the world are working in Germany and that English is, of course, the language of science. This year the move to English is complete: all our three symposia, the website and the posters are in English.

In addition, we feel strongly about the interdisciplinary nature of the TWK as a Perception rather than just a Vision conference. This year's symposia, on the role of the cerebellum in sensation and perception, visual localization in space-time, and on signal processing in the central auditory system reflect the breadth of both topics and methods in today's perceptual sciences. We are equally happy that in the poster session the computer vision and robotics section is expanding, as are the auditory perception and the neuroscience sections.

Altogether we have accepted 127 posters to be presented at the TWK 2004, an increase of over 10% compared to last year. We interpret this as a sign that both the change in language as well as the thematic shift from a vision to a perception conference are favourably received by the TWK community.

The public lecture will be given by Professor Manfred Spitzer, head of the Department of Psychiatry of the University Hospital Ulm. His talk, entitled "Die Macht innerer Bilder: Wahrnehmung, Vorstellung, Halluzination" will be given in German—we feel that the public lecture should be the one exception to the "all-in-English" rule, as this is a lecture intended not only for scientists, but for the general public of Tübingen and beyond.

Ever since the 3rd TWK in 2000 we have awarded a prize for the best poster contributed by an undergraduate or graduate student. In 2003 the poster prize was awarded to Angelika Lingnau of the Technical University of Braunschweig for her contribution "Lesen ohne Fovea? Fixationsmuster und Leseleistung beim Lesen mit einer Pseudofovea". A prize will again be awarded at this TWK. The prize is a cheque for 500 Euros, donated by the Förderverein für neurowissenschaftliche Forschung, e.V., whose support we gratefully acknowledge.

The Organizing Committee
Tübingen, January 2004

Sponsoring Institutions

Max-Planck-Institut für biologische Kybernetik, Tübingen, Germany
Eberhard-Karls-Universität Tübingen, Germany
Förderverein für neurowissenschaftliche Forschung, e.V.

Acknowledgments

The TWK website was updated, refined and maintained by Jez Hill, post-doctoral fellow in Felix Wichmann's Computational Vision Laboratory at the MPI, building on the system he had designed and programmed the previous year. Abstracts are submitted directly into a SQL-database from which they can be posted to the net and, using his PHP-based TeX generator, straight into the TWK Proceedings, typeset using LaTeX.

Dagmar Maier, Heinrich Bülthoff's secretary, reserved the Kupferbau—the conference venue—distributed our information material, contacted all our speakers and arranged their accommodation, organised coffee, tea and snacks during the TWK, drafted-in students to help put up poster-boards, and handles the on-site registration during the conference. It is difficult to imagine how TWK 2004 could have happened without her professional and friendly help.

Ralf Buckenmayer and Julia Liske of the administration of the Max-Planck-Institut für biologische Kybernetik were again dealt the burden to deal with the accounting side of the conference registration.

Reinhard Feiler, Walter Heinz, Werner Koch, Michael Renner and Uli Wandel, again helped in the background both during and before the conference—if you do not notice them, this is a sign of how well they work to ensure that the TWK runs smoothly. In addition and as in previous years, Walter Heinz produced the name-badges and the tickets for the dinner at the Museum and printed the banner outside the Kupferbau. Internet access during the TWK is possible thanks to Michael Renner. Reinhard Feiler helped organize technical support provided by *Bewegte Bilder Medien AG* and produced the programme flyers.

Finally, we would like to thank the University of Tübingen for their cooperation. Lecture halls are a scarce commodity in Tübingen at the moment due to major reconstruction works across the University, and our use of the Kupferbau is only possible because of the University's willingness to meet our requirements.

Friday 30th January 2004

15:00 Registration and hanging of posters

16:25 Welcome

Symposium 1: Contributions of the Cerebellum to Sensation and Perception
(Klaus Mathiak, Universität Tübingen)
Symposium to be conducted in English

16:30 **Introduction**
Klaus Mathiak (Eberhard-Karls-Universität Tübingen)

16:40 **Mapping Visually Activated Cerebellar Regions in Anaesthetised Monkeys with fMRI**
Fahad Sultan (Eberhard-Karls-Universität Tübingen) & Nikos K. Logothetis (MPI for Biological Cybernetics, Tübingen)

17:10 **Contributions of the Cerebellum to Visual Perception**
Thomas Haarmeier & Hans-Peter Thier (Eberhard-Karls-Universität Tübingen)

17:40 **Cerebellar Contributions to Auditory Perception**
Hermann Ackermann & Klaus Mathiak (Eberhard-Karls-Universität Tübingen)

18:10 Coffee break

18:40 **The Cerebellum as a Sensory Coordinator**
Lawrence M. Parsons (University of Texas Health Science Center)

19:10 **Does the Cerebellum Guide Attention?**
Dagmar Timmann (Universität Essen)

Pretzels and other light snacks will be served from 19:30.

Public evening lecture (to be given in German)

20:00 **Die Macht innerer Bilder: Wahrnehmung, Vorstellung, Halluzination**
Manfred Spitzer (Universitätsklinik Ulm)

Saturday 31st January 2004

Symposium 2: Visual Localization in Space-Time
(Dirk Kerzel, Universität Gießen)
Symposium to be conducted in English

09:00	**Introduction** Dirk Kerzel (Justus-Liebig-Universität Gießen)
09:10	**Compensation of Neural Transmission Delays by the Sensory and the Motor Systems** Romi Nijhawan (University of Sussex,UK)
09:40	**Representational Momentum: Perception or Cognition?** Dirk Kerzel (Justus-Liebig-Universität Gießen)
10:10	**Dynamic Mental Representations of Human Action** Ian M. Thornton (MPI for Biological Cybernetics, Tübingen)
10:40	Coffee break
11:10	**Visual Localization and Feature Processing During Eye Movements** Markus Lappe (Westfälische Wilhelms-Universität Münster)
11:40	**Spatio-Temporal Integration of Propagating Subthreshold Activity—Voltage-Sensitive Dye Imaging in Cat Visual Cortex** Dirk Jancke (Ruhr-Universität Bochum & The Weizmann Institute, Rehovot, Israel)
12:10	**A Network Model for Coding the Position of Continuously Moving Stimuli** Wolfram Erlhagen (University of Minho, Portugal)
12:40	Lunch break

Poster sessions
The posters will be divided into 4 groups. The authors should be present at their poster at least during the time allocated to their group as follows. The poster boards will be marked to indicate which group the poster is in.

14:00	Group A
15:00	Group B
16:00	Group C
17:00	Group D
19:30	Banquet at the Museum Restaurant The poster prize will be awarded during the dinner. NB: places are limited. Tickets may be reserved during online registration, and any remaining tickets will be sold at the registration desk.

Sunday 1st February 2004

Symposium 3: Signal Processing in the Central Auditory System
(Petra Arndt, Universität Oldenburg)

Symposium to be conducted in English

09:00 **Introduction**
Petra A. Arndt (Universität Oldenburg)

09:10 **Auditory Lateralization and Spatial Hearing in Patients with Acquired Brain Lesions Affecting the Brainstem or the Primary Auditory Cortex**
Rudolf Rübsamen (Universität Leipzig), Manon Grube (Universität Leipzig) & D. Yves von Cramon (MPI für Cognitive Neurowissenschaften Leipzig)

09:40 **Mechanisms of Auditory Scene Analysis**
Georg Klump (Universität Oldenburg), Mark A. Bee (Universität Oldenburg), Sonja B. Hofer (TU München) & Ulrike Langemann (Universität Oldenburg)

10:10 **Spectro-Temporal Analysis and Streaming in the Auditory System**
Torsten Dau (Centre for Applied Hearing Research, Technical University of Denmark, Copenhagen)

10:40 Coffee break

11:10 **Learning-Induced Plasticity in the Auditory Cortex**
Frank W. Ohl (Leibniz-Institut für Neurobiologie, Magdeburg)

11:40 **Effects of Auditory Localization on Intersensory and Sensorimotor Integration**
Petra A. Arndt (Universität Oldenburg)

12:10 Closing discussion, removal of posters, end of conference

Contents

Symposium 1

Contributions of the Cerebellum to Sensation and Perception

Klaus Mathiak
Universität Tübingen

Introduction

Klaus Mathiak

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The cerebellum is often neglected as concerns its function in sensory and perceptual processes. Neuroscientists in Tübingen, however, are traditionally pioneers for this ‘lesser brain.’ During this symposium we want to review critically cerebellar contributions to sensory processing and perception and outline new developments in the study of this organ. The cerebellar cortex is characterized anatomically by a very homogeneous and repetitive structure suggesting a single computational operation. Simplistic models, however, failed so far to give a good account for the observed sensory, perceptional, and cognitive functions. In particular, recent functional imaging studies documented cerebellar contributions to wide range of motor, sensory, and cognitive tasks, with activations detected in patterns suggesting orderly functional compartmentalization. Current developments towards combined fMRI and electrophysiology in the monkey might bridge the gap between the understanding of cerebellar function from single cell recordings and imaging of localized activation on a system level. The integration with clinical studies showing critical cerebellar involvement in the perception of dynamic events in vision, audition, and tactile sensation might lead to a holistic understanding that accounts for motor functions as well. Indeed, the deep but sometimes subtle sensory contributions suggest that the wide activations observed during even higher cognitive functions might merely reflect underlying basic or supporting functions. However, this supporting and mediating function of the cerebellum should be considered in any kind of sensory process.

Mapping Visually Activated Cerebellar Regions in Anaesthetised Monkeys with fMRI

Fahad Sultan[1] and Nikos K. Logothetis[2]

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Visual input handed over to the cerebellum by way of the pontine nuclei plays a crucial role in the sensory guidance of movement in primates [1]. Based on the demonstration of visual single unit activity and the results of tract tracing experiments, several cerebellar regions seem to be involved in the processing of visual signals. We therefore looked for visually evoked cerebellar BOLD activation with a vertical 4.7 Tesla MRI scanner in monkeys. This approach provides us with a direct visualisation of the complete multisynaptic cerebro-ponto-cerebellar pathway. Monkeys were scanned while being anaesthetised in order to rule out movement-related BOLD responses, induced by the visual stimuli. In a first set of experiments we looked for cerebellar BOLD responses evoked by moving large field random dot kinematograms. Our preliminary results indeed suggest that some of the previously proposed cerebellar regions are activated by such pure visual stimulus. The visual responses were most pronounced in the posterior vermis. However, visual responses were also elicited in another classical "visual" cerebellar area, the dorsal paraflocculus. In addition we also saw activation in the cerebellar hemispheres, although much less pronounced. The differences in activation strength in different cerebellar regions may be due to several factors: potentially larger physiological noise in the more caudal cerebellar regions, larger distance of the caudal regions to the RF coil, and/or different density distribution of activated afferent fiber terminals in the different cerebellar regions. The function of these sensory signals may subserve to optimize occulomotor performance [2] or sensory performance [3] such as visual motion detection.

[1] Stein M, Glickstein J. Physiological Reviews 1992; 972:67–1017.
[2] Thier P, Dicke PW, Haas R, Barash S. Nature 2000; 405:72–6.
[3] Bower JM. International Reviews in Neurobiology 1997; 41:489–513.

Contributions of the Cerebellum to Visual Perception

Thomas Haarmeier and Hans-Peter Thier

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While the cerebellum has been traditionally viewed as a part of the brain exclusively devoted to motor control, there is converging evidence that the cerebellum might also contribute to a much wider range of functions including cognitive functions such as visual perception. This view is supported by (i) clinical studies demonstrating visual disturbances in patients suffering from cerebellar disease and (ii) by functional imaging studies of healthy human subjects. Two different types of visual disturbances have been observed in cerebellar patients. A first one is due to impaired eye movements and can be explained solely by the retinal consequences of the eye movement disturbance. Such deficits include the analysis of moving objects tracked by eye movements. A second type of deficit is present also during stationary fixation, i.e. when the retinal parameters are the same for patient and control groups. An example of this type of deficit is the impairment of the discrimination of visual motion. This disturbance likely reflects a dysfunction of cortical areas devoted to the analysis of visual information due to a loss of cerebellar projections. This view is supported by anatomical studies showing extensive connections that link the cerebellum with areas of the cerebral cortex known to be concerned with higher order behavior and by recent functional imaging studies showing that our perception of visual motion such as the motion aftereffect or the perception of visual motion during eye movements involves synchronous activity in a cortico-cerebellar network.

Cerebellar Contributions to Auditory Perception

Hermann Ackermann and Klaus Mathiak

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Temporal processing is of particular high importance in the auditory system. Based upon models of timing functions of the cerebellum (e.g. [1]), we investigated auditory time perception in cerebellar disorders. Patients with diffuse cerebellar atrophy showed specific deficits in duration categorization in speech perception and in delayed matching-to-sample tasks for auditory durations. In speech perception, these deficits emerged only under constrained conditions and could be compensated by using other auditory cues. Thus, they are rarely reported and usually not noted by the patients in everyday life. To explore its significance in normal neuronal processing, we conducted two functional magnetic resonance imaging (fMRI) studies: A right-hemispheric cerebellar cluster in crus I emerged, first, during the same lexical identification task based on occlusion time as compared to aspiration noise and, second, during a working memory as compared to an identification task of auditory pause durations. The neurobiological origin of the timing hypothesis has bee challenged. Our data, however, suggest that during certain perceptual and cognitive processes that demand precise temporal evaluation of acoustic signals, the cerebellum has an obligatory function exhibiting compartimental organization. In both experiments, prefrontal activation was concurrent with the cerebellar clusters. Similar activation patterns emerge frequently under verbal working memory conditions. Conceivably, thus, temporal processing as required for sequence organization contributes to cognitive operations such as covert speech. This function might contribute to cerebellar activation in various cognitive tasks.

[1] Ivry RB, Fiez JA in Gazzaniga, M.S. (Ed.): The New Cognitive Neuroscience 2000; Plenum, NY; 999–1011.

The Cerebellum as a Sensory Coordinator

Lawrence M. Parsons

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The cerebellum contains approximately 70% of human neurons, its microcircuitry is remarkably conserved across the vertebrate line, it receives input from every sensory system, and has reciprocal connections with a variety of non-motor cortical areas. New anatomical, neurological, and neuroimaging findings appear to implicate selected regions of anterior and posterior cerebellum in a wide variety of non-motor information processing. Such processes include: (a) language generation (semantics); (b) perception of auditory tone duration (e.g., 500 ms range); (c) executive functions (organizing, sequencing); (d) kinesthetic/proprioceptive processing; (e) verbal working memory; (f) spatial reasoning; (g) tactile/cutaneous processing; (h) selective visual attention (target search); (i) perception of phonemes; (j) regulation of affect; (k) food hunger; (l) thirst (sensory and cognitive effects); (m) air hunger (sensory and cognitive effects); (n) olfaction (sensory aspects of regulating sniff rate); (o) perception of visual motion, speed, and direction; and (p) the fine discrimination of auditory pitch. Dysfunction of the cerebellum has recently been suggested to contribute to a significant degree to autism, dyslexia, ADHD, problems in short term phonological memory, specific language impairment, alcoholism, and schizophrenia. Hypotheses for one kind of operation that could underlie these varied phenomena have included attentional processes, timing and sequencing mental operations, optimizing functions for all mental and affect processes, and optimizers for the control of the acquisition of sensory information. This presentation will discuss the latter hypothesis, but with an eye toward making explicit variants of each of these hypotheses in order to discriminating amongst them using PET, ERPs, MEGs, fMRI, close testing of various kinds of cerebellar patients, among other methods.

Does the Cerebellum Guide Attention?

Dagmar Timmann

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There is some controversy about a possible role of the cerebellum in non-motor functions. Disability of cerebellar patients in rapidly shifting attention is one frequently used example to support cerebellar involvement in mental skills. The original proposal was based on findings in five cerebellar children with chronic surgical lesions and a young adult with degenerative disorder. The aim of the present study was to repeat Akshoomoff and Courchesne's [1] initial findings in a larger group of children with focal cerebellar lesions. Ten cerebellar children and ten age- and sex-matched controls were tested. Neocerebellar areas were affected in all cerebellar children except one based on detailed analysis of MRI scans. Subjects had to perform a focus and a shift attention task. The ability of target detection did not significantly differ in the cerebellar compared to the control children in both the focus and the shift attention tasks. In particular, cerebellar children showed no significant impairment in rapid (< 2 s) shifts of attention. The present findings indicate that the cerebellum may be less critical in attention related processes as suggested previously. Courchesne's view that the cerebellum plays a role in shifting attention has recently been challenged. Ravizza and Ivry [2] found deficits in adult cerebellar patients in shifting attention. Deficits, however, showed a significant improvement when the motor demands of the task were reduced. Findings of a recent fMRI study in healthy subjects of the same group supported Ivry's hypothesis that the role of the cerebellum in shifting attention tasks is involvement in motor response reassignment rather than attention [3]. Differences in findings between the present and the initial study by Akshoomoff and Courchesne [1] may be explained at least in part by differences in the severity of deficits in motor performance. In [1] reaction times were significantly longer in the cerebellar children as compared to controls, whereas no significant group differences were found in the present study. The present data agree with Ivry's assumption that the cerebellum's role in attentual tasks is likely related to motor requirements of the task.

[1] Akshoomoff NA, Courchesne E. Behavioral Neuroscience 1992; 106: 731–8.
[2] Ravizza SM, Ivry RB. Journal of Cognitive Neuroscience 2001; 13: 285–97.
[3] Bischoff-Grethe A, Ivry RB, Grafton ST. Journal of Neuroscience 2002; 22: 546–53.

Symposium 2

Visual Localization in Space-Time

Dirk Kerzel
Universität Gießen

Introduction

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A key visual function for animals and humans is spatial localization. We need to know where an object is before we can grasp it, hit it with a tennis bat, or catch it. However, there are significant information processing delays within the nervous system. For instance, it takes about 30–100 ms between the stimulation of the photoreceptors and a neural response in primary visual cortex. While this delay may not be a problem for actions toward static objects, it poses a major problem when dealing with moving objects: Moving objects change their position while information is being relayed. If visual processing delays were not taken into account, our actions would therefore lag behind the real-world positions of moving objects. However, successful performance in high-speed ball games such as tennis or baseball, as well as experimental investigations, show that motor responses to moving objects are highly accurate. One of the themes in this symposium will be how and where neuronal delays are compensated for, and what mechanisms have evolved to deal with moving objects.

A related problem is that moving objects are often hidden from view. They may go out of sight, or may be covered by other objects. Human actions therefore often rely on mental representations of object position and motion. For successful performance, it would be advantageous if object motion was extrapolated in visual-short term memory such that the represented target position would closely follow the true target position. As a consequence, position information may be distorted in visual-short term memory.

Finally, the visual system has to consider that retinal motion may not only be produced by object motion, but also by eye or body movements. To distinguish between these two possibilities, extraretinal information about eye movements and motion signals from the retina have to be combined. The question is whether and how the visual system achieves accurate synchronization of incoming extraretinal and retinal information. Current evidence indicates that temporal mismatches on the order of 100 ms go uncorrected such that spatial errors result.

Compensation of Neural Transmission Delays by the Sensory and the Motor Systems

Romi Nijhawan

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For more than a hundred and fifty years, scientists have known that neural processes are relatively slow. This implies that the visually experienced world, which involves the activation of higher cortical areas that are several synapses removed from the visual input, is forever lagging the real one. Consequently, events should be perceived after a delay and moving objects should appear where they were about a tenth of a second ago. However, the demands of quick and precisely timed interceptive (or avoidance) behaviors imposed on an animal's nervous system require compensation of these delays. Various investigations of the nervous systems of animals, particularly of the motor system, have revealed mechanisms that compensate for these delays. Suggestions of compensation within the visual system per se are relatively recent, and controversial. I will argue for a visual mechanism compensating for neural processing delays. This suggestion is based on a fascinating phenomenon (the flash-lag effect) in which a flashed object presented at the same position as a moving object appears in a position lagging the moving object. The flash-lag effect manifests itself in many forms, and impacts areas as diverse as color vision, perceptual filling-in, and feed-forward control in motor behavior.

Representational Momentum: Perception or Cognition?

Dirk Kerzel

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When observers are asked to memorize the final position of a moving object, judgments are often displaced in the direction of motion. So far, this distortion of visual short-term memory has been explained with reference to high-level, cognitive processes. The classical explanation has been that mental representations of moving objects reflect properties of the physical world. In analogy to the physical momentum of moving objects, the remembered target position possessed "representational momentum" and overshoots the true final target position. This idea has its roots in Shepard's proposal that many cognitive activities are guided by internalizations of invariant real-world constraints. In contrast to these knowledge-based proposals, more recent low-level accounts hold that errors in visual short-term memory are accounted for by properties of motion perception, attention and eye movements. First evidence for this account is the distinction between smooth and implied motion. Whereas a shift of the remembered final target position is reliably observed with implied motion, no shift occurs with smooth motion when fixation is maintained. Paradoxically, weak or second-order motion signals produce more forward displacement than real motion. The second important distinction concerns the response mode. When motor judgments such as mouse or natural pointing movements are used, displacement in the direction of motion is larger than with relative judgments that involve a comparison with a probe stimulus. Contrary to current theorizing, this suggests that the distortion is larger in a motor map of environmental space than in a cognitive/perceptual map. It may be that the forward error in pointing movements compensates for neural delays.

Dynamic Mental Representations of Human Action

Ian M. Thornton

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The visual presentation of real, apparent or implied object motion is often accompanied by systematic errors in localization. In this talk, I will concentrate on one form of error—representational momentum—in which observers systematically misremember a stopping point as being further forward in the direction of motion or change. While representational momentum has been demonstrated using a wide variety of stimuli, in this talk I will focus specifically on the perception and production of human actions. I will begin by reviewing a number of studies that have examined our ability to anticipate simple human actions, such as walking. I will then discuss recent work in our lab that has directly compared anticipation in visual perception with the production of grasping movements. Finally, I will discuss an ongoing project that explores how prior experience in manipulating physical objects that differ in weight affects subsequent visual anticipation when those objects are seen moving.

Visual Localization and Feature Processing During Eye Movements

Markus Lappe

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Localization of briefly flashed stimuli around the time of a saccade Visual localization is distorted for stimuli that are briefly flashed in the wake of a saccadic eye movement. Objects flashed in the dark appear shifted in the direction of the eye movement. Objects flashed on a structured background appear compressed towards the saccade target. Also, the apparent position of the saccade target is influenced by a presaccadically flashed object. In the dark, the saccade target position appears shifted towards the flashed object. In the presence of a background, the saccade target is accurately localized. These results suggest that perisaccadic mislocalization arises from compression of the visual distances between elements of the presaccadic scene plus an uncertainty about postsaccadic target location. The compression affects only the location of the presented objects, not their visual properties or identity. When multiple objects with different colors are flashed before a saccade they appear to overlap in one place but their individual colors can still be distinguished.

Spatio-Temporal Integration of Propagating Subthreshold Activity—Voltage-Sensitive Dye Imaging in Cat Visual Cortex

Dirk Jancke

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Our percepts depend on the context within which local features are embedded, both in space and time. In a dynamic context, even stationary stimuli can give the impression of motion. For example, the "line-motion" illusion simply consists of a flashed dot briefly followed by a bar. Instead of sensing the bar at once, subjects report motion progressively away from the cued side. We used optical imaging of voltage-sensitive dyes in area 18 of the anaesthetized cat in order to visualize cortical line-motion. We found that the flashed dot or the bar alone evoked subthreshold propagating activity that gradually decreased its speed with increasing amplitude. Only at high levels activity stayed local, i.e. motionless. In the line-motion condition however, the cued activity was progressively boosted producing a suprathreshold wave of activity starting closest to the initialized location. As similar expanding wave-fronts of propagating activity where observed in response to real moving dots we suggest that synaptic spread must serve a fundamental processing strategy that facilitates anticipation of motion and strongly affects spatio-temporal interactions in response to any natural sensory input. Generally, it has been suggested that intra-cortical long-range horizontal connections mediate contextual lateral interactions across visual space. In order to further investigate their functional role in integrating visual information, we extended our studies towards another important visual stimulus parameter: orientation selectivity. Anatomical and extracellular studies have suggested that horizontal axons connect preferentially neurons of similar orientation preference. Using voltage-sensitive dye signals as a direct functional measure, we here re-evaluated synaptic orientation selectivity of horizontal spread. In response to a small local oriented grating, activity spread horizontally, far beyond retinotopic borders. However, orientation selectivity was preserved only locally, closely around retinotopic sites, while it was lost exponentially across less than 1 millimeter. Preliminary experiments led us propose that orientation selectivity may emerge from integrative cortical mechanisms.

A Network Model for Coding the Position of Continuously Moving Stimuli

Wolfram Erlhagen

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In everyday life, we are frequently faced with the problem to plan or avoid contact with objects undergoing smooth change in location. The goal of the visual system becomes one of estimating their current state and predicting their future states. How this is accomplished is still a matter of debate. In my talk I will present a modelling approach, which aims to critically discuss possible mechanisms underlying the processing of position of a stimulus in motion. The proposed dynamic model consists of interacting excitatory and inhibitory cell populations coding for stimulus position. In response to an apparent motion paradigm the network develops a self-stabilized wavy activity pattern in parametric space. The non-linear interactions among the neurons lead to a partial compensation of processing delays compared to a stimulus presented in isolation. They may also cause the continuation of the dynamic transformations upon offset of the moving target, resulting in an extrapolation of past trajectory information. A second mechanism for motion extrapolation is based on an integration of additional top-down information into the processing. This top-down contribution may represent a learned internal model of the moving stimulus or actions plans directed at the stimulus in motion. The coded position of the stimulus appears to be shifted forwards along its trajectory of motion compared to the case when the bottom-up input alone drives the neuronal population.

The model predictions are discussed with respect to recent findings in studies of localization errors observed with moving stimuli such as the flash-lag effect and the representational momentum. In particular, I will focus on the question whether the temporal coding of position (i.e. latency to perception) and/or a spatial mechanism (i.e. spatial shift) may account for the observed localization errors.

Symposium 3

Signal Processing in the Central Auditory System

Petra Arndt
Universität Oldenburg

Introduction

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Sensory systems are designed to detect and identify relevant objects and events in the environment. Although the purpose is similar, different sensory systems are confronted with dissimilar problems in performing this task. Specific problems are evoked by the properties of the signals the respective system has to analyze and by properties of the sensory system itself. The auditory system differs from (most) other sensory systems in the early representation and in the processing of the spatial positions of stimuli. The spatial location at which the sensory surface is stimulated is independent of the spatial position of the object or event which evokes this stimulation. The position of objects and events has to be reconstructed on the basis of non-spatial pieces of information. From this it is obvious that spatial hearing depends on specific mechanisms to reconstruct the position of auditory events in the environment. In the first talk Rudolf Rübsamen, Manon Grube & D. Yves von Cramon discuss this issue and the role of brainstem and primary auditory cortex in spatial hearing. The presented results reveal differences and interesting parallels between auditory and visual system. However, the characteristics of spatial hearing do not only affect stimulus localization. They have also an impact on higher processes, e.g., the segmentation of objects. In the visual system figure-ground-segmentation is based on spatially defined boundaries. Such a feature is not provided by acoustic signals. Thus the auditory scene analysis must be based on alternative cues. Possible underlying mechanisms are explored on the basis of behavioral and electrophysiological investigations (Georg M. Klump, Mark A. Bee, Sonja B. Hofer, Ulrike Langemann) and by analyzing models of spectro-temporal pattern analysis (Torsten Dau). The remaining two talks deal with subsequent processing of auditory stimuli. The talk given by Frank Ohl addresses characteristics of auditory processing on a higher, more cognitive level: Category learning in the auditory system is discussed in the context of plasticity in the auditory cortex. The last talk (Petra A. Arndt) analyzes effects of spatial processing in the auditory system on perceptual processes and on the control of action. Influences on intersensory interaction of auditory and visual signals are investigated as well as effects on sensorimotor integration.

Auditory Lateralization and Spatial Hearing in Patients with Acquired Brain Lesions Affecting the Brainstem or the Primary Auditory Cortex

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The principle role of primary auditory cortex (PAC) in spatial hearing is not yet known, as previous studies yielded controversial results. In animals, cortical single units with panoramic response characteristics and peak responses located in the contralateral hemifield were recorded, while in behavioral studies with brain-lesioned animals the apparent contribution of PAC to spatial hearing depended on the nature of the task. The two prevailing hypotheses on auditory space perception suggest dominant representations of the contralateral hemifields or a general right-hemisphere dominance. However, the evidence mainly stems from lateralization, i.e., headphone experiments, or from studies in patients with lesions of higher, i.e., supramodal parietal cortical areas. In this study, we specifically aimed at the functional significance of PAC in sound localization. The ability to spatially segregate auditory events was investigated in patients with acquired brain lesions affecting left or right Heschl's Gyrus (HG, the PAC anatomical correlate), in that HG was either directly damaged or deprived of its afferents. Minimal audible angles (MAA) in the horizontal plane were measured for low and high-frequency noise bursts as a function of reference direction. We applied an adaptive three-alternative forced-choice paradigm proven suitable for working with naive subjects and patients. The patients' direction discrimination thresholds critically depended on the site of lesion. Compared to data from naive control subjects, spatial resolution was severely impaired in patients with lesions affecting right HG. Thresholds were elevated for reference directions in both hemifields, with the deficit being more pronounced for low-frequency than for high-frequency stimuli. The performance of patients with left-hemispheric lesions tended to be poorer in the right hemifield rather than in the left, if it was impaired at all. The results of our study support the assumption that, corresponding well to the generally accepted functional specialization in human space perception, a right hemisphere dominance in spatial hearing is already established at PAC level. At the same time, our findings yielded evidence for the existence of dominant contralateral representations of auditory space in human PAC.

Mechanisms of Auditory Scene Analysis

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In analysing the acoustic environment, the auditory system has to solve the problem to segregate the sounds that arrive at the ear at the same time but originate from separate sources. This task has been termed "Auditory Scene Analysis" by Bregman [1]. Spectral characteristics provide one cue that is used for sound source separation. Different spectral components of a sound that contribute to a complex signal originating from one source, however, should not be separated but should be grouped together to be analysed as a unit. Evidence from psychoacoustic studies in various animal species suggests that their auditory systems employ similar mechanisms to perform auditory scene analysis as have been described in humans. Examples are the use of correlated amplitude modulations of spectral components of a sound originating from one source to improve segregation of a signal from background noise (an effect termed "Comodulation Masking Release"), the use of common onset and offset of spectral components of a sound for grouping, and the use of spectral separation and temporal proximity for segregating sounds into separate perceptual streams ("Auditory Objects"). The similarities in the perception of the different species indicate similar underlying mechanisms of auditory processing. This provides the opportunity for parallel studies of the psychoacoustics and the neuronal responses in the auditory pathway of a species to elucidate the functional principles of the circuits involved in auditory scene analysis. Using examples from our work in a bird species, the European starling, we will demonstrate how bottom-up processing mechanisms can contribute to object segregation in auditory scenes.

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Spectro-Temporal Analysis and Streaming in the Auditory System

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Many real-life auditory stimuli have intensity peaks and valleys as a function of time in which intensity trajectories are highly correlated across frequency. This is true of speech, of interfering noise such as “cafeteria” noise and of many other kinds of environmental stimuli. Across-frequency comparisons of temporal envelopes are a general feature of auditory pattern analysis and play an important role in extracting signals from noise backgrounds, or in separating competing sources of sound. For example, comodulation of different frequency bands in background noise facilitates the detection of tones in noise, a phenomenon known as comodulation masking release (CMR). The mechanisms underlying such a spectro-temporal pattern analysis in hearing are still unclear. There has been recent interest in elucidating the possible physiological basis for CMR [1, 2] and in confirming its presence in non-human species. CMR is usually assumed to depend on comparisons of the outputs of different auditory channels. However, “within-channel” cues can also facilitate the detection of a signal in modulated noise leading to a measured CMR without any necessary involvement of across-channel mechanisms [3]. In this presentation, the extent to which CMR reflects within- and/or across-channel processes is investigated by assessing the influence of concurrent and sequential streaming cues on CMR [4]. Effects of auditory object formation are commonly associated with higher-level processes. The dependence of CMR on auditory grouping places strong constraints on potential neural substrates for CMR. Consequences for models of spectro-temporal pattern analysis in the auditory system are discussed.

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Learning-Induced Plasticity in the Auditory Cortex

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Research on learning-induced plasticity in the auditory system will be briefly reviewed. It will be concluded that this research has predominantly been physiologically motivated and central questions on the role of neuronal plasticity (a physiological concept) for learning (a psychological concept) have remained unanswered. It will be shown that the study of category learning (concept learning) can resolve some of the conceptual problems inherent in the physiologically oriented learning research. During category learning equivalence classes of meaning (categories) are established over stimuli that enable an organism to adequately respond even to novel, previously unfamiliar, stimuli when they are encountered. A particular type of auditory category learning in a suited animal model (Mongolian gerbil) will be considered in detail. Typically, the formation of categories arises in a sudden rather than gradual process in the behavioral data ('Aha'-event) and can be modeled as a behavioral state transition. Measurement of single trial multichannel electrocorticograms during category formation reveals that the behavioral state transition is accompanied by a state transition in the neurodynamics in auditory cortex. The state transition is accompanied by the emergence of identifiable transient spatiotemporal activity patterns in the ongoing cortical activity ('late states') which can be differentiated from the known stimulus-evoked activity patterns ('early states'). While early states reflect the representation of physical stimulus parameters in the framework of a topographically organized cortical map (a structure grossly identical across individuals), the late states establish a newly formed metric which reflects the perceptual scaling of stimuli exhibited by individual animals. These data suggest the coexistence of separate coding principles for information relevant for stimulus identification using physical features and for information subjectively relevant for an individual's categorization of stimuli. The data will be discussed with reference to the problem of objective physiological measurements of subjective cognitive structures, and with reference to the general problem of identifying physiological correlates of learning.

Effects of Auditory Localization on Intersensory and Sensorimotor Integration

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The position of an auditory stimulus has to be reconstructed from spectral, temporal and intensity cues provided by the auditory signal. The localization in the horizontal plane is mainly based on differences in intensity and timing between the left and right ear. In contrast vertical localization is derived from the spectral cues in a more time consuming process. The temporal progression of the underlying processes is reflected in behavioral data. For example, the measurement of manual reaction times has shown that localization latencies for auditory stimuli are remarkably longer than detection latencies. This even holds true for stimuli in the horizontal plane, although the processing of horizontal position is relatively fast. A typical effect of the time difference between horizontal and vertical localization are curved saccadic trajectories found for auditory target stimuli above or below the horizontal plane. A more detailed analysis has shown that the perceived position of an auditory signal changes during the time course of auditory processing [1]. During this process a first rough estimate of stimulus position is replaced by a later representation with a higher spatial resolution. Based on the data of reaction time experiments the effects of this process on sensorimotor integration is discussed. In case of incomplete processing of the auditory stimulus a rough estimate of the position might be used to control motor activity. Alternatively the perceived spatial position of the auditory stimulus might be determined by top-down processes. To elicit responses at early, incomplete processing stages of the auditory signal, we used a visual stimulus as target and the auditory stimulus as accessory. As a behavioral measure saccadic latencies and trajectories were examined. Our eye movement data favor the assumption that a default value is used in this experiment, i.e., the top-down hypothesis. To analyze whether this result is specific for saccadic eye movements we examined pointing movements under similar conditions. The results allow for conclusions on the effects of the time course of auditory processing on different motor systems. Moreover they give insight in processes of intersensory interaction and in the relationship between saccadic and manual motor control.

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Attention and Awareness

Variations in the Visual Hallucinatory Response to Flickering Monochromatic Light

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It is generally assumed that conscious visual states represent an interaction between spatially structured variations in the environment and the nervous system. Visual hallucinations, both of pathological origin [1,2] and induced experimentally [3–6], question the assumption that our conscious percepts are necessarily determined by spatial structure in the distal stimulus. Here we show that complex colour and form hallucinations can be evoked by flickering monochromatic light and that the type of hallucination varies with flicker frequency and phase.

A specially constructed box with LEDs controlled by a timer card allowed the presentation of a spatially homogeneous field of flickering light. In Experiment 1 we determine the type of hallucinatory experience and the range of flicker frequencies over which hallucinations were experienced in a free report design for frequencies of 1–60 Hz. Observers reported eight colour hallucinations: purple, blue, green, yellow, red, black, white and grey and nine spatially structured hallucinations: lines, waves, circles, radials, spirals, gratings, points, rectangles and zigzag patterns, each of them being reported at a specific range of frequencies. The reports of hallucinations were not uniformly distributed over frequency and report distributions differed significantly for some of the hallucinations.

Experiment 2 examines the onset time of colour and form hallucinations relative to the phase of intermittent stimulation by asking the observers to press a response key on first experiencing a particular hallucination. Analysis of the relation between the times of the onset of hallucinations expressed in terms of phase angle relative to the frequency cycle of intermittent stimulation revealed all responses, except those involving purple hallucinations, to be normally distributed. This indicates that, irrespective to the absolute time at which a hallucination starts to be perceived, the onset time of the hallucination relates specifically to a particular phase of the evoking flicker. Certain hallucinations appear at close phases in the flicker cycle (i.e. lines and rectangles; blue and purple), while others are clearly separated in phase space (i.e. rectangle vs. spiral; blue vs. yellow).

The hallucinations described here are experiences of visual form and colour that are entirely independent of the presence of particular spatial structure or colour in the distal stimulus, but relate specifically to the frequency and phase of the flicker presentation. This evidence indicates that conscious visual experience may be evoked directly by particular variations in the flow of spatially unstructured light over time and therefore supports theories of consciousness that stress temporal aspects of perceptual processing.

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Spatial Neglect: Offset from Normal Resting Position

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The characteristic deficit of patients with spatial neglect is a bias of their exploratory movements towards the right. When searching for targets, copying, or reading, the patients direct their eye and hand movements towards the ipsilesional side, leading to neglect of the contralesional side. How elementary is this disorder? Is it linked with active behaviour (such as drawing or exploring) or is it inherently obvious without any specific requirements? To address this issue we investigated the patients' spontaneous resting position while sitting in the wheelchair, just waiting and "doing nothing". Using magnetic search coil technique, we recorded spontaneous gaze, eye-in-head, and head orientation of 10 right hemispheric neglect patients while they were "waiting for an experiment". In a subsequent condition, patients were instructed "to look exactly straight ahead". In comparison to controls, neglect patients showed a marked rightward deviation in both conditions. Their spontaneous resting position thus corresponded with the subjective "straight ahead" orientation. Spatial neglect seems to be associated with a very elementary disturbance of spatial information processing which might be understood as a re-adjustment of the normal resting position to a new, more rightward located origin.

The Time Course of Attentional Selection Among Competing Locations: Experiment and Model

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Recent experiments found evidence for a split of spatial attention [1, 2]. This raises the question, whether these findings argue for a static selection of two locations on a master map of locations or if the findings support a model of dynamic continuous spatial reentry [3] that initially supports several locations but finally settles onto a single location.

By modifying the paradigm that was used by [1] to show that attention can be "split" among 2 separate locations, we demonstrate that such a split of attention does only occur at intermediate stages of (incomplete) attentional selection. Our subjects were asked to discriminate the shapes (circle or square) of 2 oddly colored targets within an array of 8 stimuli. After a certain SOA, 8 letters were flashed at the previous stimulus locations, followed by a mask. For a given SOA, the performance of subjects at reporting letters in each location was taken to reflect the distribution of spatial attention. In particular, by considering the proportion of trials in which none or both of the target letters were reported, we were able to infer the respective amount of attention allocated to each target without knowing, on a trial by trial basis which location (if any) was receiving the most attentional resources. Our results show that for SOAs around 100–140 ms, attention can be equally split between the two targets, a conclusion compatible with previous reports. However, with longer SOAs, attention ultimately settles at a single location. We simulated this experiment with a novel model of visual perception which comprises areas V4, IT, PF and FEF. In the model spatial attention emerges from a reentry signal reflecting the plan to move the eye: movement related cells compete for the target location of an eye moment and their activity feeds back continuously to extrastriate visual areas. Thus, the SOA in our experiment determines the state of this competition at the time the letters were flashed and ultimately the distribution of attention at different locations. This model better fits our data than a model that simply selects two locations simultaneously.

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Attention Shifts to Masked Stimuli. Results of an Event Related Potential Study.

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Recent studies (e.g. [1]) have investigated the effects of masked stimuli on lateralized components of the ERP. While the motor effects of these stimuli are well known (e.g. [2]), attention related asymmetries are a new field of study ([3]). The poster presents results of a series of experiments that were specifically designed to assess the impact of masked stimuli on attention related asymmetries.

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Attention Processes in Narcoleptics

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Narcolepsy is a common neuropsychiatric disorder characterized by increased daytime sleepiness, cataplexy and hypnagogic hallucinations. Although attentional deficits are responsible for many difficulties patients with narcolepsy experience in everyday life, these deficits have not been addressed in quantitative scientific investigations. The purpose of this study was to test different aspects of attention in patients with narcolepsy. We compared performance of subjects with and without narcolepsy in four attention tests: sustained attention (d2-test), attention shift (a visual conjunction search test), alertness (a vigilance test) and a test for kataplexies. Ten narcoleptics recruited through announcements and 10 healthy subjects matched for age and gender participated in the study. The narcoleptics showed no significant deficits in the visual search task. There was a tendency for longer reaction times and higher error rates, but the differences did not reach statistical significance. The narcoleptics showed a deficit in sustained attention: performance was slightly poorer, they made many more errors and the fluctuation margin of performance was very high. Specific deficits appeared in the vigilance test. Reaction times were consistently longer, error rates and number of missed reactions were much higher in narcoleptics than in the control subjects. Except for one subject, we did not succeed in eliciting cataplexies in our experimental setting (not illustrated). The trigger factors seem to differ from one narcoleptic subject to the next. Our results are in accordance with the hypothesis that attentional impairments in narcolepsy are a result of impaired vigilance. Deficits in attentional capacity and attentional control can also play a role. These possibilities could be investigated in further experiments with sleep-deprived control subjects.

Split Foci of Attention in Prior Entry

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Attending to a stimulus speeds up its processing and leads to a pre-dating of its onset. This prior entry effect (e.g. [1 ,2]) is defined as the relative facilitation of an attended compared with an unattended stimulus: Two stimuli are presented successively. Attention is drawn to one of them shortly before its presentation, e.g., by a peripheral location cue. Temporal order judgments reveal that the attended stimulus is perceived as the earlier one if it is presented simultaneously with the unattended stimulus, and even if it trails the unattended stimulus by a short interval. In recent studies, prior entry has been used as a methodological tool to investigate attention-related topics such as contingent capture by masked peripheral cues [3] and gradients of attention [4]. The present experiments are concerned with the notion of split foci of attention. Most models of visuo-spatial attention include the notion that attention is dedicated to a single location in space. However, several researchers found evidence that under appropriate circumstances attention may be allocated to noncontiguous locations (e.g. [5, 6]). In the present experiments, the spatial distribution of attention is assessed via prior entry elicited by either one or to spatially non-contiguous peripheral cues. The experiments revealed a robust attentional priming effect at two noncontiguous locations of the visual field, simultaneously with little or no priming of the intervening location.

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EEG Channel Selection for Brain Computer Interface Systems Based on Support Vector Methods

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A Brain Computer Interface (BCI) system allows the direct interpretation of brain activity patterns (e.g. EEG signals) by a computer. Typical BCI applications comprise spelling aids or environmental control systems supporting paralyzed patients that have lost motor control completely.

The design of an EEG based BCI system requires good answers for the problem of selecting useful features during the performance of a mental task as well as for the problem of classifying these features.

For the special case of choosing appropriate EEG channels from several available channels, we propose the application of variants of the Support Vector Machine (SVM) for both problems. Although these algorithms do not rely on prior knowledge they can provide more accurate solutions than standard filter methods [1] for feature selection which usually incorporate prior knowledge about neural activity patterns during the performed mental tasks.

For judging the importance of features we introduce a new relevance measure and apply it to EEG channels. Although we base the relevance measure for this purpose on the previously introduced algorithms, it does in general not depend on specific algorithms but can be derived using arbitrary combinations of feature selectors and classifiers.

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Unfocussed Spatial Attention Underlies the Crowding Effect in Indirect Form Vision

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When targets are seen in the presence of neighbouring patterns or contours, their visibility is reduced. This phenomenon, known as the crowding effect, is particularly pronounced in indirect view. By the measurement of recognition-contrast sensitivity of a character with flankers to the left and right, we studied mechanisms underlying the crowding effect in indirect form vision. Attentional and featural contributions to the effect can be separated by a new paradigm that distinguishes pattern location errors from pattern recognition errors and further by manipulating the focusing of spatial attention through a transient positional cue, appearing 150 ms before the target. Measurements were on the horizontal meridian, at 1°, 2°, and 4° eccentricity, and a range of flankers' distances. Our results show that in normal indirect view the impairment of character recognition by crowding is—in particular at intermediate flanker distances—caused by spatially imprecise focusing of attention. The enhancement of performance by a transient positional cue seems mediated separately such that locus and intensity are independent characteristics of attention in form vision.

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Do Depth Cues Affect Attentional Modulations of the Stroop Effect?

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The task of naming the color of stimuli is facilitated by the presence of congruent color words, and impaired by the presence of incongruent color words (Stroop effect). Usually, the Stroop effect is attributed to the automaticity of word reading. A recent study suggests that object-based attentional selection may additionally contribute to the robustness of the Stroop effect. Participants named the color of one of two rectangles, and color words in the relevant object produced larger Stroop effects than words in the irrelevant object, or words in the background. Wühr and Waszak [1] attributed the difference to an object-based mechanism of attentional selection that amplifies processing of all the features of an attended object. Yet, an alternative explanation is possible because, in the display used by Wühr and Waszak, occlusion suggested the presence of different depth planes. Hence, the increased Stroop effect may have resulted from perceiving the words in the same depth plane as the relevant object, and not from perceiving the words as parts of the relevant object. Two experiments tested the depth-based hypothesis against the object-based hypothesis by using displays without monocular depth cues: Participants had to name the color of one of three non-superimposed rectangles, and to ignore words that appeared either in the relevant object, in the two irrelevant objects, or in the background. The results of both experiments replicate those of Wühr and Waszak, supporting their object-based account.

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Dynamic Spatial Shifts of Neuronal Receptive Fields Toward Attended Locations in Macaque Area MT

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Attention excerts a multiplicative modulation on sensory responses of neurons in visual cortex. This modulation is particularly strong with multiple stimuli within a neuronal receptive field (RF). This could be due to a space-based mechanism involving shrinkage and shift of the RF toward the attended location [1, 2]. Alternatively, the response could reflect gain changes in the neuron under study, leaving shape and position of the RF unchanged [3, 4]. We examined these hypothesis directly by obtaining quantitative RF profiles of macaque area MT neurons while attention was directed at different positions within the RF. Our task required spatial attention to one of three moving random dot patterns (RDPs) in order to detect a direction change of the target RDP. Two RDPs were always placed within the RF of direction-selective neurons in MT. While one of the three stimuli was attended, quantitative RF maps were obtained by recording the responses to irrelevant, moving probe RDPs briefly appearing at the intersections of a dense virtual grid covering the RF. The resulting maps reveal a systematic shift of the sensitivity profile (the RF) toward the location of attention. We did not observe a corresponding shrinkage when attention was directed inside versus outside the RF. Our results provide the first direct evidence for a dynamic change of spatial RF position with selective attention to different subregions of the RF—on a trial-by-trial basis and under identical visual stimulation and task difficulty: Attention enhances sensitivity close to the attended location and reduces it at distant position. While the spatial response weighting corresponds to a non-multiplicative modulation, the RF-shift could also result from an attentional gain mechanism acting multiplicatively on pre-synaptic neurons with smaller RFs at attended and unattended locations. The observed spatial sensitivity increase near attended locations at the single neuron level could provide the neuronal substrate for behavioral consequences of the spatial distribution of attention: Perceptual facilitation has been reported to follow a spatial gradient centered on the attended location. At the population level it reflects the additional recruitment of neuronal resources devoted to feature analysis at and near attended positions.

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Auditory Perception

The Perception of Dichotic Shepard Tone Intervals—Fusion or Suppression?

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90% of all people tend to use their right ear when eavesdropping through a door. Investigations of the Octave Illusion show, that people preferably use one ear for pitch detection: It turns out to be the right ear for right-handed subjects (Deutsch, 1974 [1]). This suggests, that as for a concept of Harmony Generalization—harmonies are perceived independent of stereo distribution—certain errors can be expected.

Shepard tones are used to test the assumption, that mainly one ear is responsible for the perception of intervals played across the center frequency. Thus if the top five octaves of a Shepard tone are presented to the right and the bottom five to the left ear, perception should be dependant on the ear responsible for pitch detection and different from information integration of both ears.

Conducted experiments investigated if the stereo distribution of specific tone components of Shepard tones influence the perception of musical intervals. Subjects were presented two subsequent, computer generated tones of different intervals. Their task was to judge pitch difference by reporting if the second tone was higher or lower compared to the first. Subsidiary seconds, thirds, fourths and tritones were applied in three different conditions differing in their stereo distribution. In condition 1 Shepard tones were presented mono, in condition 2 octaves of Shepard tones were distributed alternating in the stereo image and in condition 3 subjects were presented the top five octaves of a Shepard tone to their right, and the top five to the left ear.

Results show, that stereo distribution does not effect perception of the interval for subsidiary seconds and thirds. However, in condition 3, fourths—with the center frequency lying in between—are perceived as quints. Furthermore, there are different individual perceptional patterns. Some subjects perceive all the intervals as could be expected by the theory of binaural fusion, others confirm the hypothesis by Deutsch. A third of the subjects perform differently depending on the interval tested. A third of the subjects perceive the intervals as follows: they confirm the binaural fusion theory for subsidiary seconds, for thirds, no reliable pattern can be found. For quarts, their results apply to the theory of binaural suppression.

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Representational Momentum in Spatial Hearing

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When observers are instructed to localise the final position of a moving visual object, they usually remember its position to be displaced in the direction of motion [1]. This phenomenon was termed "representational momentum" because of its analogy to physical momentum in which a physical object continues along its path of motion due to inertia. The occurrence of representational momentum has been shown to depend on a number of variables, such as object velocity [2] and direction of motion [3].

A potential analogue of the representational momentum was investigated here in the auditory modality. In a dark anechoic environment, an acoustic target (continuous noise or noise pulses) moved from left to right (LR) or from right to left (RL) along the frontal horizontal plane, covering an angular range of 36°. Ten listeners judged the final position of the target sound by using a hand pointer. Target velocity was 8 or 16 deg/s. In a reference condition, stationary target sounds were presented at the final positions of the motion stimuli used in the main condition.

Generally, the final target positions were localised as displaced in the direction of motion. The most prominent displacements occurred with pulsed-noise stimuli: In comparison with the stationary condition, the overall displacements were 2.9° (SE +/-0.8°) for the lower target velocity and 3.8° (SE +/-1.2°) for higher velocity. With the continuous stimuli, there was a strong influence of target velocity, revealing larger displacements with lower (5.2°, SE +/-0.9°) compared to higher velocity (1.3°, SE +/-0.8°).

These findings suggest that the phenomenon of representational momentum is not restricted to the visual modality, although its origin remains unclear. Following a neurobiological approach, one may assume that sound movement initiates a process that results in a shift in the neural representation of auditory space [4]. Alternatively, more cognitive approaches of explanation of the visual representational momentum, dealing with principles of "internalised dynamics" [5], could be transferred to the auditory modality.

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Audiovisual Interactions During Speech Perception: A Whole-Head MEG Study

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The perceptual fusion of visually-presented phonetic features into the auditory processing stream during encoding of an acoustic speech signal has been described as the “McGurk effect”. For example, the acoustic syllable /ba/ can be perceived as /da/ when synchronized with a video recording of a speaker uttering the syllable /ga/. The present study was performed to determine the time course and hemispheric asymmetry of speech-related audiovisual interactions by means of magnetoencephalography (MEG). Video recordings of the syllables /pa/ and /ta/ were selected as prototypical video templates with respect to bilabial and alveolar place of articulation, respectively. Each of these two video syllables was synchronized with two different synthetic acoustic traces resembling the syllables /pa/ and /ta/. In order to have a non-speech control condition, two missing-fundamental complex tone signals, differing in pitch by one semitone (106 Hz, 112 Hz), were synchronized with the same two video templates as well. An oddball design was used during the MEG recordings. As concerns the speech conditions, audiovisually congruent signals served as frequent stimuli, rare events deviating from the standard events either in the visual or in the acoustic domain. Under the non-speech conditions, the video frequents and deviants were identical to the speech condition whereas the acoustic deviants were always the lower-pitch items within a series of higher-pitch standards. Subjects had to watch the video and to attend to the acoustic signals. In order to direct attention to the auditory channel, a behavioral response was required in case the subjects did not hear the frequent syllable or tone, respectively. The MEG results showed, as expected, a strong mismatch response to acoustic deviants, peaking ca. 170–190 ms post acoustic stimulus onset, that could be modeled by a bilateral diople structure within the region of the auditory cortex. Visual deviants elicited a mismatch response (latency ca. 220 ms) irrespective of the acoustic signal representing speech or non-speech, the magnetic source being located within the visual rather than the auditory cortex. Furthermore, subspace projection of the responses to visual deviants onto the ‘auditory’ mismatch dipole structure yielded a significant speech/nonspeech x hemisphere interaction, the speech condition giving rise to left-pronounced MEG responses with a latency of ca. 280 ms. No significant effects of visual mismatch were found within the time window of acoustic mismatch. These findings indicate that the phonological operations underlying the McGurk effect occur relatively late during perceptual processing and do not coincide with sensory memory operations reflected in the auditory mismatch response.

Temporal Limits of Melodic Music Perception

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Are there rate limits beyond which the perception of auditory event sequences breaks down? Are they fixed or subject to neural plasticity? In spite of a wealth of experimental studies on speech and music perception, the answers to such questions show remarkably little consistency. For example, a recent study [1] reports that listeners are able to discriminate two differently ordered tone sequences presented at rates of up to 30 Hz; however, when the task was to identify known melodies, performance deteriorated when the rate at which tones followed each other exceeded 6 Hz. The latter finding is surprising, as it stands in conflict with results on the perception of compressed speech [2], and on estimates of the fastest tempi in performed music, e.g., recorded performances of Chopin's piano études. To study the issue experimentally, we constructed a task that required listeners to perform temporal-order judgments on two tones embedded within musically meaningful tone sequences of 32 tones. Sequences were based on advanced piano exercises [3], and consisted of chromatic or harmonic (arpeggiated chords) tone material. Sequences were composed of eight identical 4-tone contours on the chromatic or the chord scale, following a global pitch trajectory that was either ascending (chromatic condition) or ascending-descending (harmonic condition). The listener's task was to decide whether all patterns followed the same contour, or whether the two middle tones within the fifth, sixth, or seventh pattern were reversed. Note that spectral differences were minimized because the deviating contour pattern contained the same tones as the corresponding regular pattern. The musical key of sequences were randomly chosen, such that there were 12 x 4 x 2 = 96 different regular sequences, which were played on ROLAND synthesizer under MIDI-control. Five listeners participated for two test sessions and five training sessions each. Training sessions presented the chromatic (harmonic) sequences at fixed IOI of 90 ms, and the harmonic (chromatic) sequences at IOIs that decreased by 4 ms per block, starting at 96 ms and ending at 42 ms. Almost all listeners showed better-than-chance performance at rates far below those reported in the literature; one listener (an expert accordionist) achieved recognition d's around 2.0 even at rates of up to 24 Hz. Additional control conditions were run to elucidate the factors that enable melody perception at tempi far beyond those predicted by current wisdom.

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Auditory Memory in Humans, Cats, and Gerbils

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Sensory memory for auditory stimuli has been demonstrated in humans [1], cats [2], and gerbils [3]. However, while the lifetime of auditory memory in humans extends to several seconds, it is shorter than 500 ms in both cats and gerbils. It is intriguing to consider that long-living auditory memory might have evolved with the evolutionary need to process long streams of auditory input such as speech. A possible test for this hypothesis would be the evaluation of the lifetime of auditory memory in songbirds.

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Comparison of ERPs to Complex Sounds and Simple Tones in Patients with Altered States of Consciousness

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In the literature there is a controversy to what extent the processing of spectrally rich sounds in the human auditory cortex is related to the processing of single frequencies. The issue of the present studies was to assess whether complex sounds are processed differently from simple tones in patients with severe brain injuries. We performed two studies. In the first study three auditory oddball paradigms (with simple tones, ST, complex sounds, CS, and vowels, V) were presented to 46 patients with severe brain injuries (most of them in persistent vegetative state or minimally conscious state) while P300 were recorded. Deviant stimuli elicited significantly more frequently the P300 to complex tones than to simple tones (CS: 28 %, ST: 7 %). Evidence of P300 to vowels lied in between (13 %). Likewise, the second study was investigated to ascertain whether the mismatch negativity (MMN) to complex sounds can be recorded more frequently than to tones. Two auditory oddballs were performed in 79 patients with severe brain injuries. Again, MMN to complex sounds were found more often than to tones (ST: 24 %, CS: 50 %). Both ERP components were larger in amplitude to complex sounds than to tones. Moreover, although in some patients P300 or MMN were absent to tones both ERP components were detectable to complex sounds. Thus, simple tones using in clinical populations may underestimate the ability of patients to distinguish between two different stimuli. The findings are also in line with the supposition of independent processing of complex sounds in the auditory cortex.

Gender-Specific Asymmetry in Spatial Hearing

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A multitude of studies have focussed on functional hemispheric asymmetries in audition by investigating differences in performance, depending on which ear receives the sound stimuli. Two main effects of laterality have so far been demonstrated. Firstly, language-related stimuli (e.g., speech) are usually recognized more accurately when presented to the right ear, suggesting a dominance of the left hemisphere (in right-handers) for speech perception. Secondly, complex tones with rich harmonic structure (e.g., melody) are perceived more accurately when presented to the left ear, suggesting preferential right-hemispheric processing of non-verbal acoustic parameters. These two laterality patterns depend on gender in quite distinct ways: males exhibit stronger asymmetry for verbal auditory stimuli, while females a stronger asymmetry for non-verbal stimuli [1]. This apparent dichotomy seems to reflect a complementary gender-based pattern of laterality in the functional organization of the cerebral hemispheres. Until now, the question of how the processing of auditory spatial information can be integrated into these conceptions of laterality has remained open. The primary aim of this study was to fill this gap. To this purpose, the precision of monaural localization of non-verbal stimuli in the median sagittal plane was tested with female and male dextral subjects. In a simple pointing task, subjects localized vertical positions of sound sources (broadband-noise bursts) in darkness with one ear blocked by a plug. Results show that females were significantly more precise when listening with the left ear, while males did better with the right. However, significant differences in monaural localization performance as a function of gender occurred exclusively when listening with the right ear, with males performing substantially more precisely than females. These findings suggest gender-related differences in the intrahemispheric functional organization of the left hemisphere for the processing of monaural spatial cues. It is proposed that the results may be related to the sexual dimorphism of the posterior parietal cortex [2], or planum temporale [3], both areas known to be involved in spatial auditory functions.

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Computer Vision and Robotics

A Graph Representation Applied on Miniature Robots for Modelling Territorial Behaviour

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Comparable to all other traits in animals, cognitive abilities are adapted to the animal's ecological niche[1]. The formation of an internal representation of the environment during spatial learning is such an essential capability needed in territorial behaviour.

To investigate the cognitive background of animal behaviour, computer simulation is a powerful tool. Hence, a well described model of animal territorial behaviour is required for our work. Such a model of territory establishment is presented by [2] for anolis lizards. The individual thereby assigns values to areas of its environment. The value reflects the probability of returning to the corresponding area. It decreases if an opponent is met in the area, but increases with every visit without opponent encounter. Thus the assigned value mirrors the attractiveness of its area. This model is implemented in computer simulation and on miniature robots.

As underlying representation for territoriality, a graph is used in our experiments. As shown in [3], robots are able to establish a territory using a grid representation. In contrast to the grid, the graph is built up stepwise and not determined from the beginning. Different influences of already visited areas on each movement decision lead to differences in space use.

The robots are able to establish a territory with the graph representation. The more existent nodes are used for movement decision, the smaller but more stable territories can be observed. The influences of different parameters of the graph on territorial behaviour are determined. Such paramaters are step length, weighting of the attractiveness value, and number of nodes used for movement decision.

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Local Processing in Spatiotemporal Boundary Formation

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Patterns of abrupt changes in a scene, such as the dynamic occlusion of texture elements (causing their apppearance and disappearance), can give rise to the perception of the edges of the occluder via a process called Spatiotemporal Boundary Formation (SBF). It has previously been shown that SBF can be disrupted by very small amounts of dynamic noise spread globally throughout a scene. We recently developed a mathematical model of SBF in which groups of local changes are used to extract edges, which are then combined into a figure and used to estimate the figure's motion. The model implies that SBF relies on local processing and predicts that SBF should be impaired when noise is added near the edges of the figure, but not when it is added far from the edges. This prediction was tested in a shape-identification task in which the location of noise is varied. Indeed, performance was not impaired by noise far from the figure, but was markedly disrupted by noise near the figure, supporting the notion that changes are integrated locally rather than globally during SBF. In the second part of this project, the mathematical model of SBF was implemented in software. Reichardt-based motion detectors were used to filter the experimental stimuli and provide the input to the software implementation. Three simple geometrical figures, similar to those used in the psychophysical experiment, were reconstructed using this method, demonstrating one way in which a mid-level visual mechanism such as SBF could connect low-level mechanisms such as change detection to higher-level mechanisms such as shape detection.

Direct Estimation of Pose and Illumination—An Analysis by Synthesis Approach

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Visual object recognition, localization, tracking and scene reconstruction all face the challenge, that the transformation of an image of a 3D scene to a geometrical model (analysis) is ambiguous. On the other hand, image synthesis from a geometrical model is well-defined and well-understood. Analysis by Synthesis takes advantage of this fact by utilizing a feedback loop for parameter estimation. It solves above-mentioned computer vision problems with methods of computer graphics: Modern graphics hardware is used to synthesize the predicted visual appearance of the scene. The difference between the rendered image and the captured camera image is utilized to compute a new and improved set of model parameters. Recent advances in graphics hardware have tremendously accelerated the processing involved in the feedback loop. This led to an increased attractiveness of Analysis by Synthesis methods for computer vision. Other appealing properties of these methods are:

1. Multi-modal sensor fusion can be solved in a straightforward way, if only the model can be rendered to the different sensor data representations. Besides images from multiple cameras we have utilized laser range scanners.

2. In contrast to other methods using only few features in a scene for parameter estimation, all available sensor data is taken into account.

3. It is not necessary to explicitly solve a data association problem like finding correspondences between image and model features.

The application of Analysis by Synthesis methods involves the following challenges: An adequate model in conjunction with an initial model parameter set must be available. This set has to be within a sometimes very limited convergence radius, which cannot be found in a high dimensional space without applying special techniques. During temporal tracking, it is crucial that the convergence radius is not lost.

The most important methods to increase the convergence radius are filtering of the input data and hierarchical processing. In certain cases, preliminary locking of parameter combinations during the iteration process can be employed to increase the speed of convergence.

For temporal tracking, Analysis by Synthesis can be combined with Sequential Monte Carlo methods. This means that the measurement of the Monte Carlo method is implemented in Analysis by Synthesis style with all its advantages.

Due to its inherent flexibility, Analysis by Synthesis methods show high potential in a wide area of applications. We have used it for estimation of illumination, pose and material properties of simple objects, panorama composition and map generation from laser range scans.

Focussing Object Recognition on Regions of Interest

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While humans are able to detect and recognize objects in their environment effordlessly, these tasks belong to the hardest problems in computer vision. One of the difficulties lies in the huge amount of data that has to be processed. In this work we restrict object classification to regions of interest detected by biologically motivated attention mechanisms. This yields a significant increase in speed of classification.

The sensor data used for our experiments are acquired by a 3D laser scanner mounted on top of an autonomous mobile robot. The scanner yields illumination independent range and reflection data, both visualized as gray-scale images. The advantage over camera images is, firstly, the illumination independence enabling the acquisition of the same data in sunshine as in complete darkness and secondly, the precise and dense depth information that is only achievable from camera data with difficulties.

The laser images are fed into a biologically motivated attention system. In human vision, attention helps identify relevant parts of a scene and focus processing on corresponding sensory input. Inspired by the psychological work of Treisman [1], computational attention models determine saliencies according to different features like intensity, color, and orientations in parallel and fuse them into a single map. The most salient region in this map determines the focus of attention. In contrast to other models, our approach fuses saliencies of both laser modalities, depth and reflection, to achieve a single focus of attention. The fusion of sensor modalities is performed in analogy to humans who use information from all senses and enables considering more object properties.

The regions of interest detected by the attention system serve as starting points for a fast cascade of classifiers [2]. In contrast to the conventional approach, we search for a previously learned object only near the focus of attention instead of considering the whole image. This enables a concentration on relevant image regions and a significantly faster classification, requiring only 30% of the time of an exhaustive search (60ms vs. 200ms, Pentium-IV-2400 MHz). Considering also the time for the attention system (230ms), the system performance already increases for two learned object classes and the time saving increases proportionally with the number of object classes.

In future work, the recognized objects will be registered in semantic 3D maps that are automatically created by the autonomous robot. The maps will support self-localization of the robot and serve as an interface between robot and humans.

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Efficient Approximations for Support Vector Classifiers

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In face detection, support vector machines (SVM) and neural networks (NN) have been shown to outperform most other classification methods. While both approaches are learning-based, there are distinct advantages and drawbacks to each method: NNs are difficult to design and train but can lead to very small and efficient classifiers. In comparison, SVM model selection and training is rather straightforward, and, more importantly, guaranteed to converge to a globally optimal (in the sense of training errors) solution. Unfortunately, SVM classifiers tend to have large representations which are inappropriate for time-critical image processing applications.

In this work, we examine various existing and new methods for simplifying support vector decision rules. Our goal is to obtain efficient classifiers (as with NNs) while keeping the numerical and statistical advantages of SVMs. For a given SVM solution, we compute a cascade of approximations with increasing complexities. Each classifier is tuned so that the detection rate is near 100%. At run-time, the first (simplest) detector is evaluated on the whole image. Then, any subsequent classifier is applied only to those positions that have been classified as positive throughout all previous stages. The false positive rate at the end equals that of the last (i.e. most complex) detector. In contrast, since many image positions are discarded by lower-complexity classifiers, the average computation time per patch decreases significantly compared to the time needed for evaluating the highest-complexity classifier alone.

Learning Depth

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The depth of a point in space can be estimated by observing its image position from two different viewpoints. The classical approach to stereo vision calculates depth from the two projection equations which together form a stereocamera model. An unavoidable preparatory work for this solution is a calibration procedure, i.e., estimating the external (position and orientation) and internal (focal length, lens distortions etc.) parameters of each camera from a set of points with known spatial position and their corresponding image positions. This is normally done by iteratively linearizing the single camera models and reestimating their parameters according to the error on the known datapoints. The advantage of the classical method is the maximal usage of prior knowledge about the underlying physical processes and the explicit estimation of meaningful model parameters such as focal length or camera position in space. However, the approach neglects the nonlinear nature of the problem such that the results critically depend on the choice of the initial values for the parameters.

In this study, we approach the depth estimation problem from a different point of view by applying generic machine learning algorithms to learn the mapping from image coordinates to spatial position. These algorithms do not require any domain knowledge and are able to learn nonlinear functions by mapping the inputs into a higher-dimensional space. Compared to classical calibration, machine learning methods give a direct solution to the depth estimation problem which means that the values of the stereocamera parameters cannot be extracted from the learned mapping.

On the poster, we compare the performance of classical camera calibration to that of different machine learning algorithms such as kernel ridge regression, gaussian processes and support vector regression. Our results indicate that generic learning approaches can lead to higher depth accuracies than classical calibration although no domain knowledge is used.

Image-Based Homing: Accuracy and Thresholds

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Localization based on (panoramic) images is often applied in mobile robots because of the low computational costs, e.g. [1]. Insects, e.g. honey bees and desert ants, also seem to use only slightly processed images to return to important places, like the hive or the location of a food source [2, 3]. We investigate the accuracy of visual homing with panoramic images considering sensor noise and image contrast. Based on Taylor expansion for small deviations from the goal location we present a mathematical description of the expected positional errors. We show that the results are directly related to the rate of change of the image with observer position, more formally defined as the "local image variation" (liv) in [4]. Evaluation of an image data base consisting of 1250 panoramic images recorded in the robot environment reveals that a higher liv-value corresponds to a lower positional error of image based localization. We also propose an extension of the widely used "Sum of Squared Differences" (SSD) measure of image similarity which normalizes for image contrast. Preliminary results show that—compared to SSD and image correlation—the "contrast normalized SSD" simplifies the choice of thresholds for image based homing in environments with strong variation of image contrast.

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Multimodal Interactions: Sensory Integration

Vestibulo-Ocular Reflex Eye Movements During Multiaxial Whole Body Rotations

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Vestibulo-ocular reflex (VOR) responses of humans to whole body rotations are well known. Along with other parameters, the "VOR-gain" (eye velocity / head velocity) may be used to evaluate the functional status of the VOR. Although VOR gain is known to show great individual variability, we sought to determine whether the adaptive plasticity of VOR gain may give insight about individual strategies for optimal spatial orientation. The question of whether the oculomotor responses would be different between a group of experts ("gym" - high performance gymnasts), with a high degree of spatial abilities, and a control group of non-athletes ("control"), was of particular interest. The subjects' (gym: n = 9, age: 10–12 years, control: n = 10, age: 10–12 years) eye movements were recorded using a video nystagmography system (SMI). They were seated with head fixed in a software controlled multiaxial whole body rotator. The test consisted of a combination of a two simultaneous sinusoidal 360° rotations about the pitch and yaw axes, followed by the reverse motion, simulating movements of "twisting somersaults". The maximum velocity was 113 deg/s in each axis, and duration was 10 sec for the whole test (0.1 Hz). Each subject was first rotated without knowledge of the nature of the stimulus, followed by a repetition where the subjects knew the same test would occur. This was compared to a standard sinusoidal monoaxial (horizontal) test (0.1 Hz, 100 deg/s). Although correctly directed eye movements were observed during all phases of the whole body rotation (including in a companion study with double twists), initial comparisons were performed on the horizontal components of eye movements and whole body rotation. The results show no significant difference between the gymnasts and controls for the sinusoidal test (gain ± s.d.,gym.:0.48±0.06, n=9, non.:0.45±0.14, n=9; p=.565, Z=-.575, Mann-Whitney-U), and the first (w/o prior knowledge) multiaxial stimulus (gym.:0.48±0.05, n=8; non.:0.47±0.07, n=9; p=.596, Z=-.531, Mann-Whitney-U). For the second (prior knowledge) multiaxial stimulus, the difference was significant ((gym.:0.39±0.05, n=6; non.:0.45±0.06, n=6; p=.037, Z=-2.085, Mann-Whitney-U). Finding no difference for the tests without expectations of the stimulus show that the reflexive response has not been adapted in this context. But the significant difference following preparation of the stimulus shows the gymnasts suppress even reflexive eye movements. This is consistent with the companion poster indicating that gymnasts may rely heavily on visual orientation mechanisms at the expense of vestibular responses, both cognitive and oculomotor.

Feeling what you Hear: an Auditory-Evoked Tactile Illusion

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Previous research indicated that sound can bias visual [1–4] as well as tactile perception [5,6]. The present experiment tested whether auditory stimuli can alter the tactile perception of sequences of taps (2 to 4 taps per sequence) delivered on the index fingertip. The taps were delivered using a PHANToM force feedback device. The subjects did not have any visual or auditory feedback about the tactile stimulation and their task was to report after each sequence how many taps they felt. In the first experiment, for some trials, auditory sequences of beeps were presented concomitantly with the tactile sequences (through earphones). The number of beeps diffused in the auditory sequence could be the same as, less, or more than the number of taps of the simultaneously presented tactile sequence. Though irrelevant (subjects were instructed to focus on the tactile stimuli), the auditory stimuli systematically biased subjects' tactile perception, i.e. subjects' responses depended significantly on the number of diffused beeps. The results also suggested that for such an auditory-tactile interaction to occur, a certain amount of "structural" congruency between the simultaneously presented stimuli is required. Indeed, the diffusion of an auditory stimulus obviously incongruent with the tactile sequence failed to evoke any bias of tactile perception. In the second experiment, we tested whether the auditory-tactile interaction also requires temporal congruency or whether a bias can be evoked without temporal overlapping between the auditory and tactile presented sequences. The tactile and auditory stimuli were the same as in the first experiment (the structurally incongruent auditory stimulus was not used here) but the auditory sequences were presented either simultaneously with, before the beginning, or after the end of the tactile sequences. Audition strongly biased tactile perception when the stimuli were temporally concomitant (reproduction of the results obtained in the first experiment). With a temporally asynchronous audio-tactile stimulus the interaction gradually disappeared. We conclude that auditory and tactile sensory signals are integrated when they both provide redundant information in good temporal coherence.

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Visual-Vestibular Integration in Gymnasts

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Berger et al. [1] have shown the general dominance of visual to vestibular perception in a setting of combined stimulation requiring integration of sensory modalities. In the present study we evaluate different integration strategies during presentation of dissociated visual-vestibular stimuli as a function of the individual spacial orientation ability of the subjects. We present the results of the gymnasts for discussion. The subjects (n = 10, age: 10–13, height: 140,33 +/- 4,09, mass: 32,89 +/- 2,32) were rotated in a spherical chamber, with simultaneous presentation of a planetarium type visual stimulus with an independently controlled velocity. Testing consisted of a standardized randomized sequence of 26 horizontal rotations in both directions with different visual-vestibular dissociation factors (the difference between the velocities, normalized to the rotational velocity). The factors presented were in steps of 0.2 between 1 and -1, and additionally 2 and -2. Auditory stimuli were blocked using headphones. The rotatory stimulus consisted of a velocity step of 60deg/s with a duration of 6 seconds. After each turn, two questions were asked: 1. “Which direction did the stars turn in relation to you?” (to control for visual perception and concentration) 2. “Which direction did the stars turn in relation to the room?” (to test the visual-vestibular integration). Correlation analysis of correct responses to question 2 against the individual “perrotatory space orientation ability” (PSO) as independantly evaluated by three coaches was performed. Results: A positive correlation between the visual-vestibular dissociation factors and the number of correct answers to question 2 was found [Pearson: r = 0,81 with positive dissociation factor (determination coefficient: 0,65); r = 0,81 with negative dissociation factor (determination coefficient: 0,66)]. However, there was a negative correlation tendency between the ratio of the correct answers and the PSO of the subjects (Spearman, rank using the coach questionnaires:k=0.60, determination coefficient: 0,36). Discussion: The first result corresponds to previous work and demonstrates the dominance of visual to vestibular perception for lower dissociation factors. More remarkable is the second result showing the higher the PRO, the worse the ability to determine the stars’ direction. The results require one to consider that perhaps the gymnasts have learned to give a superior weight to the visual information over the vestibular sensation, not as an integrative strategy, but rather a form of sensory filtering. This opens the discussion for how best to evaluate the integrative or filtering abilities of the age-matched group of non-athletes.

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Multisensory Interaction Modulates Spatial Selectivity of Auditory Processing

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Crossmodal interactions are suggested to affect spatial attention selectively. Two different mechanisms are proposed to account for spatial attentional functions. A covert top-down mechanism is located in intraparietal and superior frontal regions, whereas a stimulus-driven, bottom-up process includes temporo-parietal cortex and inferior frontal cortex and is largely lateralized to the right hemisphere. Multisensory representations of spatial objects interact within the central nervous system at different levels. Recently, the modulation of preattentive responses (MMNm) at the level of the auditory cortex has been shown to depend selectively upon oculomotor, visual, and tactile pre-cues in the absence of attention. Auditory virtual reality allows to position auditory objects at arbitrary positions in the perceptual space during whole-head magnetoencephalographic recordings. We showed in a first experiment neuromagnetic responses of the auditory cortex to virtual auditory sources following visual pre-cues placed at 15° distance in the frontal semicircle. Early components like P50m were enhanced for the contralateral side of the respective hemisphere but did not exhibit a selective influence of the pre-cues. In contrast, the N100m depended on the place of pre-cues at both hemispheres. In a second experiment, auditory stimuli located at both left and right face and hand were preceded by tactile pre-cues at these locations. The lateralized stimuli yielded a contralaterally enhanced P50m and a "proximity" effect, i.e. larger responses to close stimulation at the face. If pooled together, somatosensory pre-cues interacted in such way with auditory responses that both P50m and N100m components were reduced afterwards. These unspecific effects were followed by spatially selective interactions: when facial tactile stimuli preceded auditory stimuli at the same side, the N100m was larger over both hemispheres. Thus, at this level, the tactile pre-cues facilitate and prepare an attentional switch into the desired direction. Conceivably, a cortical supramodal network is sensitive for spatial cues at the level of long-latency components. However, earlier responses are mainly governed by exogenous stimulus onset properties and multisensory interaction is arising in a rather unspecific form only. These multisensory networks are modulated in a spatially selective way. We suggest, thus, that integrated multisensory networks act as a base for a spatial attentional control system.

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Reference Frames of Multisensory Space Representations

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Primates can use different sensory signals to localize objects in the environment. Depending on the behavioral situation, the brain chooses the modality conveying the most reliable information to guide behavior. Accordingly, neural structures encoding signals from more than one sensory modality are best suited for representing information about space. The posterior parietal cortex (PPC) is a key structure for spatial representations. One substructure within human and macaque PPC is the ventral intraparietal area (VIP), known to represent visual, vestibular, and tactile signals. In the present study we were interested in the question whether VIP neurons would respond to auditory stimuli and if so, in which reference frame this response would occur.

We recorded neuronal activity in area VIP of two awake macaque monkeys and mapped visual and auditory receptive fields within the central 60°x60° of space while the monkeys fixated at different azimuthal positions (-10°,0°,10°). To map auditory responses we used a virtual auditory environment based on the monkeys' individually measured head related transfer functions (HRTFs). We positioned white noise bursts via calibrated headphones at various virtual positions within the mapping range. The visual responses of the cells were mapped with spatially non-overlapping moving white bars. We computed receptive fields for each modality and determined their spatial shift for different fixation positions by means of a 2D cross-correlation analysis. This allowed us to reveal the signals' reference frames.

Spatially localized auditory and visual receptive fields could be determined for 91 and 124 neurons, respectively. In most neurons the auditory and visual RFs largely overlapped. Early visual areas provide position information in retinal coordinates. Auditory information is initially encoded with respect to the head. Yet, we found that not only visual but also auditory spatial representations were transformed into a continuum between these two reference frames. Accordingly, our data provide for the first time experimental evidence for the hypothesis of a simultaneous encoding of multisensory signals in different reference systems as put forward in modeling studies on the sensorimotor function of the PPC in normal human subjects and its malfunction in parietal patients.

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Multimodal Interactions: Sensory-Motor Integration

Expansion Plays a Role in Quickly Determining whether a Ball will Land in Front of you or behind you

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Chapman [1] proposed that ball catchers run backwards when they see the projection of an approaching ball accelerate, and forwards when they see it decelerate. However, the threshold for distinguishing acceleration from deceleration is too high to account for catchers' performance in selecting the appropriate running direction. We propose an alternative cue, which is based on a combination of estimates for the ball's horizontal and vertical speed. These estimates are based on the rate of expansion of the ball's projection, and its angular velocity, respectively. In order to test this alternative cue we simulated the first 300 ms of an approaching ball on a large screen. The rate of expansion was either simulated realistically, or else the simulated ball either expanded too fast or too slowly. Subjects indicated whether they expected the ball to land ahead of them or behind them. If subjects use the Chapman strategy, our manipulation of the rate of expansion should not make a difference, because the vertical acceleration of the projection was not varied. If they use the cue that we propose, they should be biased to respond 'ahead' when the rate of expansion is reduced and 'behind' when it was increased. We did find such biases. However, the difference between the conditions was not as large as we predicted. This may indicate that subjects use additional cues to estimate the ball's horizontal speed.

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Does Non-Visual Motor Training Influences the Recognition of Biological Motion?

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Introduction: Neurophysiological and fMRI studies seem to support an involvement of the motor system in perception of biological motion. These results have been interpreted as support for a "common coding" of perception and action [1]. One prediction of a "common coding" of action and perception is that learning of new motor skills should influence the visual perception of similar motor behaviors. Unfortunately most studies so far have focused on how perceptual judgments are influenced by concurrent motor actions. Only few experiments have focused on motor learning [2]. We evaluated this prediction by testing whether motor learning, without visual feedback, influences the perception of biological motion.

Methods: Subjects had to discriminate between point light walkers in a same/different paradigm. Arms and legs of point light walkers realized coordination patterns that are either frequent, or very infrequent (i.e. implementing phase shifts between 0 and 180 deg, but maintaining synchrony between contralateral arms and legs). Subjects were then blindfolded and trained to execute an uncommon phase relationship with their arms. During this training only non-visual feedback was provided. Also any cues that would provide explicit temporal rhythms were avoided.

Results: Our preliminary data shows that before training subjects show significantly better discrimination results for common phase relationships (close to 180 deg). After the motor training performance in the visual recognition task increases selectively for the trained unfamiliar phase relationship, even though no visual input was provided during training.

Conclusion: Our result seems consistent with a top-down influence of internal motor models, or abstract representations for relative timing on the recognition of biological motion.

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Where Action Impairs Visual identification—Action-Induced Blindness in Two Event-Related fMRI Experiments

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Behavioral studies revealed an impact of action on visual perception. If participants are engaged in a motor task they proved to be worse in identifying a visual stimulus (Action-Induced Blindness effect [1,2]). In two event-related fMRI experiments healthy participants had to accomplish a visual identification task combined with a GO-NOGO task. Thus, we were able to investigate the influence of a motor response on visual identification. Three different stimulus onset asynchronies (SOAs) were used that provided different overlaps between the motor task and the visual task. We compared visually identical trials with and without a concurrently-performed motor response. Behavioral data revealed an impairment of visual identification in GO trials compared to NOGO trials. This discrepancy is most pronounced at short SOAs, i.e. when the motor task and the visual identification task processing overlap to a great extent. In a GO vs. NOGO contrast fMRI results showed an action-dependent BOLD response modulation in the extrastriate visual areas V3/V3A and, additionally, V4 in Experiment 2. Thus, results demonstrated that the planning of an action has modulatory effects in brain areas concerned with early processes in visual encoding, resulting in an identification impairment.

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The Quality of Feedback does not Affect the Rate of Visuomotor Adaptation.

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Under many conditions, the human visuomotor system quickly adapts when confronted with spatially discrepant stimuli. This adaptability can easily be demonstrated with for example the change in pointing behavior when first wearing prism glasses. Here we asked whether the quality of feedback, that is its reliability, has an effect on the rate of adaptation. The hypothesis was that the system should adapt more quickly if the feedback was more reliable. To investigate this question we conducted two adaptation experiments: One pointing experiment (closed-loop), in which we measured the rate of adaptation to a lateral prismatic displacement, and a grasping experiment (open-loop), in which we measured adaptation to a size conflict of visually magnified objects. The experiments were conducted in three phases: A pre-adaptation phase to establish baseline performance, an adaptation phase in which the visuomotor conflict was introduced, and a post-adaptation phase to determine the after-effect. We determined the rate of adaptation from the change in visuomotor behavior during the second and third phases. In several conditions the reliability of feedback was manipulated. In the pointing experiment we varied the feedback reliability by blurring the target stimulus, which was a Gaussian blob of 10% contrast (sigma = 4, 32, 48 deg). In the grasping experiment we presented rectangular blocks of five different sizes for open-loop grasping. Here the feedback was manipulated by either adding noise to the visual display or by varying the haptic presentation time. The effectiveness of all feedback manipulations was assessed by measuring discrimination thresholds. To our surprise, in both experiments, closed-loop pointing and open-loop grasping, there was no significant effect of the reliability of feedback on the rate of adaptation. We conclude that the rate of visuomotor adaptation depends on the sensory estimate that determines the conflict but not on its reliability.

Cortical Modulation of Extrageniculocortical Binocular Processing: A Comparative Single-Unit Analysis in Pigeons (Columba Livia)

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Within the geniculocortical processing pathway visual information is transferred from retinal ganglion cells via the corpus geniculatum laterale to V1 of the visual cortex. Furthermore, retinal information becomes processed via the colliculus superior to the pulvinar, a diencephalic nucleus, which structure and function is mainly unknown. Pigeons show homologue visual processing pathways, but compared to mammals their optic nerves are completely crossed. Therefore they are ideal models for studying the characteristics of neuronal cell responses in the pulvinar during the processing and integration of visual information. We recorded from 162 single neurons in the homologue of the left and right pulvinar of 26 pigeons. During our recordings we stimulate the eye either monocularly or binocularly for 500 ms using a wholefield light stimulus. Control measurements without any stimulation were done for the measurement of spontaneous cell activity. Our results reveal a fast response component of “pulvinar” neurons after contra- and bilateral stimulation of the eyes that can be explained by an extrageniculocortical processing pathway. Moreover, many neurons (49% in the left and 22% in the right “pulvinar”) show a second delayed response component in form of a plateau (sustained activity) after binocular stimulation of the eyes. The summation of the delayed component with the fast extrageniculocortical response leads to a significant delay of adaptation of bilateral cell responses. The latencies of delayed response components are compatible with the notion of cortical feedback neurons which innervate neurons of the pulvinar via the colliculus superior. Indeed we could demonstrate, that temporal blocking of the V1 homologue in pigeons with lidocaine lead to a significant reduction of the amplitude of plateau components in the “pulvinar”. The behavioral relevance of the cortical modulation of binocular cell responses in the extrageniculocortical pathway is still unclear. Mechanisms of attention, signal enhancement and sensorimotor integration will be discussed.

Our research was performed under guidelines established by the German Welfare Law and were permitted by the responsible state authority.

Is there a Dynamic Illusion Effect in Grasping?

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Glover and Dixon [1] suggested that the effects of visual illusions on grasping vary over the time course of the grasp movement. For example, the Ebbinghaus illusion should exert a large effect at the beginning of the movement, while the effect should decay at the end of the movement. Glover [2] interprets this result as evidence for two different processes which guide movements: An early "planning" process which should reside in the ventral cortical pathway and a late "control" process in the dorsal cortical pathway. In an number of experiments I tested these claims. Participants grasped disc surrounded by Ebbinghaus figures and the temporal dynamics of the grasp trajectories was determined. Grasping was performed with and without visual feedback. Special care was taken to determine the time point at which participants touched the target object, because from this time on the measured illusion effects will be contaminated. I found surprisingly constant illusion effects over time. This result challenges the planning-control model.

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The Problem of Limited Capacity of Computational Resources

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It is widely accepted that our ability to direct attention towards either a specific location or towards a specific property of our environment is essential for successfully handling the huge amount of data being transferred from the sensory organs to the central nervous system. Attention is either directed as the consequence of an external event (exogeneous, bottom-up) or, alternatively, as the consequence of internal reflections (endogeneous, top-down). Here, we ask whether events in the environment, absolutely irrelevant for the task completion of subjects, are able to allocate computational resources of our subjects. We speculate that this allocation might be visible by the change of either saccadic latency or the dynamic saccadic parameters.

The IR (infra-red) tracker recordings of 7 healthy subjects revealed that target position (-10, -5, 5 or 10°) did not affect saccade latency. None of the latencies, post-saccadic error and the dynamic parameters (main sequence) was different when the saccade target was either presented on a dark background or a structured background. However, if the orientation or the luminance of all background lines was changed at the same time that the saccade target was presented, a massive, statistically significant (ANOVA with subsequent post-hoc test, $p < 0.01$) increase in saccadic latency was observed. It is important to note that neither the post-saccadic error nor the main sequence was affected in this condition. To reveal whether this increase in saccadic latency results simply from another sensory stimulation concomitant to the target presentation, we ran additional experiments in which we used an additional auditory stimulus irrelevant for the saccade task. In contrast to the change in visual background property, the saccadic latencies were not affected at all in this condition (ANOVA, $p > 0.05$).

We conclude that the changes in the visual background reflexively allocate computational resources. This direction of attention is neither confined to a specific location nor to a specific feature in the display. As a consequence of the allocation, the latency, but not the execution of the saccades was delayed. However, this effect of re-allocation of capacity is not present across different modalities.

Real Walking in Virtual Environments

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Experiments in VR are increasingly useful for research of human navigation and orientation. But they suffer from different problems. One of these problems is the incompatibility between field of view and real movableness. Wearing a head mounted display gives the possibility to walk around like a pedestrian in reality. But visual field of view and resolution of the image of the virtual world are poor. Standing in the middle of the projection sphere of a high-resolution projection system, the optical image fills the whole field of view and the scene could look very realistic. But is not possible to move more than one step away from the focal point without loosing the realistic visual impression. To solve this problem, different theoretical and practical approaches have been made. Some labs use fixed based wheelchairs or bicycles to supply the experimental subject with some of the stimuli of real moving without leaving the focal point. We have constructed a treadmill to give our experimental subjects the possibility to walk freely like a pedestrian in reality. A system of infrared emitters, infrared cameras, and scene analysing software located the longitudinal position and heading of the experimental subject. The movement of the treadmill holds the subject regardless of his or her movement speed in the same distance to the projection sphere. The projected image itself reacts to the heading movements of the subject and centres his or her lateral deviations back to the middle of the treadmill path. We present the first results with this new equipment and discus them with respect to the usability of the equipment in navigation experiments in large-scale VR areas.

Contributions of Primate Area MST to Goal-Directed Behavior

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When we perform goal-directed movements towards a moving target, a precise estimation of the target's velocity is essential. Earlier investigations of neuronal activity in primate area MST have shown that neurons respond directionally selective during smooth pursuit eye movements. Additionally, intracortical micro-stimulation (ICMS) in area MST as well as lesions in this area were shown to affect the velocity of smooth pursuit eye movements. Here, we addressed the following two questions:

1. In which frame of reference do area MST neurons code for the trajectory of a moving target? 2. Are the contributions of area MST confined to the execution of eye movements or alternatively, do they have also an impact on goal-directed hand movements elicited by moving targets?

In our studies concerning the single-unit responses of MST neurons, we used two different tasks: on one hand, we trained our monkeys to perform either isolated eye movements or combined eye and head movements to track a moving target. On the other hand, we used a combination of pursuit task and vestibular stimulation. The outcome of both series of experiments indicated that single-units in area MST code for target movement within an external frame of reference. If we applied ICMS in area MST, we were able to demonstrate that this stimulation accelerates movements towards the preferred direction of the stimulated site. This effect was present for eye movements as well as for hand movements. Finally, we applied transient lesions of area MST by injections of small amounts of muscimol. These lesions resulted in deficits in the estimation of ipsiversive target velocity. This effect was again present for eye as well as for hand movements.

We conclude from our results that the neuronal activity of primate area MST represents target velocity in a world centered frame of reference. This information is not only used to generate an appropriate eye movement program, i.e. smooth pursuit eye movements. In addition, this information is also used to generate goal-directed hand movements, so it might represent a very general representation of target trajectory independent of the actual performed tracking action.

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Contributions of the Skeleton to the Organization of Sensation and Perception.

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Sensation and perception always has a biomechanical basis to allow avoidance and approach, and clearly the performance of spatiotemporal movement has to fit the spatiotemporal performance of sensation and perception. On the biomechanical side the performance is the result of the specific geometry of the skeleton. But vertebrate mechanics is not only the basis of movement. The skeleton also has incorporated elements, which define the performance of sensation and perception. This is the contribution of the geometry of the skeleton to sensation and perception. The focus on this aspect allows to distinguish general incorporated patterns and the pattern of higher signal processing . This distinction is very important in the construction of autonomous robots and their self-reference, also in environmental contact and machine-man communication.

Acoustic signals are processed in the central auditory system. But if we look at the organization of the signals, mirrored e.g. by the MIDI notation of sound, the sensation clearly has a specific layout, which allows (or forces) to perceive the same tone in different octaves. So it may be questioned, to understand this as a signal processing performed by the central auditory system—or to understand this auditory sensation and perception to be forced by incorporated patterns.

A method to evaluate this question is a generalization of the organization of sensation and perception to fit related cranial patterns.

A good candidate for a bodily forced auditory sensation and perception is the specific geometry of the cochlea. Its geometry visibly is the pattern of higher order sensation and perception. Also the cochlea is part of the cranium, and thus integrated in the total vertebrate system and it spatiotemporal performance, accordingly.

The Perception of one's Own Hand Movement Depends on an Adaptable Internal Model of the Action

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The brain continuously makes predictions on the outcome of our behavior by resorting to internal representations (=internal models) of the input-output properties of the sensorimotor apparatus. These predictions should be constantly optimized in order to guarantee that the prediction matches the behavior it simulates. While intriguing, the concept of internal models improving perception is still lacking compelling empirical support. In order to test this concept, we studied the perception of one's own hand movements. We wanted to know if this specific perceptual faculty builds on an adaptable internal model of the movement and, moreover, if the internal model facilitating perception is congruent with the one optimizing motor performance. Seven human subjects carried out center-out pointing movements in complete darkness. Hand position was fed back visually using a virtual-reality configuration. This allowed us to move a visual cursor in the same plane as the hand either according to the actual movement or, alternatively, according to a 30° clockwise rotation of the cursor movement vector relative to the hand movement vector. In the latter case, visual feedback was no longer congruent with motor intention and proprioceptive feedback. The question was, if subjects are able to adapt to these distortions, allowing them to attribute what they see to their own agency, an interpretation which would require a modified expectation of the visual consequences of their hand movement, i.e. a modified internal model. Indeed, when applying distorted visual feedback the perceived pointing direction shifted significantly ($p<0.01$) in the direction of the trajectory rotation, on average 40% of the rotation of 30°. The same perceptual reinterpretation could be observed on catch-trials, in which no visual feedback was available ($p<0.001$). As demonstrated by controls, in which we could show that the subjective visual horizontal and vertical are stable, the perceptual reinterpretation is not secondary to shifts of a low-level visual reference frame. Although there was a tendency for compensatory movements opposite to the direction of the imposed rotation, these changes in movement trajectories were not statistically significant and on average smaller than the perceptual adaptation (20% of the rotation). These observations are in full accordance with the notion of internal models in perception. Not only do they show that the perception of one's own action depends on adaptable internal models, but also they demonstrate that the internal model for perception is at least partially independent of the one guiding the action.

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How the West was Won: Reactive Vs. Intentional Movements

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In the Wild West, legend has it that the guy who draws his gun first is the one who gets shot. The idea behind this is that intentional actions are slower to execute than reactive actions. To see if there is any truth in this notion we staged mock duels in the laboratory. Initially 12 observers were trained to make a speeded sequence of button presses for three keys located in front of them. After subjects had become proficient at the task (40 minutes training), we paired them up and they dueled against each other. The two subjects in a duel had different roles: one was the initiator and the other the reactor. A computer randomly determined which subject was the initiator on every trial. Initiators were free to start their movement sequence when they wanted. Subjects played against each other to be first to complete the movement sequence. The first person to complete the sequence scored points off the other player. Reactors rarely beat initiators (i.e. reactors normally got shot); however, the within-subject analysis of movement times made when the subject was the reactor versus the initiator suggested an average of a 20ms advantage for reactive movements. These preliminary results suggest that even though the guy who draws second gets shot, reactive movements may be faster than intentional ones.

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Motor Significance Overrides Attentional Modulation—Premotor Cortex Investigated with fMRI

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The lateral premotor cortex is known to be modulated by attention to different stimulus properties. This has been suggested to reflect a representation of perceived stimuli according to a habitual pragmatic body map. We used functional magnetic resonance imaging (fMRI) to investigate whether an arbitrarily assigned motor significance for a particular stimulus property influences the premotor activation during a purely perceptual serial prediction task. To this end, subjects trained a sensorimotor mapping linking either four objects of different size or four spatial orientations to the four fingers of one hand. We employed a two by two mixed design with between-subject factor TRAINING (motor significant stimulus property object size vs. spatial orientation) and within-subject factor PROPERTY (attended stimulus property object size vs. spatial orientation). During the experiment, all subjects performed in both serial prediction of object sizes as well as of spatial orientations. Additionally, we introduced catch trials (11%) for the motor significant property, where subjects were required to reproduce the encoded sequence, in order to test the sensorimotor mapping. In a first step, activation during encoding a sequence was contrasted with activation in control trials separately for sequences with and without motor significance. In the following, these contrasts were compared between subjects who were attending to object sizes and subjects who were attending to spatial orientations. We expected attending to object sizes to elicit more ventral premotor activation as compared to attending to spatial orientations, which we expected to elicit more dorsal premotor activation [1]. Results showed that this pattern was present in trials without a motor significance, whereas it vanished in trials with a motor significance. These results were further confirmed by discriminant analyses on sagittal and axial location of individual activation peaks. Subjects attending to objects could be discriminated from subjects attending to spatial orientations on the basis of their axial location within the left hemisphere in trials without motor significance, while this was impossible in trials with motor significance. Moreover, the mean coordinate of maximal activation in trials with motor significance was located in a more dorsal part of the premotor cortex, regardless of whether subjects attended to object sizes or spatial orientations. Thus, an arbitrarily assigned motor significance influences premotor activation, overriding the property specificity. This points to an extreme flexibility of premotor cortex in the adaptation to different task demands.

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Sequential Modulations of Logical-Recoding Operations in the Simon Task

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The Simon effect consists of faster responses to the color (or another non-spatial feature) of spatially corresponding stimuli than to spatially non-corresponding stimuli. Recently, several studies observed the Simon effect after corresponding predecessor trials, but not after noncorresponding predecessor trials. To explain these sequential modulations, Stürmer et al. [1] proposed a mechanism modulating the ability of stimulus position to automatically activate a response. The present study investigated which events are effectively triggering this mechanism. Possible triggers are the (non-) correspondence between stimulus and response position, or the (non-) correspondence between the response activated by stimulus color, and the response activated by stimulus position. To test between these hypotheses, a Simon task was used, in which both stimuli and responses varied in color (participants wore colored gloves) as well as in horizontal position. In the same-color task (e.g. green stimulus—green response/hand) a normal Simon effect showed up after corresponding trials, but no effect occurred after noncorresponding trials. In the alternate-color task (e.g. green stimulus—red response/hand) no effect occurred after spatially corresponding trials, whereas an inverted Simon effect was found after noncorresponding trials. Additional analyses showed that repetition (or alternation) effects did not affect the results. The results are consistent with a conflict-monitoring mechanism as an explanation for sequential modulations of the Simon effect [1]. Moreover, these results suggest that the relationship between the response activated by stimulus color and the response activated by stimulus position triggers the conflict-monitoring mechanism. Yet the results are also consistent with an alternative, feature-integration account for sequential modulations of the Simon effect [2].

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Perception of Time

Does Covert Attention Impair the Temporal Resolution of the Visual System? Not Always!

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When covert attention is oriented to a particular location in space, a stimulus at this location is easier to detect and to identify. Thus the bulk of studies on visual attention clearly supports the notion that attention enhances the spatial resolution of the visual system. Recently, however, Yeshurun and Levy [1] reported that covered attention impairs the temporal resolution of the visual system. When their subjects attended the stimulus location, the detection of a single temporal gap within an otherwise continuous stimulus was lowered. To assess whether this surprising finding generalizes to another temporal discrimination task, we examined the influence of covert visual attention on temporal-order judgments. In a first experiment, subjects judged the temporal onset order of two adjacent dots. An exogenous cue shifted attention either toward the target location (valid trials) or toward the non-target location (invalid trials). Consistent with the results of Yeshurun and Levy [1], discrimination of temporal order deteriorated in the valid condition. In a second experiment, we also employed neutral cueing conditions to assess temporal interference effects. The results of this experiment, however, suggest that the negative cueing effect in our first experiment is due to non-attentional interference, which degrades performance at the cued location. The whole pattern of our study supports the notion that attention does not generally impair the temporal resolution of the visual system.

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Perceptual Development

Statistical Structure and Serial Learning in Children

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Serial learning has recently been predominantly investigated with the serial choice reaction task (SRT): Individual stimuli are successively presented to participants. The participants are required to react to the stimuli as quickly as possible with different responses. Typically, a screen is used for the presentation of stimuli and key pressings on a keyboard are the corresponding responses. Reaction times and error rates are measured. In general, statistical structures in the sequence of stimuli and responses decrease reaction time, indicating sequential learning. Moreover, it has also been shown that learning is caused by redundancies in the sequence of stimuli as well as in the sequence of responses. However, it is still an issue as to whether or not serial learning of stimulus and response sequences is based on a single learning mechanism and how this learning process develops. In the present experiments, the sequences of responses (Study 1) and the sequences of stimuli (Study 2) were separately varied. The statistical structures of stimuli and responses, including frequencies (condition a) and transitions (condition b), were also separately varied in each study. A total of 24 six-year-old children, 24 eight-year-old children, 24 ten-year-old children and 24 adults took part in each study. In the current SRTs, 16 cards from a deck of playing cards with four numbers (1, 2, 3, 4) and four colors (red, green, yellow, blue) were used as stimuli. Four different keys of a keyboard were the respective responses. In Study 1, neither age nor condition had a significant effect on the results. Children and adults performed equally well. They displayed explicit knowledge and a structure specific decrease in reaction time during the task. In Study 2, children's learning was effected by frequencies, but not by transitions, and the children showed implicit knowledge of the frequencies. Adults demonstrated explicit learning of both varied statistical structures. In both studies, children's reaction times were consistently slower than adults' reaction times, however the error rates were nearly the same. In conclusion, the results show that, when frequencies and transitions are investigated separately, children and adults differ with respect to stimulus learning. With regard to response learning, however, children and adults perform comparably. Therefore, statistical regularities as frequencies and transitions, and variations in stimulus and response sequences, should be considered in future SRT studies on the development of serial learning.

Perceptual Neuroscience

Processing of Shape from Coherent Motion in the Human Visual Cortex.

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Interactions in our dynamic environment require that the visual system processes both the shape and motion of objects. Different cortical areas have been proposed to be involved in the processing of visual motion (hMT+/V5 = human middle temporal homologue), kinetic boundaries (KO = kinetic occipital) and object shape (LOC = lateral occipital complex). The goal of this study was to investigate whether these areas are involved in the perception of shapes defined by motion coherence. To this end, we used human event-related fMRI and employed stimuli in which the shape was defined by the relative motion of random dots in the shape and the background. We manipulated the perception of these shapes by independently varying the motion coherence of the dots in the shape and the background. Increased motion coherence in either the shape or the background improved the behavioral performance of the observers in a shape categorization task. FMRI responses in the LOC and KO were consistent with the behavioral performance; that is, enhanced fMRI responses were observed with increased motion coherence in either the shape or the background. Interestingly, hMT+/V5 showed activation patterns similar to the LOC, suggesting strong interactions between ventral (LOC) and dorsal (hMT+/V5) visual areas in the perception of shape from motion. To further investigate shape representations from motion in the different visual areas we tested for selectivity for shape and motion direction information. To this end, we used an fMRI adaptation paradigm in which lower fMRI responses are observed for two identical than two different stimuli presented consecutively in a trial. Recovery from adaptation was observed across changes in shape in the LOC, KO, and hMT+/V5, but not in early visual areas. In a third study, we tested whether shape and motion related areas are selective for the 3D structure of shapes. To this end, we employed an fMRI adaptation paradigm and similar stimuli as in the two previous studies. In addition, these stimuli were rendered with 3D structure using horizontal disparity cues. Recovery from adaptation was observed across changes in 3D structure in the LOC, KO, and hMT+/V5. In summary, these findings suggest that not only object (LOC) but also motion-related areas (hMT+/V5) are involved in the selective representation and perception of shapes defined by coherent motion.

Temporal Instability in Amblyopic Vision

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Two different methods were used for the evaluation of spatial and temporal distortions in strabismic and anisometropic amblyopic vision. In both, the quantitative and qualitative procedure, main focus was on the temporal instability which has been reported quite often in amblyopic research but never investigated in detail. First, the amblyopic participants were asked to describe their subjective percept of patterns of different spatial frequencies. Three out of four strabismic and two out of three strabismic-anisometropic amblyopes and only one out of four anisometropic amblyope sensed temporal instability. This was only true for the higher spatial frequencies, spatial distortions in low spatial frequency had a stable character. The type of temporal instability was twofold: either the whole pattern was perceived as jittering or some lines or parts in the pattern were perceived as moving. Second, we used a circle-construction-method to acquire quanitative data of the spatial distortions and spatial uncertainty in the amblyopic eye. The subjects had to reconstruct circles with different radii point by point monocularly with each eye. Radius of each circle was presented visually, the twelve different points of the circles were marked by a recorded voice presented through loudspeakers. Considerable distortions and spatial uncertainty were shown in the amblopic eye for strabismic and strabismic-anisometropic amblyopes. Anisometropic amblyopes did not exhibit significant spatial distortions. Subjects who perceive temporal instability showed an additional significantly lowered performance in adjusting the angle of the auditivley presented points. These results suggest that amblyopes with temporal distortions need visual assistance for handling the construction task. Further experiments need to be conducted to confirm our data and corroborate the results of quantitative and qualitative methods.

Quantification of Anterogradely Stained Axons in the Cerebral Cortex

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One of the main features of the cerebral cortex is its vast internal connectivity. Understanding this connectivity will most likely play a major part in understanding cortical function. Theoretical studies based on quantitative neuroanatomical data are one important approach to reveal fundamental processing principles in this complex structure. In order to provide such data, we are studying cortico-cortical connections in the mouse cortex by way of the anterograde tracer BDA (biotinylated dextran amine). One of the aims of this study is to gain knowledge about the strength of connections between distant places in the cortex. The number of synapses one region makes with another is closely related to the total length of axonal ramifications the projecting neurons make in that terminal region. This implies that the density of these axonal ramifications reflects the influence from the injection site onto this region. Therefore, the length and density of labeled axons in a terminal region is a measure of the connectivity from the site of injection to this region. A method was developed for estimating axonal length density (length per volume) of stained axons in regions of termination using stereological priciples (i.e. deriving higher dimension features based on measurements made in a low dimension). The method consists mainly of counting intersections between labeled axons and specially designed test lines, providing a simple quantification of tracing results.

Shape Processing in Basic Level Categorization—An fMRI Investigation

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How is basic level categorization achieved in the human brain? Deforming shape (morphing) transformations are well suited to describe the shape variability of members of common basic level categories. Behavioral experiments showed that categorization performance deteriorates systematically with increasing amount of morph transformation [1, 2]. A possible explanation for these findings is that categorization relies on time-consuming compensation processes (deformable template matching). If spatial compensation processes are involved, then categorization might not only comprise the ventral visual pathway, as generally assumed, but also the dorsal stream. We investigated this question with functional MRI.

Objects from 25 common basic level categories were generated by morphing between two members of the same category (using 3ds max). Eleven subjects participated in two tasks, starting with the categorization task. Subjects had to decide as fast as possible whether two sequentially presented objects belonged to the same basic level category. The transformational distance between category members was varied (event-related design). In a second task, the same observers perceived intact morphing sequences, scrambled morphing sequences, and static presentations of different morph exemplars (block design). fMRI data were acquired on a 3T scanner (Siemens Trio), measuring 24 slices of 64x64 voxels every two seconds (resolution of 3x3x5 mm^3).

In the categorization task, the response latencies for same trials increased with increasing morph distance between two category members. Correspondingly, the contrast long vs. short morph distance revealed an increasing BOLD signal in LOC (lateral occipital complex). Moreover, activation increased also in the superior parietal cortex (BA 7) and in the frontal cortex (BA 44). Control analyses showed that this pattern of activation cannot be reduced to task difficulty, or increasing dissimilarity between the objects. In the second task we found dorsal activation for the comparison between intact vs. scrambled morphing sequences. This activation spot was close to the dorsal activation in the categorization task, but was not identical.

The results suggest that basic level categorization is not limited to the ventral pathway, but rather relies on a network of ventral, dorsal and frontal activation. The activation within this network is systematically dependent on the amount of shape transformation. The dorsal activation seems related to compensational processes taking place in parietal cortex, i.e. spatial (deforming) transformation processes. These findings are in accordance with an alignment approach of object recognition and categorization.

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Selective Attention to Auditory Stimuli: a Brain-Computer Interface Paradigm

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During the last 20 years several paradigms for Brain Computer Interfaces have been proposed—see [1] for a recent review. They can be divided into (a) stimulus-driven paradigms, using e.g. event-related potentials or visual evoked potentials from an EEG signal, and (b) patient-driven paradigms such as those that use premotor potentials correlated with imagined action, or slow cortical potentials (e.g. [2]).

Our aim is to develop a stimulus-driven paradigm that is applicable in practice to patients. Due to the unreliability of visual perception in “locked-in” patients in the later stages of disorders such as Amyotrophic Lateral Sclerosis, we concentrate on the auditory modality. Specifically, we look for the effects, in the EEG signal, of selective attention to one of two concurrent auditory stimulus streams, exploiting the increased activation to attended stimuli that is seen under some circumstances [3].

We present the results of our preliminary experiments on normal subjects. On each of 400 trials, two repetitive stimuli (sequences of drum-beats or other pulsed stimuli) could be heard simultaneously. The two stimuli were distinguishable from one another by their acoustic properties, by their source location (one from a speaker to the left of the subject, the other from the right), and by their differing periodicities. A visual cue preceded the stimulus by 500 msec, indicating which of the two stimuli to attend to, and the subject was instructed to count the beats in the attended stimulus stream. There were up to 6 beats of each stimulus: with equal probability on each trial, all 6 were played, or the fourth was omitted, or the fifth was omitted.

The 40-channel EEG signals were analyzed offline to reconstruct which of the streams was attended on each trial. A linear Support Vector Machine [4] was trained on a random subset of the data and tested on the remainder. Results are compared from two types of pre-processing of the signal: for each stimulus stream, (a) EEG signals at the stream’s beat periodicity are emphasized, or (b) EEG signals following beats are contrasted with those following missing beats. Both forms of pre-processing show promising results, i.e. that selective attention to one or the other auditory stream yields signals that are classifiable significantly above chance performance. In particular, the second pre-processing was found to be robust to reduction in the number of features used for classification (cf. [5]), helping us to eliminate noise.

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Quantification of the Spatio-Temporal Characteristics of Walking Trajectories of Patients Suffering from Cerebellar Disease

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Cerebellar dysfunctions can cause disturbances of gait by causing disequilibrium, and by altering the leg and trunk kinematics and interlimb coordination (for review: [1]). Such disturbances are characterized by an instable stumbling walking path, increased step width, and a high variability of gait. Few approaches for quantitative description of cerebellar gait patterns have been proposed. In particular the disturbances caused by impairment of limb coordination cannot be appropriately described by elementary features used in classical gait analysis [2],[3]. For a more accurate characterization of coordination changes it seems desirable to take the full spatio-temporal characteristics of the movement trajectories into account. To model such spatio-temporal characteristics we applied the method of Hierarchical Spatio-Temporal Morphable Models (HSTMMs) [4],[5] that generates accurate models of complex trajectories by linear combination of example patterns. In this way complex trajectories can be mapped onto low-dimensional parameters that characterize or pathological changes of movement patterns. The linear combination model is defined by the weighted linear superposition of spatio-temporal correspondence fields between the example patterns and a reference trajectory.

For the analysis of cerebellar walking disorders we trained a HSTMM with prototypical examples trajectories from cerebellar patients, Parkinson patients, and normal controls (3 per class). Walking movements were recorded with a VICON motion capture system. The linear combination model obtained was used to approximate new trajectories. The resulting linear weights were mapped onto a score that describes the degree of cerebellar disease using nonlinear regression techniques. This score was correlated with the ratings of the same patients on the common clinical ataxia scale ICARS [6]. The algorithm was tested with different feature sets in order to determine feature combinations that are optimally suited for the characterization of cerebellar gait disorders.

For the evaluation of the method we analyzed 12 cerebellar patients. The scores obtained using HSTMM correlated highly with the clinical ICARS scale (Spearman rank correlation: $r_s = 0.9$, $p < 0.01$). Ongoing work focuses on finding feature sets that are maximally predictive for subsets of items from the ICARS scale that characterize balance and coordination problems respectively.

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Can Visual Stimuli Affect the Phase of Brain Oscillations?

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The function of brain oscillations is seen in the context of various sensory, behavioural or cognitive states, and for the visual system a number of hypotheses have been proposed based on synchronized activity of different populations of neurons . A prerequisite for the type of synchronisation suggested is that visual stimuli are capable of affecting (resetting) the phase of brain oscillations.

A change in the phase of brain waves assumingly also occurs in the "Berger effect" : If observers open their eyes, the amplitude of EEG oscillations in the alpha band (8 13 Hz) decreases or disappears completely. One interpretation is that due to visual stimulation oscillations in different neurons or neuronal populations are desynchronised.

For a functional interpretation of brain oscillations it therefore seems crucial to find out whether or not the phase of these brain oscillations can be affected by visual stimuli. To answer this question one has to examine whether brain waves are generated by linear or nonlinear mechanisms. If they are due to linear band pass filtering or linear oscillators, no phase resetting is possible, as the superposition law holds: the response to a stimulus is just superimposed on the ongoing oscillation, no phase resetting is possible. In contrast, in nonlinear oscillators (as described e.g. by the van der Pol equation), phases can be reset e.g. by an impulse.

We analysed the question of linearity of alpha waves by investigating whether or not the superposition law holds: Light flashes were presented randomly, as usual, or at particular phases of the alpha waves. The result: the evoked potential to a flash, given at a particular phase, basically is the superposition of the alpha wave and the evoked potential to flashes presented randomly (which is without alpha contribution). This holds only, however, if one assumes that within 200 to 300 ms after a light flash the amplitude of alpha waves decreases in a flash intensity dependent degree.

Conclusion: the phase of alpha, perhaps also of gamma waves cannot be reset by visual stimuli. This questions existing theories about the function of these waves. The "Berger effect" is not due to event related de- synchronisation. The amplitude of alpha waves after a flash are reduced in the same way as that of evoked potentials, due to the loss of sensitivity by light adaptation.

More Evidence for Early Visual Processing in Perceptual Disambiguation of Ambiguous Figures

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Background. Ambiguous figures (e.g. the Necker cube) fascinate observers because perception spontaneously changes while the observed figure stays unchanged. Event related potentials (ERPs) can trace the time course of the neural processes underlying perception. To synchronize EEG averaging to such endogenous reversals we used the fact that reversals typically occur at stimulus onset after a brief blank period. Using this technique we had found ERP correlates to the perceptual reversal of the Necker cube, beginning with a surprisingly early component (120 ms after onset), which occurred at occipital locations only [1]. We here present results of ERP experiments with the famous “Mother and Daughter in Law” figure [2]. Methods. An ambiguous “Mother and Daughter in Law” figure appeared repeatedly for 800 ms after blank periods of 40 ms. Our subjects indicated whether they perceived a “reversal” at stimulus-onset. EEG was recorded from 7 channels in 16 subjects; the difference traces between reported “reversal” and “stability” were analyzed. Results. The first significant signal ($p<0.01$) after stimulus-onset regarding the difference traces (reversal minus stability) occurred at 110 ms at the occipital location. It was followed by signals at temporal, frontal and frontopolar positions around 100 ms later. Discussion. We interpret the earliest occipital signal as a direct correlate of the neural processes underlying perceptual reversals. Timing, location and polarity of this signal is similar to a signal found with reversals of Necker cubes. Early processing in visual areas seem to be necessary for disambiguation of both, geometric ambiguous figures (e.g. Necker cube) and “semantic” figures like the “Mother and Daughter in Law”. The signals at the temporal locations may reflect neural activity in areas that are known to be active during processing of faces (e.g. [3]). Neural processes in higher cortical areas (temporal and frontal) seem to be secondary to the initial early occipital activity.

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Synchronization of Oscillatory Neural Dynamics in a Model of the Thalamo-Reticular System

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The thalamus has a key position in information processing in the brain: first, it is the major gateway for sensory information to the cortex. Second, thalamo-cortical pathways are reciprocated by massive feedback connections from the cortex back to the thalamus. Thalamic relay neurons are coupled to cortical neurons, as well as to the inhibitory neurons of the reticular nucleus of the thalamus and the resulting reciprocal interactions generate synchronous oscillatory patterns in the thalamo-cortical system depending on input frequencies, phase deviations, and delay time. We present a simple model of the thalamo-reticular system based on the Wilson-Cowan model of neuronal oscillatory behavior and show how different input patterns result in several spatio-temporal patterns of synchronous activity. A main finding of the numerical simulations is that the network connectivity and the intrinsic oscillatory properties result in distinct characteristic collective spatio-temporal behavior within the network. By studying different connectivity schemes comparable with lesionated or damaged brain regions our results are in good agreement with experimental results, for example suppressing sensory input results in temporal oscillatory activity in the beta and gamma range and a strong spatial dependence of the network dynamics.

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Blindsight, the Pupil, and the Stimulus Probability Effect.

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Blindsight is the capacity of patients with visual field defects from retro-geniculate lesions to respond to visual stimuli they do not consciously see (Stoerig & Cowey, 1997, for review). It can be assessed with psychophysical as well as –physiological methods. To learn whether the pupil displays better sensitivity to stimuli presented in the blind field, we here tested a hemianopic patient (HK) in a detection task while simultaneously recording his pupillary responses. In a 2AFC paradigm, a grey disk disc (5° diameter, 19 cd/m, delta t 300ms, 8.9° eccentricity on the horizontal meridian, background 77cd/m2) appeared in pseudo-random alternation with blank trials. Targets and blanks were announced by a brief beep, and HK pressed different buttons to indicate whether or not he thought a stimulus had been presented. We varied the stimulus probability (20, 35, 50, 65 and 80% targets), and gave feedback in half of the 42 series of 100 trials each. Only when no feedback was given was HK not informed about the stimulus probability. During the behavioural tests pupil responses were recorded with an infra-red eye tracking system (I-View-System; SMI) that also served to control HK's fixation. Psychophysical detection results were highly significant throughout, regardless of whether he knew the stimulus probability or received feedback. Especially when no feedback was given he produced very few false alarms. When he missed a target—32% overall—pupillometry still revealed a probability-dependent effect of the stimulus. This task-evoked pupillary response (TEPR), a dilation, is well-described for normal-sighted subjects (Qiyuan, 1985), but has to our knowledge not previously been described to occur in cortically blind fields. In addition, and in contrast to published reports of a close similarity between pupillometrically and psychophysically determined sensitivity (Weiskrantz, 19992), our results show that the pupil responds even when the subject fails to detect the stimuli.

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Congenital Periventricular Lesions Specifically Affect Cortical MEG Response to Biological Motion

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Although recent findings point to the great compensatory potential of the developing brain, the mechanisms of the functional plasticity and, in particular, limitations on it remain largely unknown. Periventricular leukomalacia (PVL), a subcortical lesion pattern of early origin and high structural homogeneity [1,2] serves a proper model for addressing this issue. Here, we ask whether and, if so, how cortical brain activity might be modulated by congenital bilateral damage to periventricular regions. With this purpose, we assessed the changes in the neuromagnetic cortical responses during visual perception of biological motion. Adolescents with bilateral PVL and matched healthy term-born controls saw a randomized set of 200 stimuli consisting of a point-light canonical walker and a scrambled configuration for which the spatial positions of dots were randomly rearranged on the screen.. Each stimulus appeared very briefly, for 650 ms, on a blank screen. Participants performed a one-back repetition task: they pressed a button following the offset of the second of two consecutive identical stimuli of each type [3]. We calculated the miss (and false alarm) rate as a ratio of the number of failures to respond to the second identical stimulus of this type to the total number of the required responses. Patients had greater number of misses than controls in response to the point-light walker, whereas no difference was found between the patients and controls in response to the scrambled configuration. Overall, the psychophysical data nicely dovetail with the MEG response: At several latencies (in particular, at 140–180 ms post-stimulus) the brain activation in response to biological motion over the parietal sensors was weaker in patients, but did not differ between the patients and controls in response to the scrambled noise. Overall, the data suggest that integration of the local motion of dots in different locations into a cohesive percept of a point-light walking figure is compromised in patients with congenital periventricular brain damage. Moreover, this is the first evidence that periventricular lesions specifically affect cortical brain activity.

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On the Best Way to Remove Trend Artifacts from Steady-State Visual Evoked Responses (VEPs)

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Problem. The application of fast visual stimulation rates and the recording of steady-state VEPs is a useful paradigm to study the visual system. One of the advantages is the easy evaluation of the response via Fourier analysis. For conditions near threshold, statistical tests are available that evaluate whether a response is significantly different from noise. These tests exploit the scatter of all individual trials within the complex Fourier plane. However, individual trials may be contaminated by trend artefacts induced by eye movements. The easiest method for trend rejection is to subtract the linear increments or decrements from the VEP waveforms. However, this procedure might introduce additional contaminations of the Fourier components whenever the VEP recording interval does not contain an integer number of cycles of the mains interference at 50 Hz. We here present a method to decouple both types of trend artefact and to remove them from the VEP recording.

Methods. We introduced (A) a linear trend function, (B) a 50 Hz sine function, and (C) a 50 Hz cosine function as three base functions. After orthogonalizing these new functions with the sine and cosine functions of the standard Fourier transform, we achieved a new set of base functions for a combined analysis of response magnitude, trend, and mains interference. To test this modified Fourier transform, we synthesised VEP waveforms by adding trends and mains interferences with varying relative weights to a VEP response of given magnitude. The data were analysed with a standard Fourier transform and with the modified Fourier transform.

Results. Significant differences were found between the given VEP magnitude and the VEP estimate after standard Fourier analysis. In contrast, the modified Fourier transform was able to predict the given VEP magnitude exactly, regardless of the amount of trend and mains interference.

Conclusions. The modified Fourier transform is a helpful tool to separate trend artefacts from steady-state VEP recordings. As the analysis of individual VEP trials is required to separate a low magnitude response from noise, the new trend rejection method may help to improve the objective estimation of sensory thresholds.

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Sensory Saltation on the Abdomen

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Research is presented on the psychophysics of sensory saltation, one of several spatiotemporal illusions [1]. In saltation subjective localization of a cutaneous stimulus is altered by a second stimulus at a different place following the first one closely in time. The amount of mislocalization decreases linearly with the stimulus onset asynchrony (SOA). According to neurophysiological evidence, saltation can be explained by quantitative dynamic behavior of the neural network in the primary somatosensory cortex [2]. The psychophysical characteristics of saltation may be used to quantify the dynamic behavior of this network noninvasively. Assuming that neural behavior of the network leads to spatial anisotropy due to temporally associated stimulation, we expected that in saltation the amount of mislocalization not only depends on the SOA, but on the orientation of the stimulus pattern in relation to the body axes. The abdomen was chosen as stimulus area because previous studies focused on extremities show that subjective localization is affected by the position of the limb in relation to the trunk [3]. Studies using truncal stimuli, however, are rare [4]. We applied a stimulus sequence, consisting of a warning stimulus (S0) and two short stimuli 7cm apart (S1, S2) in a repeated measurement design (29 healthy subjects), varying time delays between S1 and S2 (SOA: 57–500ms) and sequence of the stimuli in relation to the longitudinal body axis (direction "upwards": S1 near the spina iliaca anterior superior, S2 near the costal arch; direction "downwards": S1 near the costal arch, S2 near the spina iliaca anterior superior). In all subjects an effect of SOA—saltation effect—could be elicited. The amount of mislocalization of S1 towards S2 increased linearly with a decreasing SOA. Furthermore direction had an effect on the amount of mislocalization, showing a greater amount of mislocalization of S1 towards S2 in direction "downwards". We hypothesize that this effect reflects anisotropic distribution of the spatiotemporal tactile map of the abdomen.

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Probing Feature Binding by TMS and Light Masking

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Introduction: The binding problem The mammalian brain analyzes features of the outer world in separate parts of the brain in parallel. How these features are bound to the percept of a unique object is known as the binding problem. Whereas the neural mechanisms underlying feature binding are heatedly debated less is known about the spatio-temporal characteristics of binding itself. Here, we focus on one of the very basic binding processes, namely, feature fusion. In feature fusion two elements are rapidly presented one after the other at one spatial position. Because of rapid presentation only one element is perceived combining the features of both elements [1]. To test feature binding we used a vernier discrimination task.

Materials and Methods: A vertical vernier consists of two abutting lines slightly offset in the horizontal direction. If this vernier is followed by another vernier, with offset in the opposite offset direction, only one vernier is subjectively perceived which combines both offsets. Feature fusion has occurred. The second anti-offset vernier is called the antivernier. Offset size of vernier and anti-vernier was identical in all experiments. Vernier segments were 600" long and separated by a small vertical gap of 60". The task of the observers was to indicate the offset direction of the fused vernier. We used vernier and anti-vernier durations of 40/20ms or 40/25ms, depending on observer, yielding to a performance level of 50%, i.e. offsets cancel each other. To probe the time course of feature fusion, we masked the two verniers by either a light masking field or by a single magnetic pulse (TMS) over the occipital lobe for various SOAs (stimulus-onset-asynchrony). Light masks had a length of 1260 1260 arc seconds and were presented for 20ms. Magnetic stimulation was applied with a Medtronic MagPro stimulator and the standard figure-eight coil. Intensities were adjusted to 80% - 90% of maximal output. The coil position was registered and monitored throughout the experiment with a stereotactic positioning device.

Results: 1. Varying the SOA between the light mask or a TMS pulse and the vernier onset changes feature fusion strongly. 2. For light mask onsets occurring before the first vernier the anti-vernier dominates perception, for onsets after the anti-vernier onset the vernier dominates. Analogous results are found for TMS onsets if SOAs are shifted by about 130ms indicating that the major cortical processing occurs at that time in the occipital lobe. 3. Modulation depends on the spatial layout of the light mask. 4. Modulation of dominance is the stronger the longer both verniers are displayed. 5. Strong modulation of dominance can occur in the vernier/anti-vernier paradigm even when virtually no masking effects occur if the vernier is presented alone, i.e. without the anti-vernier.

Conclusions: TMS masking yields similar effects as light masking suggesting a common mechanism. Feature fusion is a long lasting process that selectively can be disturbed favoring either one of the vernier.

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Cortico-Cortical Connectivity in the Human Brain. A Study on the Cortical White Matter

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The human cortical white matter has a volume nearly as large as the grey matter. Most of it is composed of fibers connecting the cortex to itself. These fibres can be divided into the following systems: 1) short fibres which follow the gyri and sulci of the grey matter (the U-fibre-system), 2) longer fibres which make short-cuts between more distant gyri, 3) long fibres which run in fascicles in the depth of the white matter and connect the different cortical lobes with each other, and 4) fibres of the Corpus callosum. In this study we make an estimate of the quantitative composition of some of these sytems. This gives insights into the organization of cortico-cortical connectivity in the human brain which is otherwise difficult to approach.

In a first approach, we dissected the long-range fascicles in the depth of the white matter. Measuring their cross sectional areas and multiplying these by the assumed density of fibres one can estimate the number of fibres in these fascicles. It turned out to be of the orders of 10^6 and 10^7 in the individual fascicles and to add up to the order of 10^8 for the fascicles of one hemisphere. Thus, the number of fibres connecting the lobes of one hemisphere to each other is similar to the number of fibres in the Corpus callosum [1]. Both of these long fibre systems comprise only a few percent of the total number of cortico-cortical fibres [2].

In a second approach, we made estimates on the number of short cortico-cortical fibres (up to a few centimeters) in the white matter (based on volume measurements of the U-fiber system) and on the number of horizontal axon collaterals which connect the cortex in itself up to a few millimeters within the grey matter. It turns out that there is an inverse relation between number and range of fibres connecting the cortex in itself. The fibres in the U-fibre system outnumber the cortico-cortical fibres in the rest of the white matter by a factor of 10, and are themselves about 10 times less than the horizontal collaterals in the grey matter.

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Visual Properties of Neurons in the Ventrolateral Thalamus of the Pigeon (Columba Livia)

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Visual information processing in the pigeon encompasses two major ascending pathways: A) the tectofugal system which is generally considered as homologue to the colliculothalamo-cortical pathway in mammals (superior colliculus -> pulvinar -> temporal cortex); B) the thalamofugal system corresponding to the geniculocorticostriate pathway in mammals (lateral geniculate nucleus -> striate cortex). In the present study we examined, in which way the ventrolateral thalamus (VLT), a hardly studied thalamic nucleus, might be involved in the pigeon's processing of visual information. Urethane-anesthetized pigeons were subjected to photic visual whole-field stimulation either unilaterally or bilaterally for a duration of 500ms. In either the left or the right hemisphere single cell recordings during visual stimulation were performed. We discovered visual responsive neurons within the VLT which reacted to the onset of the applied stimulus. Two types of single cells could be isolated: Type I) responding to uni- and bilateral stimulation with response latencies of 110–120ms and 145ms, respectively; and Type II) responding exclusively to bilateral stimulation with response latencies of 80–85ms. These results are of interest not only because this is the first study to demonstrate visual response characteristics of VLT-neurons but also in view of anatomical data indicating a considerable projection from the visual Wulst, homologue of the mammalian striate cortex, to VLT. It is argued that the response characteristics of the observed single cells are most likely due to such a top-down influence. The avian VLT, like mammalian VLT, might be involved in the integration of visuomotor information.

Get Real Close if you Want to Disturb: a Magnetoencephalography Study on Short-Term Tactile Memory

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A common assumption about sensory cortices is that they are mostly involved in extracting characteristics of sensory input. However, recent findings in different sensory cortices have revealed that memory retention and retrieval processes also exist within sensory cortices, and seem to follow a topographical representation (Dill et al., 1997). Likewise, this study supports the view that the primary somatosensory cortex plays a role in sustaining the working memory trace for vibratory stimuli topographically (Harris et al., 2001).

Vibro-tactile steady-state stimulation was employed (Diesch et al., 2001) to investigate the role of the primary somatosensory cortex in short-term memory. Cortical responses to an interference stimulus interpolated between two tactile stimuli that had to be compared with respect to their frequency were studied and the somatotopical influence of this interference on subjects' discrimination accuracy was examined. Specifically, the stronger the influence of the interference stimulus was on the hemisphere 'encoding' the first stimulus, the less accurate was the tactile discrimination. The influence of the interference stimulus manifested itself in terms of the finger distance the interference stimulus was located away from the digit experiencing the comparison stimuli (i.e. the closer the interference was to the site of comparison stimuli presentation, the stronger was its effect), and also in terms of the influence it had on the hemisphere responsible for encoding the first comparison stimulus. This apparent hemispheric influence is suggestive of a bilaterally activated primary somatosensory cortex in response to unimanual tactile stimulation (Hansson and Brismar, 1999).

In addition, this study demonstrated that the steady-state stimulation technique which has been adopted from time-saving mapping of digit representations of the somatosensory cortex, can be applied in a cognitive task paradigm to show interactions of neural sources. Bilateral activation of somatosensory cortex was found for both the comparison stimuli and the interference stimuli, with more activity on the side contralateral to the stimulation. These sources could be located in primary somatosensory cortex using dipole analysis.

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Lesion Analysis in Spatial Neglect using SPM Normalisation

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Traditionally, the neglect syndrome in humans (a lack of orienting to and attending to space on the side of the body contralateral to a brain injury) has been associated with damage to the right inferior parietal lobule (IPL) and the right temporo-parietal junction (TPJ). Thus, it was surprising when a recent study by Karnath et. al. (2001) found that the centre of lesion overlap covered right superior temporal gyrus (STG) and planum temporale (PT), suggesting that the superior temporal cortex rather than the inferior parietal lobule is the critical substrate for spatial neglect in humans. In this study lesions were demarcated by hand onto standard template T1-weighted magnetic resonance images (MRI) to allow comparisons across individuals. To overcome this limitation we here use a lesion analysis method that does not rely on the manual transfer of lesions to standard template slices, rather employing a technique where the location of the lesion is drawn directly on the patient's own MRI scan. Combining all slices produces a lesion region of interest (ROI) for each patient. Both the scan and lesion shape are then mapped into stereotaxic spacing using the spatial normalisation algorithm provided within the software package SPM2 (http://www.fil.ion.ucl.ac.uk/spm/). For determination of the transformation parameters, cost-function masking is employed, i.e. the 3D lesion ROI is used for masking those areas used in the calculation of image difference so that the lesion does not bias the transformation (Brett et al. 2001). This procedure avoids the requirement of the investigators making (observer-dependent) decisions. We investigated a new sample of 15 consecutively admitted patients with acute right-hemisphere ischaemic strokes and spatial neglect. Patients with additional visual field defects (e.g. hemianopia) were not excluded. We used T2-weighted fluid-attenuated inversion-recovery (FLAIR) imaging if conducted 48 hours or later after the stroke (10 patients) and diffusion-weighted (DWI) imaging if conducted within the first 48 hours after the stroke (5 patients). All patients showed severe spatial neglect (clinical behaviour on the ward, cancellation tests, copying) at the time when the images were taken. We found that lesion overlap was centred on the STG, the insula and the operculum. The center continued further into the pre- and postcentral gyri, middle temporal gyrus, and the putamen. The data thus clearly argue against the traditional view that the IPL and TPJ are the critical substrates for spatial neglect in humans. References

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Research Methods and Techniques

m-Alternative Forced Choice—Improving the Efficiency of the Method of Constant Stimuli

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We explored several ways to improve the efficiency of measuring psychometric functions without resorting to adaptive procedures. a) The number m of alternatives in an m-alternative-forced-choice (m-AFC) task improves the efficiency of the method of constant stimuli. b) When alternatives are presented simultaneously on different positions on a screen rather than sequentially time can be saved and memory load for the subject can be reduced. c) A touch-screen can further help to make the experimental procedure more intuitive. We tested these ideas in the measurement of contrast sensitivity and compared them to results obtained by sequential presentation in two-interval-forced-choice (2-IFC). Qualitatively all methods (m-AFC and 2-IFC) recovered the characterictic shape of the contrast sensitivity function in three subjects. The m-AFC paradigm only took about 60% of the time of the 2-IFC task. We tried m=2,4,8 and found 4-AFC to give the best model fits and 2-AFC to have the least bias.

Computer Based Vision Training in Amblyopia: Selected Results of a Nation Wide Multicentric Prospective Research Study

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The poster presents results of a nation wide multicentric prospective research study. Our research aimed at the test of a software-based stimulation method as a supporting procedure additionally to occlusion treatment of amblyopia. A drifting sinusoidal grating of a spatial frequency of 0,3 cycles per degree and temporal frequency of 1,5 .Hz, co-ordinated with each other, served as the stimulus. This pattern was implemented as a background stimulus in simple computer games in order to bind the attention by sensory-motor co-ordination tasks. According to an earlier proposed hypothesis, the stimulation aims to the provocation of stimulus induced phase coupling and to contribute to the refreshment of synchronisation and co-ordination processes in the visual transmission channels. A number of strabologic departments in eye clinics and private offices as well, co-operating with us, have been partners of this study. 192 patients took part in a half year treatment with the computer based vision training. The therapy started at the hospitals or in outside offices performed by othoptists. This supervised period of treatment lasted maximally two weeks. After that the children received the software on disk in order to use it at home under the supervision of their parents. The training was performed according to a predefined time scheme. To assess the outcome of the therapy we studied the course of the visual acuity and other parameters during a period of six months. Besides the assessment of the therapy outcome, the study aimed at the evaluation of selected etiological or differential-diagnostic questions. Statistical evaluations with a detailed screening material (case history data, anamnesis at the beginning, during and after the half-year-period) and with the help of a stratification method within the patient sample we aimed to assess, whether strabologic amblyopia vs. refraction amblyopia are differently effected by the therapy.

Signal Detection Analysis of Experience-Induced Contextual Effects in Size Discrimination

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In signal detection tasks, it is typically assumed that varying the base rates of stimuli is a powerful means for changing the observer's response tendencies independently of simulus discriminability [1]. Our recent data on category judgments of visual speed [2,3] question this assumption, suggesting that experience-related statistical context (base rates and serial order of stimuli) can alter both the response tendencies and sensory representation of stimuli. Here, we examine if the two contextual variables affect judgments of visual size in a simple two-category discrimination task without feedback. We also analyze the time course of changes both in discriminability and in response bias across the experiment. By using of two categories ("small" and "large"), four groups of participants had to judge two grey disks of slightly different sizes presented one per trial. The disk sets varied between groups in the base rates (with frequent small or large disks; ratio 3:1) and the serial order of stimuli (either frequent of infrequent disks mainly occurred on the initial trials). The results indicate that on overall, (i) the frequent occurrences of small disks induce more liberal criteria (more "large" responses over the 400 trials) than the frequent large disks. Furthermore, (ii) the serial order interferes with the base rate of stimuli, yielding a greater discriminability with the concordant base rates and serial orders (frequent stimuli presented early in a presentation series) than with discordant ones (when mainly infrequent stimuli occur earlier). These effects do not change substantially in the course of the experiment. Notably, the effects found in this two-category task with the stimuli that only slightly differ in size resemble those reported previously for much larger stimulus differences and a greater number of categories [4]. The findings suggest that in a standard discrimination task, the experience-related statistical context exerts effects not only on the observer's response tendencies, but also on the sensory representations of stimuli.

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Tactile Perception

Haptic Magnitude Estimates of Size for Graspable Shapes

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Studies of visual size perception with the method of magnitude estimation have shown a linear relationship between actual sizes and magnitude estimates [1]. Similar studies for touch do not yield unequivocal evidence for a linear relationship; in some cases, a positively accelerated power function described best the relationship between stimulus sizes and estimates [2]. We have investigated haptic magnitude estimation for length in two haptic experiments with different methods of haptic exploration (whole hand, finger span).

The haptic stimuli consisted of 15 rectangular shapes. The only difference from one shape to another was the length of the horizontal side, which ranged from 40 mm to 68 mm in equal intervals. For all shapes, the depth and height were 10 mm and 40 mm, respectively.

In the Multiple cues Experiment, blindfolded participants used their dominant hand to feel each shape freely. The shape was presented fixed flat onto a support, so they could feel the entire shape under their hand. The participants' task was to give a modulus-free magnitude estimate for the horizontal side. All shapes were presented once in random order in each block.

In the Single cue Experiment, blindfolded participants were restricted to grasping the horizontal side of a shape between the thumb and index finger of their dominant hand. Their task was to give a magnitude estimate for the length of that side.

Magnitude estimates for side length could be fitted by a two-parameter linear function with a high goodness-of-fit statistic in both experiments ($R2 > .97$). Thus, when participants were given a size range of 40 to 68 mm, their magnitude estimates increased linearly with each physical increment, independently of the exploration method used.

Because of the small range of total size variation present in the shape set, we do not conclude from our results that haptic magnitude estimation of unidimensional size is generally linear. It should be noted that the present linear functions had a negative y-intercept and that when a power function was fit to the data, the exponent was greater than 1.0 in both experiments, and goodness-of-fit was also high. Our results suggest, however, that haptic perception of size can safely be considered linear within this small part of the size continuum. These results are important for considering further psychophysical studies with shapes within this size range.

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Cue Reliabilities Affect Cue Integration in Haptic Shape Perception

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When sliding a finger across a bumpy surface, the finger follows the geometry of the bumps/holes providing positional cues for the shape. At the same time the finger is opposed by forces related to the steepness of the bumps/holes. With a specific device Robles-de-la-Torre and Hayward [1] dissociated positional and force cues in the haptic perception of small-scale bumps and holes: Participants in this experiment reported to predominantly feel the class of shapes (bumps or holes) indicated by the force cues. Drewing and Ernst [2] extended this research by disentangling force and position cues to the perception of curves more systematically and by also quantifying the perceived curvature. The result was that the perceived curvature could be predicted from weighted averaging of the two cues. This is consistent with current models of cue integration [e.g., 3].

These integration models further predict that the cue weight is proportional to the cue's reliability. Here, we aimed at testing this prediction for the integration of force and position cues to haptic shape by manipulating the shapes' material properties: high softness can be assumed to decrease the reliability of the position cue as compared to low softness, and high friction to decrease the reliability of the force cue. Using the PHANToM force-feedback device we constructed haptic curve stimuli. We systematically intermixed force and position cues indicating curvatures of 14 and 24 /m. Using the method of double-staircases, we measured the point of subjective equality (PSE) of the curvature of these as compared to 'natural' stimuli (i.e., with consistent position and force cues). From the PSE data we determined the cue weights. This was done under each combination of material properties (low vs high softness X low vs high friction). We found that material properties affected the cue weights in a manner consistent with our predictions. These results further confirm the validity of existing models of cue integration in haptic shape perception.

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Differential Effects of Synchronous and Asynchronous Tactile Coactivation on Somatosensory Cortical Organisation and Tactile Discrimination Performance

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The mammalian neocortex has an amazing capacity for plastic remodelling. This is the basis for lifelong adaptation to alterations in sensory environments and behavioural demands. Hebbian mechanisms seem to play a key role in use- and input-dependent cortical plasticity. We used functional MRI together with a spatial discrimination task to investigate in detail the effects of synchronous and asynchronous tactile coactivation on cortical organisation in the human primary somatosensory cortex (SI) and its behavioural consequences. Coactivation, which is the Hebbian-like associative pairing of tactile stimulation, was applied for three hours to the distal phalanges of index, middle and ring fingers of the right hand either synchronously or asynchronously. Strengthening previous findings we show here that somatosensory cortical representations in SI for synchronously coactivated fingers move closer together resulting in an integration of those representations. On the other hand, cortical representations for asynchronously coactivated fingers become segregated and move further apart. This coincides with a reduced number of mislocalisations between fingers that have been coactivated asynchronously and an increased number of mislocalisations between fingers that have been coactivated synchronously. These results were reversible within one week after stimulation. Thus, not only synchronous but also asynchronous coupling of passive tactile stimulation is able to induce short-term cortical reorganisation that is associated with functionally relevant changes in the perceptual and behavioural capacities of an individual without active training or attention directed to the stimuli.

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The Role of the Posterior Parietal Cortex in the On-Line Control of Grasping Movements

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Lesions of the posterior parietal cortex (PPC) in humans cause severe visuomotor deficits. These patients demonstrate large deviations of pointing and reaching movements to peripheral targets and an inability to adjust their grip aperture to different object sizes. In addition, a deficit to adjust movements to perturbations of target positions during movement execution has been recently shown. However, it is unclear whether such a deficit of an on-line correction mechanism also affects the distal component of grasping movements, i.e. whether patients with lesions of the PPC can adjust their grip aperture to perturbations of object size during movement execution.

We compared the performance of a patient with bilateral lesions of the PPC with the performance of healthy controls in a virtual grasping task. A virtual disc (36 or 44 mm in diameter) was rendered using stereo computer graphics. Virtual, haptic feedback was given using two robot arms (PHANToM TM). In half of the trials, the virtual disc either increased to a size of 52 mm or decreased to a size of 28 mm. Otherwise the objects size was stable during the trial.

The patient's performance towards the unperturbed discs was not impaired compared to the grasping kinematics of the healthy controls. In contrast, her grasping movements towards the perturbed objects seemed to be more prone to error than the movements of the healthy controls. This finding supports the previously suggested crucial role of the PPC in the online control of visuomotor actions and suggests that the PPC is also involved in the online control of the distal component of grasping movements.

Visual Cognition: General

A Computerized “Wisconsin What-And-Where Task”: Preliminary Results

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The present project goes back to neuropsychological studies of control functions in the prefrontal cortex (PFC), which were traditionally investigated with the Wisconsin Card Sorting test. These PFC processes should be connected with those mediated by the occipital-temporal “what” and the occipital-parietal “where” pathway of visual information processing. A task which combines both parts is the “Wisconsin what-and-where task” by Deco et al. (2003). Our goal was to develop an experimental version of this task. Such a diagnostic tool can provide differential information about neuropsychological deficits in visual information processing and PFC control. We demonstrated that a “what-and-where delayed-match-to-sample” task can be designed by using multidimensional stimuli that require selection of either object or space information. Of special interest are conditions where object and space information were either congruent, i.e., requiring the same responses (e.g., object and space match), or incongruent, i.e., requiring different responses (e.g. object match, space no-match).

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Emergent Illusory Shapes Interfere with Kanizsa-Type Target Detection.

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Illusory contours as seen in Kanizsa-type figures [1] demonstrate the capability of the visual system to integrate separate features into coherent wholes in the absence of luminance-defined borders. Physiological studies have consistently shown that this process of illusory-contour completion can be related to activity in primary and extrastriate visual cortex (areas V1, V2) comparable to responses related to line-defined contours or light-dark edges [2, 3, 4]. In agreement with these findings, Davis and Driver [5] reported in a visual search study, that Kanizsa-type figures can be detected without focal attention at parallel stages of the human visual system. By contrast, a reply to this study [6] stated that the efficiency to detect a target is independent of whether or not illusory contours are present in search displays. In the present contribution, we address this controversy by showing that the detectability of a Kanizsa-type target square is disrupted if the similarity of emergent illusory shapes increases between target and distractors, suggesting an important role for filling-in processes in search performance. In addition, our results suggest that this modulation of search efficiency can be related to the subjective goodness of figural grouping.

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Is “Direction of Pointing” a Visual Feature?

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In a visual search paradigm the presence of targets has to be detected among a varying number of distractors. There are two extreme cases: when targets differ from distractors in easily recognisable single features, search is usually fast and independent of the number of distractors; when the difference is a combination of features, the detection is slow and linearly increasing with the number of distractor items. However, it is not always clear what a feature is and whether a certain stimulus property can become a feature. Perceptual learning can aid in the identification of “featurisable” stimulus properties. We used two different kinds of stimuli in our experiments: wedges and semicircles, both pointing either upwards or downwards. A target was defined as a single item pointing to the opposite direction than the distractors.

In a first experiment we had two groups of 16 subjects each. One group was presented with wedges, the other with semicircles. In both groups response times were significantly higher for 16 than for 8 items and this increase was significantly higher in non-target trials. Thus, there was no feature search in either case. However, the semicircle group turned out to be significantly faster. We attribute this effect to the fact that a target wedge is composed of the two components of the distractor wedge, whereas this is not the case for semicircles.

In a second experiment we wondered whether experience with “pointing” can be transferred from the wedge task to the semicircle task. Twenty-two subjects had to do both experiments in succession. Half of them (Group W) started with wedges the other half with semicircles (Group S). Again, in the semicircle task response times were significantly shorter and in both tasks responses were faster for 8 items than for 16 items, with a higher increase in non-target trials. Furthermore, Group W benefited in the semicircle task from previous learning to use the pointing direction in order to detect a target in the wedge task. Group S on the other hand learned to use curvature in the semicircle task but this learning was obviously not useful in the wedge task.

We conclude that “direction of pointing” can be learned and is therefore a candidate for a featurisable visual attribute.

Working Memory Related Neuronal Activity and Theta Oscillations in Extrastriate V4

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Working memory is used to store information for brief periods. The mechanism of working memory is studied in both humans and monkeys. While in monkeys working memory is thought to depend on elevated firing activity in prefrontal cortex during the memory period of a cognitive task, EEG studies in humans have linked oscillations to working memory not only in the frontal but also in the occipital cortex. It is not known, whether these two findings -the delay activity and the oscillatory phenomena- interact with each other and how they may support working memory. We addressed this issue by recording simultaneously single unit activity (SUA) and local field potentials (LFP) from an occipital brain region -area V4- in monkeys. The monkeys had to perform a delayed-matching-to-sample task. The task started with a 1000 ms fixation period, followed by a 300 ms presentation of a sample object. After a delay of 1000 ms a probe object was presented and the monkeys had to decide whether the probe matched the sample by releasing a lever. The objects were natural images of the size 10°x10°. The sample stimuli had contrast levels between 5% and 100%, while the probe objects were always at 100% contrast. The monkeys' performance was almost at ceiling for contrast levels higher than 25% and at chance for low contrast levels. We compared the delay period to the fixation period by assessing power in the theta band of the LFP during the last 800 ms of the delay and the fixation respectively. Compared to the fixation period we observed increased theta oscillations for high contrast stimuli at many recording sites during the delay. Almost all sites showed reduced theta oscillations at 5% contrast level, when the monkeys were performing at chance. Unlike in prefrontal cortex there was no elevated neuronal activity during the delay period. SUA during the delay was similar to values during the fixation. But examining at the relationship between theta phase and SUA, we found that many neurons fired preferentially at a particular phase of the theta cycle. These findings suggest that theta oscillations increase during the delay period in visual cortex, and that these oscillations serve to structure neuronal activity.

Visual Short-Term Memory During Smooth Pursuit Eye Movements

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In the current study, we investigated contributions of spatial and retinal target position to visual short-term memory (VSTM). In previous studies (e.g. [1]) using a change-detection task, spatial and retinal position were confounded, because memory and probe image were presented at the same position, and observers maintained fixation. The question is whether the spatial and retinal positions of items to-be-remembered are encoded in VSTM. Our purpose was to examine effects of continuous displacement of the spatial or retinal position of to-be-memorized items, while some conditions involved continuous displacements of the eye (smooth pursuit eye movements, SPEM). In Experiment 1, we tested whether VSTM for position would suffer when the memory image was presented during SPEM. We compared a fixation condition with two SPEM conditions. In one SPEM condition, the memory image was stationary such that its spatial positions did not change. However, this condition produced changes in retinal position. Because the eyes moved, the optical projection of the memory image moved across the retina. In another SPEM condition, the memory image moved with the same velocity as the pursuit target. Here, the spatial position of the memory image changed, but remained stable on the retina. If the spatial and retinal position of items were stored in VSTM and were used to retrieve an item's position from VSTM, a decrease in performance would be expected in both SPEM conditions. This performance impairment is exactly what we found. However, performance in SPEM conditions may not only be governed by spatial or retinal stability. It may be that the execution of SPEM binds attentional resources. In this case, the execution of SPEM would reduce performance but this reduction would be unrelated to changes in an item's position. Experiment 2 was designed to test the different accounts of the decrease in performance in the SPEM conditions in Experiment 1. To this end, miniature memory and probe images were presented that were fully contained in the pursuit target (i.e., in the fovea). The highly reliable performance drop between fixation and SPEM conditions disappeared. It appears that during SPEM, attention "zooms in" on the pursuit target such that processing of the peripheral image in Experiment 1 was impaired. Because the changes in spatial location were the same in the moving eye / image conditions in Experiments 1 and 2, we conclude that spatial position does not appear to play a major role in VSTM performance.

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Visual Cognition: Objects and Faces

Human Classification Behaviour Revisited by Machine Learning

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We attempt to understand visual classification in humans using both psychophysical and machine learning techniques. Frontal views of human faces were used for a gender classification task. Human subjects classified the faces and their gender judgment, reaction time (RT) and confidence rating (CR) were recorded for each face. RTs are longer for incorrect answers than for correct ones, high CRs are correlated with low classification errors and RTs decrease as the CRs increase. This results suggest that patterns difficult to classify need more computation by the brain than patterns easy to classify. Hyperplane learning algorithms such as Support Vector Machines (SVM), Relevance Vector Machines (RVM), Prototype learners (Prot) and K-means learners (Kmean) were used on the same classification task using the Principal Components of the texture and flowfield representation of the faces. The classification performance of the learning algorithms was estimated using the face database with the true gender of the faces as labels, and also with the gender estimated by the subjects. Kmean yield a classification performance close to humans while SVM and RVM are much better. This surprising behaviour may be due to the fact that humans are trained on real faces during their lifetime while they were here tested on artificial ones, while the algorithms were trained and tested on the same set of stimuli. We then correlated the human responses to the distance of the stimuli to the separating hyperplane (SH) of the learning algorithms. On the whole stimuli far from the SH are classified more accurately, faster and with higher confidence than those near to the SH if we pool data across all our subjects and stimuli. We also find three noteworthy results. First, SVMs and RVMs can learn to classify faces using the subjects' labels but perform much better when using the true labels. Second, correlating the average response of humans (classification error, RT or CR) with the distance to the SH on a face-by-face basis using Spearman's rank correlation coefficients shows that RVMs recreate human performance most closely in every respect. Third, the mean-of-class prototype, its popularity in neuroscience notwithstanding, is the least human-like classifier in all cases examined.

Early Stages (P100) of Face Perception in Humans as Measured with Event-Related Potentials (ERPs)

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According to current ERP literature, face specific activity is reflected by a negative component over the inferior occipito-temporal cortex between 140 and 180 ms after stimulus onset (N170). A recently published study [1] using magnetoencephalography (MEG) clearly indicated that a face-selective component can be observed at 100 ms (M100) which is about 70 ms earlier than reported in previous studies. Here we report these early differences at 107 ms between the ERPs of faces and buildings over the occipito-temporal cortex using electroencephalography. To exclude that these effects were caused by low-level features of the pictures, like contrast or luminance, we compared the P100 component for faces and totally scrambled faces in a second study. The result of higher P100 amplitudes for intact faces compared to the scramble faces confirm that face processing starts already at $\sim$ 100 ms with an initial stage which can be measured not only with MEG but also with ERPs.

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Global and Local Mechanisms of Shape Processing in the Human Visual Cortex

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Coherent visual perception requires the integration of local elements into global shapes. However, the involvement of the various visual areas in the integration of local features into global shapes remains largely unknown.Event-related fMRI was used to test for local and global mechanisms of shape processing in higher visual object related areas. We tested for responses in the Fusiform Face Area (FFA) known to respond selectively to faces [1] and the Parahippocampal Place Area (PPA) known to be involved in the analysis of spatial layout [2]. The stimuli consisted of images of houses or faces (global shapes) rendered by smaller images of stimuli from these categories (local shapes). We tested four conditions: a) global faces rendered by local faces; b) global faces rendered by local houses; c) global houses rendered by local faces and d) global houses rendered by local houses. Subjects were instructed to judge whether global and local shapes where from the same or different categories. Our results showed strong fMRI responses for global faces in the FFA and global houses in the PPA independent of the stimulus category at the local level. Lower category specific responses to the local shapes were observed when the global shapes were from a different category than the local shapes. Further studies tested for fMRI responses at different stimulus scales and attentional shifts. Stronger responses to the local faces in the FFA and local houses in the PPA were observed compared to global faces and global houses. Our results suggest differential processing of global and local shape information in category selective areas. Furthermore, attention and spatial scale influence the processing of local and global shape information.

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Neural Correlates of the Learning of Biological Motion: An fMRI Adaptation Experiment

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Introduction: Previous experimental work indicates that biological motion recognition is dependent on learning. In order to determine neural correlates of this learning process we conducted an fMRI adaptation experiment (cf. [1]). Compared to previous studies using a classical block design, adaptation experiments have the advantage that they allow to distinguish multiple functionally distinct neural subpopulations within the same voxel, exploiting the fact that the BOLD signal decays if the same stimulus is presented repeatedly. Methods: Pairs of unfamiliar motion stimuli for a discrimination task were generated by motion morphing between triples of prototypical trajectories of human movements. The morphs were generated by linear combination of the prototypical trajectories in space-time [2]. Subjects had to discriminate between two successive stimuli presented as Johansson point light walkers with same or different linear weights of the prototypes. By choosing appropriate weight vectors the difficulty of the discrimination task can be precisely controlled. This was used to generate four conditions with identical (SAME), very similar (SIMILAR), moderately similar (DISSIMILAR), and completely different (DIFFERENT) stimulus pairs. Subjects reported whether they perceived the successive stimuli as same or different. The subjects were scanned before and after a training period. Areas relevant for the processing of biological motion (early visual areas, MT+ , KO, FFA, and STS) were localized using standard techniques. Results: Before the training subjects could discriminate the stimuli in the DISSIMILAR and in the DIFFERENT condition. After training they could also discriminate the stimulus pairs in the SIMILAR condition. Comparing the BOLD signal before and after the training period we found a significant reduction of the signal in all localized regions of interest. Before training, we obtained significant adaptation effects for the SAME and the SIMILAR condition only in area FFA and the STS. The other areas did not show selective adaptation. After training, however, no adaptation effect was observed for the SIMILAR condition any more. This result is consistent with an increased discrimination capability after training. Conclusion: We have successfully established the fMRI adaptation paradigm for biological motion experiments. The adaptation effects in area FFA and the STS are consistent with the discrimination performance of the subjects before and after training. Conforming with earlier studies, the STS and area FFA seem to be critical for biological motion recognition. The general decrease in BOLD signal observed after training might be related to a more efficient encoding of the stimuli after learning.

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Magnetoencephalographic Gamma-Band Responses to Illusory Triangles in Humans

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Increased induced gamma-band activity to illusory triangles has been reported in electroencephalogram (EEG) [1] where the activity was both spectrally and topographically widespread. While this is a typical feature of fast oscillatory responses in EEG, in magnetoencephalogram (MEG) we have consistently found highly focal increases of activity in the upper gamma range (50–90 Hz) during different types of auditory processing [2,3], suggesting that MEG may be more sensitive to local network synchronisation. Here we present a replication of the study by Tallon-Baudry et al. [1] in MEG. N = 16 subjects had to respond to two consecutive presentations of a curved illusory triangle (targets) in sequences containing also straight illusory (Kanizsa) triangles, real triangles and no-triangle stimuli (with rotated inducer disks) at equal probabilities. Three blocks of 200 stimuli were presented (duration: 0.7 s, variable interstimulus interval between 2–3 s). Induced oscillatory responses were compared between Kanizsa and no-triangle stimuli and between Kanizsa and real triangles using a statistical probability mapping. Kanizsa triangles were distinguished from no-triangles by increased activity around 70 Hz over medial occipital cortex peaking at 240 ms and over bilateral lateral occipital areas at 430 ms after stimulus onset. Kanizsa stimuli differed from real triangles by increased spectral amplitudes at 90 Hz over parieto-occipital cortex between 100–450 ms after stimulus onset. These findings suggest that illusory triangles are encoded by networks both along the visual ventral and dorsal streams.

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Time Course of the Face Identity Aftereffect

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Exposure to a face can alter the perception of another subsequently presented face. Using a computational 3-D model derived from a database of 200 scanned faces [1,2], we have previously demonstrated the existence of face identity aftereffect (FIAE) [3]. In a multidimensional “face-space”, the average prototype face occupies the central position, while individual real faces are represented as points or vectors emanating from the center. In this context, by inverting a vector corresponding to an individual face, one can create a so-called “anti-face” [4], which served as the adapting stimulus in our previous study. While the FIAE has much in common with more traditional aftereffects, such as its negative sign and its storage during brief unstimulated periods [3], its dynamic aspects have not yet been studied. The present investigation aimed to determine the effects of adaptation and test durations on this phenomenon. Subjects learned to recognize four faces at different identity levels over a period of several sessions, until they could correctly name low-identity faces. We then tested the effects of adaptation and testing duration on the FIAE. In each trial, one of the four names was shown on the screen, followed by the presentation of an “adaptation” face (the anti-face of the named individual) for a period between 1.0 and 16.0 s. Immediately following adaptation, a “test” face (the average face) appeared for between 0.1 and 1.6 s. Subjects were required to rate, on a scale of 1 to 7, the degree to which the test face resembled the individual named at the beginning of the trial. They were specifically told to restrict their judgment to the instant that the test stimulus disappeared. The results indicate that the FIAE resembles other aftereffects in that it is increased in magnitude by long adaptation times, as well as by short test times. Mean ratings showed good fits to the adaptation and test times with positive and negative logarithmic functions, respectively. However, despite this similarity, the magnitude of this proportionality in the FIAE was considerably smaller than in low-level aftereffects.

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Influence of Occlusion on the Responses of Area TE Neurons in the Macaque Monkey

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Identifying an image presented behind an occluder is in many cases easily possible. However, under certain occlusion conditions, identification fails. Critically, identification performance depends on which image parts are visible through the occluder. Area TE in the macaque visual cortex is thought to play an important role in object recognition processes. Here, we systematically test how the occlusion of different image regions affected the responses of area TE neurons. Two monkeys (Macaca mulatta) learned to identify members of sets of natural images. We then used Bubbles to assess how the occlusion of different image regions influenced an observers' performance in the identification task. Most importantly, we determined which image regions had to be visible to allow the observer to identify the image correctly (the "informative" image regions). In most cases, the visibility of a limited portion of the image consistently influenced the monkeys' performance. Based on these results, we constructed observer-specific image versions that contained informative or uninformative regions only. Recording from neurons in area TE, we compared the responses evoked by the full images to the ones evoked by the image's informative or uninformative parts. Preliminary results suggest that informative regions had a greater influence on the response and selectivity of TE neurons than non-informative regions. Thus, monkey observers tend to rely on restricted regions of complex natural scenes during identification tasks, and this has an impact on their representation in the inferior temporal cortex.

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Self-Regulation of Local Brain Activity and its Behavioural Consequences

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Compared to brain-computer interfaces (BCI) based on electroencephalography [1], a BCI based on functional magnetic resonance imaging (fMRI) allows to record non-invasively the activity of the whole brain with high spatial resolution. This allows to feed back local brain activity to learn voluntary regulation of a region of interest (ROI). Using real-time fMRI, brain responses were visualized and provided to the subject with a delay of less than 1.5 seconds [2]. As on-line feedback, the difference of the mean BOLD signal of two regions of interest approximating supplementary motor area (SMA) and parahippocampal place area (PPA) was presented [3]. Eight volunteers learned to successfully control the differential neurofeedback signal. While regulating activity in SMA and PPA, three subjects performed behavioural tasks which are known to be characteristic for these regions. Preliminary data suggest that subject's performance systematically changed depending on the self-regulated level of activity in SMA and PPA. During up/down regulation of SMA and PPA, subjects had to carry out an externally triggered bimanual finger sequence. Reaction times, i.e. onset of the movement, correlated negatively with activity in the SMA. Hence, the more the subjects increased activity in the SMA the faster the movement was executed. To test behavioural consequences of regulating the PPA we made use of the fact that it is involved in encoding information for memory. Wagner et al [4] have shown that the higher the activity of the PPA during encoding of visually presented words, the more likely the words were recognized in a memory test. We presented 106 words while subjects regulated activity of SMA and PPA. Interestingly, all subjects remembered the words better in the SMA-up/PPA-down condition than in the SMA-down/PPA-up condition. Possibly, concurring activity in the PPA might occupy resources and, thereby, interfere with other tasks utilizing the same region. Taken together, our data suggest that self-regulation of circumscribed functional areas leads to characteristic behavioural effects. This offers the opportunity to study behaviour dependent on self-regulated brain activity.

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Feature Integration in Detection of Objects and Random Patterns

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An object is detectable if it differs from its background in at least one basic visual feature. If the object differs from the background by a second feature, detectability (measured in d') is usually increased. The increase of detectability with an additive feature serves as an indicator for interaction among the two feature modules. According to traditional theories, like the feature integration theory [1], different features are processed by independent modules. This would result in an additive increase in d' with a second feature. However, recent experiments have shown, that the assumption of independence does not always hold. Kubovy et al. [2] showed that a texture border, defined by color and form, is better to detect than would have been predicted under the assumption of independent feature modules. The authors proposed interactive feature integration that is capable of synergetic processing. Our experiments aim at the side conditions of interactive feature integration, especially in terms of synergy of feature modules. We report data from three psychophysical detection and discrimination experiments. Depending on the experimental situation we find strong interactivity of feature modules for orientation and spatial frequency. The interaction is modulated mainly by two factors. First, the strength of feature contrast is inversely correlated to interactivity: With high contrast stimuli we find enhancement below additivity whereas with low contrast stimuli feature integration is above additivity, which is interpreted as synergetic feature integration. Second, synergetic feature integration seems to be limited to stimuli that can be grouped to coherent objects. With a scattered distribution of stimuli no interactivity was found. The results indicate, that the visual system is capable of synergetic feature integration if an object has to be detected and if the object is defined by features near detection threshold.

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Role of Featural and Configural Information in Recognition Across Different Viewpoints

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Everyday life requires us to identify different faces in many different poses and views, despite this complexity, we are capable of recognizing familiar faces reasonably well. In this study, we focus on the question of what kind of information human observers use to recognize faces across variations in viewpoint; specifically, whether they use only holistic information, or whether they encode and store the local information contained in facial parts (featural information) as well as their spatial relationships (configural information). Three experiments were conducted, modelled after the inter-extra-ortho experiments by Bülthoff & Edelman, 1992, who used novel objects as stimuli (wire- and amoebae-like 3D objects). Experiment 1 was designed as a base line for the subsequent experiments. Ten face-stimuli were presented in frontal view and 45° side view. At test they had to be recognized among ten distractor faces at different viewpoints. We found systematic effects of viewpoint (recognition performance: inter = extra $>$ ortho) similar to results in the original study. Experiments 2 and 3 were designed analogously to Experiment 1 except for the fact that in the testing phase the faces were presented scrambled or blurred. The results showed that human observers are capable of recognizing faces across different viewpoints on the sole basis of isolated featural information and of isolated configural information. Furthermore, we found systematic effects of viewpoint for both isolated configural information and isolated featural information. The results provide further support for two routes in face recognition and clearly show that part-based processing is at least as viewpoint dependent as configural information. This effectively demonstrates how view-based recognition pertains even to different processing routes. In addition to the psychophysical experiments, systematic differences between the effects of viewpoint are discussed in a computational framework based on key frames.

Physiologially Plausible Neuronal Model for Prototype-Referenced Encoding of Faces

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Conceptual models of face recognition have assumed that faces are encoded as points of an abstract face space relative to an average face, or face prototype (e.g. [1]). So far it has been largely unclear how such a prototype-referenced encoding of faces could be implemented with real neurons. Recent electrophysiological evidence seems to support the relevance of prototype-referenced encoding. Neurons in macque inferotemporal cortex, which have been trained with human faces, tend to show a monotonic tuning with the caricature level of the stimuli [2]. We present a neural model that accounts for these new electrophysiological results.

The hierarchical model consists of multiple layers of neural detectors modeling properties of neurons in the dorsal visual processing stream. The first layer models simple cells using Gabor filters with with physiologically realistic parameters. A second layer combines responses of Gabor filters that carry significant information about a training stimuli into more complex features. The complex features in the model are based on the Principal Components of the Gabor responses, which could be extracted using simple Hebbian-like learning rules. The highest hierarchy layer models neurons in area IT. The responses of these neural detectors increase monotonically with the distance of the input feature vector, from the previous layer, and the average feature vector over all training faces. In addition, neural detectors on the highest hierarchy level show a broad tuning with resepect to the direction of the difference vector between input feature vector and this average vector.

The model was tested with gray-level images that were generated using a morphable 3D face model [3]. The model was trained with 98 randomly chosen faces from a data basis with 200 faces. It was tested with caricatures and anti-caricatures of 4 selected faces. In addition we tested lateral caricatures of the faces, which lie on curves in face space that connect the four selected example faces. Exactly the same stimuli had been used in the electrophysiological experiments [2].

After training, a significant number of the neural units on the highest level of the model show a monotonic tuning with the caricature level of the faces, and a moderate tuning with respect to facial identity, consistent with the electriophysiological results. The model provides a physiologically plausible concrete neural implementation of face spaces. Future work will explore its computational properties and coding efficiency in comparison with classical neural models for face recognition.

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The Role of Response Conflicts for Hemispheric Differences in Global/local Processing: A Combined ERP and Response Time Study

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It is generally assumed that the local and global levels of hierarchically structured stimuli are more efficiently processed in the left and right cerebral hemispheres (LH/RH), respectively. However, in ERP studies with stimuli in the lateral visual field (VF) corresponding effects are only rarely observed [1]. What is more, in none of these studies a concordance between ERP measures and response time measures with respect to hemispheric differences was obtained. Possibly the used stimuli were responsible for this outcome. In response time studies VF effects mainly occur with stimuli where the responses to the levels are conflicting [2]. The aim of the present study was to investigate whether in this condition analogous hemispheric differences would also occur in the ERP data. Conflicting and non-conflicting stimuli were presented to the left and right VF with the task to give a speeded response to a specific level. Response times as well as ERPs were registered. The same prediction was made for both variables: If response conflicts were important for obtaining hemispheric differences, then the corresponding positive effects should show up even though the stimuli were presented laterally. In line with earlier response time studies [2], significant VF effects were obtained only with conflicting stimuli. Global targets were processed faster and more accurate in the left VF compared to the right VF, and local targets vice versa. Concordant results also showed up in the ERP data. For conflicting stimuli the potentials were more positive in response to global compared to local targets in the RH, whereas in the LH they were more positive in the local compared to the global condition. The difference was most pronounced at parietal and occipital electrodes, 340–480 ms after stimulus onset. For non-conflicting stimuli there was no corresponding effect. To sum up, the data show that response conflicts between the levels are an important condition for obtaining hemispheric differences in global/local processing. Moreover, in this situation analogous hemispheric differences were observed in the behavioral and in the electrophysiological response. To our knowledge the present study is the first to show such a concordance between these measures.

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An Advantage for Detecting Human Targets in Dynamic Versus Static Composite Stimuli

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Human observers are amazingly adept at interpreting cluttered natural scenes, whether these scenes are presented as static photographs or dynamic movies. For example, observers have little difficulty in segmenting a scene into salient objects (e.g., a pedestrian walking through a park). Of course, the environment is dynamic—therefore, we asked whether there is an advantage for dynamic scenes relative to static ones. To address this question, we devised a dynamic composite stimulus in which two separate frame sequences were "blended" into a single stimulus by averaging the luminance of corresponding frames of the separate sequences. By varying the relative weight (alpha) of the two original sequences, we can make one sequence more or less visible in the composite stimulus. Here, we blended frame sequences of pedestrians walking in a park with various machines in action. Observers were briefly presented with two composite stimuli and they judged whether a human target was present or absent in one of them. We compared the 50% alpha threshold for detection across three conditions: (1) coherent dynamic stimuli, (2) static stimuli, and (3) scrambled dynamic stimuli in which we randomized the frame order of the sequence. Overall, we found that thresholds were lower for dynamic than for static stimuli. That is, when dynamic information regarding the human target was available, observers required less static cues (i.e., lower alpha) to detect that target. We found no difference between coherent and scrambled dynamic composites, suggesting that the critical component is increased availability of information over time.

Visual Cognition: Space Perception and Navigation

The Visual Place-Memory of Humans

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Humans use the visual place-memory, with the help of visual information, to return to a location in space. An example how humans can recall a place is that they memorize a spatial configuration of their visual field without the use of object recognition. In honey bees, that kind of strategy has been shown. The honey bees memorize a panoramic picture, a snapshot, of their surrounding to recall a place. Similar mechanisms were found in rodents. But how precise and functional is the visual place-memory of Humans?

The precision and the functionality of the visual place-memory were investigated with the help of a virtual reality lab consisting of a free walking arena and video glasses. The subject should recall a place in this virtual environments, which they had memorized before. Therefore subjects were teleported to a target location and asked to memorized that location. Subjects were than teleported back to the start location and asked to walk to the target location. The precision of goal finding was the dependent variable. The experiments were based on different virtual environments, which differed in contrast, shape or richness of detail. For example: One of the virtual environments used a circular room with a colour gradient as a texture to set the contrast to different levels.

The results show that the level of contrast has strong influence on the precision of goal finding. The results indicate that goal finding is good for a range of higher contrasts, but performance drops rapidly as contrast is lowered. Furthermore, a significant gender difference was observed.

The Influence of the Horizon Height on Spatial Perception and Experience in VR

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INTRODUCTION. Despite impressive gains in computational and graphical power over the last decade, virtual reality (VR) simulations still often fail to convey a natural impression of scale, dimensions, or distances. This however is a key requirement for many potential VR applications, as for example architectural walk-throughs. Recent models of spatial vision suggest that the core of the problem lies in the way different depth cues are integrated by the human visual system similar to a mandatory weighted maximum likelihood estimation (e.g., [1]). Since most VR setups simulate only a few depth cues, strong adversary but in itself consistent depth information like a fixed physical screen distance may therefore substantially compress the perceived depth dimension. However, cue integration might also bear the key to an applicable workaround solution: Varying easily adjustable simulation parameters might offer a potential for compensating for the shortcomings of more intractable depth cues.

OBJECTIVE. The empirical study presented here investigates effects of changing the horizon height in VR by a frustum shift. Observations on distance estimates in reality, the form of the human visual field, and the so-called cognitive framing effect of a restricted simulated field of view ([2]) suggested that a raised horizon could particularly affect the perception of egocentric distances.

METHOD. In a psychophysical experiment eight participants estimated three main dimensions and two egocentric distances in 20 virtual rectangular rooms from two different scene sets. In addition, possible side effects of the experimental parameter were roughly evaluated by a semantic differential rating in eight principal experiential categories in subsets of four rooms. The stimuli were presented on a calibrated desktop VR system. Radiosity-rendered interiors were generated using a custom-made tool that allowed to hide the manipulation of the experimental parameter by a balanced variation of scene features.

RESULTS. Albeit verbal distance estimates are known for showing high variances between subjects, relative horizon height and perceived egocentric distances were significantly correlated (correlation coefficient r=0.16**, p=0.003): The underestimation of distances was reduced by 29% on average. Whereas the influence of the experimental parameter on exocentric dimensions (horizontal r=0.01, vertical r=0.07) and rated experience were below significance level and obviously irrelevant.

DISCUSSION. The results are in accordance with both the cognitive framing theory and the model of mandatory fusion of depth cues. Our findings suggest that a raised horizon height is particularly suitable for improving the perceived ego-location in VR without negatively affecting other perceptual properties. Besides this practical improvement of VR simulations, the study shows that VR can also be effectively used in basic vision research.

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Dynamics of Heading-Encoding in Macaque Area VIP

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In a first study [1] we had demonstrated that neuronal responses to optic flow stimuli in the macaque ventral intraparietal area (VIP) are modulated by the location of the singularity of the optic flow (SOF). Response modulation [for an integration time of about 2 s] could most often be approximated by a two-dimensional regression function. Yet, an integration time of two seconds obviously would be too long for navigational processes within everyday life. Accordingly, we were interested in the question, how fast the recorded neuronal responses would allow a reliable estimate of the current heading direction. We applied the previously introduced population code termed isofrequency encoding to calculate the heading direction at different temporal intervals. The error of the calculated heading direction decreased with increasing integration time down to a residual error for both expanding and contracting optic flow stimuli. These errors, as a function of integration time, were approximated by sigmoid functions. That allowed us to define the heading processing time as the time for which the error dropped to the residual level plus 5% of the total range between initial and residual errors. In this manner we estimated heading processing times of 253 ms with a residual error of 4.2° for the simulated forward motion and 276 ms with a residual error of 4.4° for the simulated backward motion. Our results are well in line with phychophysical studies on heading perception in humans [2].

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Thresholds for the Geometric Modul in Humans

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Surprising results have been published concerning the spatial behavior based on geometric information which is available ie in rectangular rooms. If rats were disoriented they based their searching behavior mainly on the shape of the cage[1]. They persisted on this behavior if one wall of the cage was painted in a different color or additional olfactory landmarks were available. Disoriented young children and non-attentive adults seem to orient in the same way [2][3]. So far it is not clear which depth information are used and which features in the world are important for the geometric modul. In psychophysical virtual reality experiments I measured thresholds for human adults (n=36 for each point) for length discrimination of walls in rectangular rooms. In a second experiment the corners of the room are just marked by objects, no other cues were available. It turns out that: 1. The relativ threshold depends on the size of a room. In larger rooms the threshold is higher and more variant than in smaller rooms. 2. This threshold is also increased if a room is defined just by a configuration of objects. This result could explain recently published data [4] which showed that toddlers use the geometric information in a small room, but not in a larger room. It seems, that geometric information is only strong in small environments and get rid of its power if the environment is bigger. Another important feature might be the contours defined by walls. Object configurations are not that effective for the geometric moduls as walls.

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The Relevance of Vertical Structures in Virtual Architecture

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Vertical structures have an important function in the orientation of humans in their real architecture. This is an influence resulting from the force of gravity [1]. In contrast to real architecture, the virtual architecture does not possess inherent principles. Virtual architecture is characterised by non-materiality and the absence of physical laws [2]. Thus it has maximum flexibility.

In an experiment the meaning of vertical structures for the orientation of the user in virtual architecture was analysed. The experiment was conducted at the Bauhaus-Universität Weimar. As technical devices a Silicon Graphics Workstation and a magnetic tracking system were used. The output device was a Head-Mounted-Display and as input device a Stylus was used.

Within psychology there is a long tradition of examining path integration abilities in humans. As a method to examine the efficiency of sensori-motor whole body information for spatial-knowledge acquisition the method of triangle completion worked satisfactorily [3]. Based on this method two virtual environments were designed.

The first environment consisted of an arena with a diameter of sixty meters, which was enclosed by a four meters high wall. In the arena two access points were distributed in the form of columns, which could be seen from every position of the participant. The columns formed a triangle with the starting point of the user. In the arena walls were distributed according to an arbitrary. All wall elements were in a vertical position to the floor. The second environment was based on the consisting arena. The difference between them was that all wall elements were in a non-vertical position to the floor. The participants were divided into two groups and assigned to one of the environments. Their task was to reach the columns successively and to return to the staring point, which was not marked on the floor. The software recorded the position of every participant. Additionally a questionnaire was developed which measured subjective orientation.

The result of statistical examination was that the participants in the environment with vertical position wall elements had a better orientation. The average values of distances reflected a significant difference between the groups. The assumption that the orientation ability in the environment with vertical structures is also better from a subjective viewpoint could not be confirmed.

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View-Direction-Graphs: a New Approach to Configurational Knowledge

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In the literature on spatial cognition in navigational contexts, it is often assumed that humans are able to build up some kind of "cognitive map" of the surroundings in which they navigate. It is thought to consist of an integrated metrical representation of spatial locations which is organized in some common frame of reference [1]. As an alternative account, a view-direction-graph-approach is brought forward here, a descendant of the view-graph-theory [2]. It assumes that participants make use of the visual scenery at single locations to gather spatial metrical information of the local directions and distances to visible adjacent landmarks. The main difference to the "cognitive map" is the negation of integrated configurational knowledge: in the view-direction-graph, the direction from location A to location B is stored independently from the reverse direction information. In a "cognitive map", both directions have to be derived from the integrated representations of the two locations. Therefore, no systematic asymmetries in the error rates of reversal directions should appear.

Method. In a virtual reality setting, participants had to travel in the training phase repeatedly between six freely visible locations which were either characterized by different or identical houses. The houses were placed in an irregular fashion and were oriented towards the middle of the configuration. In the first test phase, the participants were "transported" consecutively to the different locations and had to point from there to all other locations, whose visibility was blocked by simulated fog. In the following transfer phase, the participants were either placed in the landscape with the identical six houses or a completely different surrounding, in which the configuration was instantiated by six identical space-shuttles, located in outer space. In these settings, the participants' ability to reorient in the configuration was tested by traveling tasks which started from random as well as novel locations.

Results. Most participants were reasonably able to point at the invisible locations, and they were able to reorient themselves successfully. These spatial abilities were uninfluenced by the landmarks (different or identical), the surroundings (houses or space shuttles) and the combination of these factors. However, the pointing errors exhibited a strong dependency on the angle between the direction to a target location and the local forward axis from the actual location. In sum, this effect led to systematic asymmetries in the respective pointing errors which are incompatible with an integrated spatial representation. The results support the new "view-direction-graph"-approach.

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Top-Down Influence on Visually Induced Self-Motion Perception (Vection)

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INTRODUCTION: The prevailing notion of visually induced illusory self-motion perception (vection) is that the illusion arises from bottom-up perceptual processes. Therefore, past research has focused primarily on examining how physical parameters of the visual stimulus (contrast, number of vertical edges etc.) affect vection. In this study, we examined the influence of a top-down process: Spatial presence in the simulated scene. Spatial presence was manipulated by presenting either a photorealistic image of the Tübingen market place or modified versions of the same stimulus. Modified stimuli were created by either slicing the original image horizontally and randomly reassembling it or by scrambling image parts in a mosaic-like manner. We expected scene modification to decrease spatial presence and thus impair vection.

METHODS: Ten naive observers viewed stimuli projected onto a curved projection screen subtending a field of view (FOV) of 54°x40.5°. We measured vection onset times and had participants rate the convincingness of the self-motion illusion for each trial using a 0–100% scale. In addition, we assessed spatial presence using standard presence questionnaires.

RESULTS: As expected, scene modification led to both reduced presence scores and impaired vection: Modified stimuli yielded longer vection onset times and lower convincingness ratings than the intact market scene (t(9)=-2.36, p=.043 and t(9)=3.39, p=.008, resp.). It should be pointed out that the scrambled conditions had additional high contrast edges (compared to the sliced or intact stimulus). Previous research has shown that adding vertical high contrast edges facilitate vection. Therefore, one would predict that the scrambled stimuli should improve vection. The results show, however, a tendency towards reduced vection for the scrambled vs. sliced or intact stimuli. This suggests that the low-level information (more contrast edges in the scrambled stimulus) were dominated by high level information (consistent reference frame for the intact market scene). Interestingly, the number of slices or mosaics (2, 8, or 32 per 45° FOV) had no clear influence on either perceived vection or presence; two slices were already enough to impair scene presence.

CONCLUSIONS: These results suggest that there might be a direct relation between spatial presence and self-motion perception. We posit that stimuli depicting naturalistic scenes provide observers with a convincing reference frame for the simulated environment which enables them to feel “spatially present” in that scene. This, in turn, facilitates the self-motion illusion. This work not only can shed some light on ego-motion perception, but also has important implications for motion simulator design and application.

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Rats can Navigate in Virtual Environments

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Rats are capable of navigating and of learning complex spatial tasks in real environments. It has been shown that rats are capable of solving complex cognitive spatial problems [1], yet it is not known what information the animals use and how it is computed. Some particular properties of spatial information analysis are known, e.g. that the geometry of the environment is of greater importance to rats than the identity of individual landmarks [2]. However, important questions remain open, e.g. the role of optical flow in rodent navigation, and how rats act in large scale environments. To address such questions, we developed a new virtual reality (VR) set-up designed for rats to test their ability to navigate in spatial tasks. This set-up consists of a projection system that displays a virtual reality environment via a mirror system onto a torus-shaped screen that surrounds the rat. The animal is placed on top of a polystyrene ball in a fixed position, allowing rotations along a dorso-ventral axis. The polystyrene ball floats on an air cushion and is easily rotated by the rat when running. Motion detectors register the ball's movements and relay it to a computer system which produces the virtual environment surroundings and adjusts the projection according to the rat's movement. In a first experiment, an array of grey cylinders was set up with 1 m separation in an infinite environment. All cylinders were baited. The animal had to run under the cylinder to get a sugar water reward. After seven days of training the rats showed a significant increase of performance, reflected by the hits per minute and time interval between hits. In following experiments we enlarged the distance between this cylinder up to 15 m and the animals showed that they were still able to navigate towards these targets. When rotations of the environment where introduced, the rats where able to keep their path stably directed towards the now moving targets, indicating that the virtual environment is used. These results show that rodents are capable of navigating in virtual environments. We suggest that the animals interpret the 2D projections as a 3D environment. If the animals interpreted the projections of landmarks simply as two-dimensional projections on canvas, it would not have been possible for them to navigate and to guide their movements to the targets in VR space.

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Relevance of Dimensions in Spatial Frequency for Empirical Design Research

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We discuss the relevance of the perception as a process for the synthesis of form, the design process. Starting with the successive visual perception of details, which can be modelled as increasing spatial frequencies, we found two meaningful perspectives: What Level of Detail (LOD) is neccessary to identify a object? What LOD is sufficient for disabling the observer to discriminate the original and a low-pass-filtered artefact [1]. The successive increasing of the resolution can be represented as a degressive interpolation, reducing the radius of interpolation in time. Perception is dynamically low-pass filtered [2]. The effect strongly varies over the visual field because of the distribution of receptors in the retina. Perpherical perception is interpolated with higher values of interpolation radius than the fovea centralis is. In addition to the factors of exposition (time) and retinal angle (space) there is to be considered an intentional aspect: A directional intention is dependent on a specific medium and situation, i.e. reading on a 2-dimensional screen is of a different scanning order unlike a spatial upfolding directmailing. Usual reading directions interfer with real or virtuel movements of the observer. In this sense we have two meanings of periphery. A (local) sensory periphery in the retina and its processing. And a second (global) periphery of the observing system in its environment. We tested a spatial frequency-based method to forecast the recallable relevance of design artefacts. Those consist in media design of a combination of pictorial and typographic elements of different size and contrast. We showed, that our qualitative prognosis of the results of the study of CZAIA [3] were very close to the order which was empirically found. The paradigm of Degressive Interpolation with dynamically low-pass filtering seems to be a powerful instrument for empirical design research to test qualities of Gestalt. So we suggest a method which considers the three essential factors: exposition time, contrast and the periphericness that is both local-sensoric and a global-intentional. Furthermore we can notice that de facto in all cases the full information of an object is not perceived because of convergence of retinal an ganglion cells. Objects contain details that were not detected when the successive perception process is being stopped. For everyday proposals in categorial perception this Level of Detail is sufficient, but a strange conclusion follows, if we interpret Gestalt as a Fourier-Sum: Every real Gestalt will have an infinite number of partial waves like visual overtones because of having a fractal numbers of dimensions. Cognitive and virtual forms however will have a finite number of dimensions. If we go farther this way, we could propose such an visual overtone as an variable and in consequence could name it dimension. So every cognitive space would have a different and dynamical number of dimensions unlike a physical space which has a constant number of dimensions. In this view real Cognitive Systems could be identified by this reducing dimensions, what the Cognitivistic Artificial Intelligence ignored.

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Visual Perception: Colour

Spatial Color Vision: Spherical Geometry and Mapping

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Neuronal coding of spatial color vision is most economical performed in our brain with a smallest number of neurons. Neighboring photoreceptors (rods and cones) in the retina project to neighboring areas in the visual cortices (retinotopic mapping). The areas of highest spatial resolution in the retinas, the foveas, thus project to fixed areas in the cortices. The neuronal color coding (CC) system steers the amounts of the elementary colors and the 2D angular directions of the elemental color sensations in the 3D color space. The depth coding (DC) system determines the depth positions of the elemental color sensations. Despite the small number of neurons and the acceptance angles of the photoreceptors (for just discriminable color areas: ca. 40”), a much higher resolution for hyperacuity (ca. 3”) can be achieved. Due to small rapid and larger slow eye movements, the representations of the foveas in the finer spaced (ca. 3”) spherical geometry of the 3D color space move accordingly. The predicted spherical geometry was quantitatively confirmed by psychophysical measurements on the “Visual Effect of Enlargement with Depth” [1, 2, 3].

Now, evidence for further properties and implications of the model of spatial color vision are presented. 1) The light distribution of a scene reaching the eye is linearly mapped onto the spherical 3D color space spanned by the three linear angle and depth coordinates. Thus, the subjective representation of the scene shows the same perspective distortions as the light distribution. Railway tracks, for example, are thus not seen as parallel lines but as two narrowing straight lines with cross ties getting closer with distance. 2) The linear mapping ends abruptly at the subjective horizon, as seen in real scenes (e.g. moon and stars) or respective 3D pictures. Objects further away in reality are seen at the same maximum subjective depth (equivalent distance: ca. 5 km). 3) In addition, the model straightforward explains the phenomenon of size constancy in pictures.

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Chromatic Signal Detection Investigated with Classification Images and Classification Histograms

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The number and nature of the mechanisms for the detection of colored stimuli is still unclear. Here we use classification images and classification histograms to investigate the detection of a signal of homogeneous color added to a noisy texture.

In a yes/no experiment, subjects had to detect the presence of a low contrast signal in chromatic noise. The noise pattern consisted of 24x24 square patches of light. Each noise square subtended 0.5 deg visual angle and was assigned a color drawn randomly from the isoluminant plane of DKL color space. The signal consisted of a centrally presented square of uniform color subtending 8x8 background patches. Signal colors were chosen from cardinal and non-cardinal directions of DKL color space.

From the observers' "yes" and "no" responses, classification images and classification histograms were computed for each signal color. Classification images are computed by first sorting the noisy background textures into one of the four possible signal/response categories "hit", "miss", "false alarm", "correct rejection", depending on the observer's response, then averaging within each category and finally subtracting averaged "no" from "yes" responses. Classification histograms are computed analogously, based on color histograms of the background image instead of the background image. Color histograms of the isoluminant background images show for each color hue the amount of saturation present in the image.

For all signal colors, classification histograms peak near the signal color and have a broad chromatic tuning, suggesting underlying linear mechanisms. Classification images show that the detection is not based on the whole stimulus but influenced mostly by a small spot around the fixation point. Experimental results are compared to a basic chromatic detection model in order to estimate the number and tuning width of chromatic mechanisms.

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Response Priming by Color in Patients with Lesioned Posterior Parietal Cortex

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Dual visual systems theory (Milner & Goodale, 1995) suggests that visual stimuli are processed in parallel through separate pathways: a dorsal pathway specialized in visually guided motor responses, and a ventral pathway for recognizing visual objects and color processing. Recent studies showed, however, that color information can be used to guide fast motor responses, even though color processing should be confined to the ventral stream (Schmidt, 2002).

We investigated how patients with dorsal-pathway lesions responded to color masks preceded by hardly visible consistent or inconsistent color primes. Although clear response priming effects were found, their time-course was altered and unsystematic in all patients compared to healthy controls, when stimuli were presented in the contralesional hemifield. Results suggest that an intact ventral pathway is not sufficient to transmit color signals to motor areas with uncompromised temporal precision.

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the German Science Foundation to Thomas Schmidt ‘response priming and visual consciousness’

Color Categorization and Lens brunescence—Comparing an Indigenous Language of Vanuatu to German

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In their 1969 published book “Basic Color Terms: Their Universality and Evolution” Berlin & Kay developed rules of the distribution of basic color terms. For example when there exists a word for blue in a language then there are terms for green and yellow in this language too, but no terms for brown, purple or gray. Different classes of basic color terms define distinct stages of evolutionary development. Many languages make, in contrast to most Indo-European languages as German, English or French, no difference between “green” and “blue”. They have only one basic color term for these colors, generally called “grue”. Mostly they integrate short-wavelength stimuli into the “green” category. As an explanation for the grue category it was proposed that this is caused by altered perception through lens brunescence (e.g. Lindsay & Brown, 2002, Psychological Science, Vol. 13, No. 6, 506–512). Chronic exposure to a high amount of UV-B radiation, as in the sunlight of the tropics, could cause faster aging of the human eye, which means a yellowing of the lens. As a result of the yellowing bluish colors would appear greenish. But also purple should appear grayish and red more orange. In this study the color categories of a language of the South Pacific were compared to color categorization in German with and without simulation of aged lenses. Melanesian native speakers of the language of Lenakel, West Tanna, an island in the south of Vanuatu, were asked to categorize an array of Munsell Color Chips with their basic color terms. They possess color terms for black, white, red, yellow, grue, and one term including purple, brown and gray. For German subjects, when looking through filters simulating a lens of a 100 year old European and categorizing the same Munsell Chips, the green category was strongly enlarged into the blue category and previous “purple” colors were categorized as “gray” or “brown”. The findings contradict the rules of Berlin & Kay, according to which the grue languages should not possess color terms for brown, purple or gray. The experiments show that the different color categories in these two languages can be explained by different color perception caused by lens brunescence.

Visual Perception: Depth

Orientation Fields in the Perception of 3D Shape and Material Properties

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I present a theoretical analysis that explains how the visual system could solve two key perceptual problems. The first problem is our ability to distinguish reflections from texture markings. The second problem is the estimation of 3D object shape from monocular images.

Textures and reflections both lead to stochastic patterns in images. How can we tell them apart? We have argued previously [1] that textures and reflections have different statistical properties (e.g. specular reflections of the real world have heavily skewed pixel histograms). However, there is an additional cue, which results from the way that patterns are distorted by 3D shape.

As a textured plane is oriented away from frontoparallel, the image of the texture becomes compressed. This provides a cue for 3D shape: if the visual system can measure the compression of the texture at each image location, it can recover the first derivative of the surface (i.e. local orientation) and thus shape. I argue that specular reflections can be treated a bit like textures, because they also lead to stochastic image patterns with well-conserved statistics. When the world is reflected in a specular surface, the reflection is distorted by the shape of the object. The pattern of distortion is a function of the 3D shape, just as it is with textures. Crucially, however, for specularities the compression is a function of the second rather than the first derivative of the surface (i.e. surface curvature as well as orientation). Hence, the mapping from image compression to 3D shape follows different rules for specular vs. textured surfaces.

I show that the compressions produced by 3D curvatures reliably lead to characteristic 'fields' of orientation energy across the image of a specular surface. These orientation fields are diagnostic of 3D shape but remain surprisingly stable across changes in the scene reflected in the surface. Furthermore, I show that these characteristic orientation fields can be easily extracted from the image by populations of linear filters that resemble the oriented receptive fields of V1 cells. I show how orientation fields could allow the visual system to distinguish between reflections and textures, even when they are present simultaneously. Finally, I discuss the generalization of these principles to surfaces with arbitrary reflectance properties.

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Texture and Haptic Cues in Slant Discrimination: Measuring the Effect of Texture Type

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In a number of models of depth cue combination the depth percept is constructed via a weighted average combination of independent depth estimations. The influence of each cue in such average depends on the reliability of the source of information [1,5]. In particular, Ernst and Banks (2002) formulate such combination as that of the minimum variance unbiased estimator that can be constructed from the available cues. We have observed systematic differences in slant discrimination performance of human observers when different types of textures were used as cue to slant [4]. If the depth percept behaves as described above, our measurements of the slopes of the psychometric functions provide the predicted weights for the texture cue for the ranked texture types. However, the results for slant discrimination obtained when combining these texture types with object motion results are difficult to reconcile with the minimum variance unbiased estimator model [3]. This apparent failure of such model might be explained by the existence of a coupling of texture and motion, violating the assumption of independence of cues. Hillis, Ernst, Banks, and Landy (2002) [2] have shown that while for between-modality combination the human visual system has access to the single-cue information, for within-modality combination (visual cues) the single-cue information is lost. This suggests a coupling between visual cues and independence between visual and haptic cues. Then, in the present study we combined the different texture types with haptic information in a slant discrimination task, to test whether in the between-modality condition these cues are combined as predicted by an unbiased, minimum variance estimator model. The measured weights for the cues were consistent with a combination rule sensitive to the reliability of the sources of information, but did not match the predictions of a statistically optimal combination.

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Determining the Depth of 2D Surface Patches using Local Relative Depth Cues in a Model of Local Recurrent Interactions

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Human observers utilize cues such as T- or X-junctions to determine the depth of objects in 2D images (e.g., [1]). Such cues provide only local and relative information about the position of an object in depth. It is therefore necessary to integrate the information of all cues to compute a globally consistent interpretation of the scene (e.g., [2]). We propose a neural model which solves this task using local information about contours and T-junctions delivered by a pre-processing stage. The model consists of several depth layers containing topographical maps of model dipole cells [3]. A dipole cell has two input channels to continuously compare the activities delivered by the positive and negative output channels of the neighboring cells. Dipole auto-reset is triggered when the relation between mean positive and negative activities in the local neighborhood of a cell reverses. By this, waves of activity running along surface contours can be triggered in the two-dimensional maps of model cells. T-junctions are used to locally reset dipoles which correspond to surface contours not belonging to a specific depth layer. This results in waves of activity resetting all dipoles of the contours not belonging to a layer. In order to obtain the absolute position of a surface contour in depth, inhibitory connections between the model layers implement a scheme which recursively assigns contours to layers. By this, the surface contours being in the fore- and background are first assigned to the corresponding depth layers and all other contours are deleted from that layers by waves of activity. Afterwards, the position in depth of those intermediate contours is recursively determined. A variety of artificial images was used to demonstrate that the model obtains the correct depth sorting of several overlapping gray-scale surfaces. Furthermore, model long-range groupings create activities at illusory contours and result in, e.g., the contours of an illusory kanizsa square being in the foreground of the pacman inducers. Taken together, we demonstrate that a globally consistent interpretation of depth can be obtained from local relative cues using a recursive model in which neurons interact only in a locally restricted topographical neighborhood. Due to the recursive scheme implemented by inhibitory connections between the model layers, depth sorting is fastest for surfaces being in fore- and background and takes progressively longer the more a surface has an intermediate depth level.

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Visual Perception: Eye Movements

The Role of the Thalamus in Updating Visual Space

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Although our eye movements cause the retinal image to slip, we perceive a stable world. It is commonly believed that spatial stability is achieved by monitoring an efference copy or, more generally speaking, corollary discharge of the movement command [1,2,3]. Recent work suggests that corollary discharge information about a saccade is conveyed in a pathway from the superior colliculus (SC) via nucleus MD of the thalamus to the frontal eye field (FEF) in macaques [4]. The aim of this study was to investigate, if thalamic lesions in humans lead to deficits in using corollary discharge information. Twelve patients with selective thalamic lesions and 12 healthy, age-matched controls were examined with a saccadic double-step task. In the experimental condition retino-spatial dissonance was induced, i.e. the retinal vector of the second target and the movement vector were different. Thus the subject could not rely on retinal information, but had to use corollary discharge information about the metrics of the first saccade to correctly perform the second saccade. The first and second saccades were significantly shorter in the patient group in the experimental as well as the control condition. Saccades in the experimental condition were shorter than in the control condition in both groups. Individual patients were, however, impaired in using corollary discharge information. Four patients showed unilateral deficits, revealed by asymmetries in their performance in comparison to the other patients and to normal controls: They showed lateral shifts of second saccades in the case of retino-spatial dissonance only on one side. Two patients with dorsolateral thalamic lesions were impaired contralateral to the side of their lesions, one patient with a lesion in MD was impaired ipsilateral to the lesion. The greatest asymmetry was found in a patient with a bilateral thalamic lesion. The results show that thalamic patients can be impaired in using corollary discharge information. Not surprisingly, contralateral deficits were observed in patients with lateral lesions, because the pathway from SC to FEF passes through lateral parts of the thalamus in humans [5]. The ipsilateral deficit observed in one patient with a medial lesion is inconsistent with the findings in macaques[4].

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Contingency of Illusory Time Perception During Saccades

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During fast eye movements (saccades) visual perception is suppressed to prevent erroneous and distracting motion signals resulting from the retinal slip. Only especially salient stimuli are perceived. Although suppression can take a noticeable time interval, there is no “perceptual gap” noticed during saccades. Up to now, it is unclear what kind of perceptual mechanisms might cause this. Yarrow et al. [1] conducted experiments in which subjects had to make temporal interval discriminations of stimuli presented simultaneously to saccades. They obtained a characteristical overestimation of the first interval that starts with the landing of the eyes. Their conclusion was that the perception at the landing of the eyes is antedated to the onset of the suppression (i.e. shortly before the beginning of the saccade), thereby closing the perceptual gap. This proclaimed mechanism should be global, multimodal and independent of object properties. In contrast, Deubel and colleagues [2, 3] hypothesize that, first, visual spatial attention shifts to the new eye position before the eyes actually start to move, and, secondly, subjects misestimate the time the eyes actually reach the target. This could be a local, attention-related and thereby object-specific explanation for the perceptual timing error found by Yarrow. Here, we conducted three experiments. (1) Yarrow’s results were replicated: A numerical counter started with the beginning of the saccades, the task was a temporal interval discrimination. If the counter was the saccade target, the first interval was perceived prolonged. (2) When, in contrast, the counter was presented centric between fixation point and target (and thus not in the focus of attention) no prolongation was perceived. (3) In another modification of exp. 1, the numerical counter was replaced by an acoustic tick. Just like before, subjects made saccades that triggered the start of the acoustic signals. Again, no significant prolongation could be observed. These results argue for a local, object-specific mechanism that origins from a shift of attention preceding an eye movement. Hence, we prefer Deubel’s explanation over Yarrow’s.

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Actively Searching for Landmarks: an Eye Movement Study on Navigating in a Virtual Environment

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Using visual landmarks is a very common strategy for animal and human navigation. A wide variety of experiments using different methods have focused on the issue of landmark navigation. But so far, the basic questions about how landmarks are found and defined in a visual scene and how landmarks are exactly use in the navigation tasks remain still unclear. Our visual system favors a "top-down" mechanism and actively achieves visual information from the environment. Therefore eye movement tracking provides a possible on-line observation of covert cognitive processing. Here we introduce a method of eye movement tracking to investigate landmark identification in a virtual environment. Additionally, this study also provides an interesting aspect of eye movement research on perceiving a dynamic scene. Subjects navigated in a virtual environment, which was presented on a computer screen. They were asked to memorize a route within the environment while the eye movements of subjects were recorded. Each place in the environment has one specific landmark object and two identical distractor objects, which are the same in the whole environment. Subjects could learn the route in the environment using those landmark objects. Subsequent to an initial training phase, subjects were asked to recall the route in a test phase. The training phase would be repeated if subjects made any errors during the test phase. The results showed that the number of fixations towards landmark objects were more frequent than fixations towards distractor objects. We conclude that during the experiment subjects did actively search for landmark object for the purpose of memorizing the route.

An fMRI Study of Optokinetic Nystagmus and Smooth Pursuit Eye Movements in Humans

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Both optokinetic nystagmus (OKN) and smooth pursuit eye movements (SPEM) are subclasses of so-called slow eye movements. However, optokinetic responses are reflexive, whereas smooth pursuit requires the voluntary tracking of a moving target. We used fMRI to determine the neural basis of OKN and SPEM, and to uncover whether the two underlying neural systems overlap or are independent at the cortical level. The results showed a largely overlapping neural circuitry. A direct comparison between activity during the execution of OKN and SPEM yielded no oculomotor-related area exclusively dedicated to the one or the other eye movement. Furthermore, the performance of SPEM evoked a bilateral deactivation of the human equivalent of the parietoinsular vestibular cortex. This finding might indicate that the reciprocally inhibitory visual-vestibular interaction involves not only OKN but also SPEM, which are both linked with the control of object- and self-motion. Moreover, we could show differential activation pattern elicited by look- as well as stare-nystagmus. Look-nystagmus, which is characterized by small amplitudes and high frequency of resetting eye movements, evoked activity in cortical oculomotor centers, whereas stare-nystagmus, which in turn is characterized by larger amplitudes and lower frequency of resetting eye movements, failed to show significant signal changes in these regions. Thus, less reflexive eye movements correlated with more pronounced signal intensity. Finally, we compared activity associated with predictable and unpredictable SPEM as indicated by appropriate visual cues. In general, predictable and unpredictable SPEM share the same neural network. The knowledge about the direction of an upcoming target movement decreased the cerebral activity level.

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Seeing Green on Green

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When multiple bars are flashed around the target of an upcoming saccade they are compressed towards the saccade target [1]. Subjects asked to indicate the perceived number of bars sometimes reported to perceive just one bar, even if three or four bars were shown. Although in this case spatial positions are merged, other features like color are not. If three bars of different color are presented around the saccade target, subjects who perceive just one bar may still perceive all three colors [2]. Here we ask what happens if a small object is shifted by saccadic mislocalisation onto a broad background of the same color. Does it melt with the background like the multiple bars do, or is it perceived on top of the background? Five subjects conducted large horizontal saccades (29 °) over a red computer screen with a black horizontal reference scale. A broad (8 °) green bar was presented continuously at position 6° to the right of the midpoint of the screen. Around the time of the saccade a green triangle, 1.85° wide, with one of two possible orientations (upwards or downwards) was flashed at position 0°, i.e. left to the broad background bar. Subjects had to indicate the perceived position and the perceived orientation of the triangle, or else indicate that they failed to perceive any object. Three subjects who exhibited mislocalisations large enough so that the triangle was shifted fully onto the background were further studied. They perceived green triangles on top of the broad green bar. Furthermore they were able to correctly recognize the orientation of the triangle even if it was shifted onto the same-colored bar. This was true as long as the flash occurred just before saccade onset. If in contrast the triangle was flashed after the eyes had started to move, subjects were not able to perceive the object any more. This suppression occurred even if the triangle was of a different color than the green background, presumably because it was masked by the motion signal of the bar. We conclude that some object properties of a perisaccadic flash are retained even if—by mislocalization—the object falls onto a same-colored background.

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Quality of Smooth-Pursuit Eye Movements at Low Stimulus Contrast Around Detection Threshold

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The perception of speed and the ability to exhibit smooth-pursuit eye movements were shown to depend on stimulus contrast [1]. Most experiments in this regard have employed stimuli well above detection threshold. We studied pursuit eye movements elicited by targets with contrasts ranging from just below individual thresholds (0.8, 1, 2, 3, 4, 10*threshold) to 100% contrast. Stimuli were Gabor patches with three target speeds (1, 8, 16°/s) and four spatial frequencies (0, 1, 4, 8c/deg). Subjects were asked to rate target direction (Experiment 1) or target direction and velocity (Experiment 2) in a constant stimuli procedure. Contrast starting values were derived from a staircase procedure that was used to determine detection thresholds. We analysed only those trials where psychophysical judgement was correct. For stimuli above threshold, the quality of pursuit eye movements depends slightly on contrast. However, below a contrast level of two to three times the threshold, pursuit is severely impaired: Steady-state gain is low, pursuit latency is long, and position error is high. For fast targets with high spatial frequency most of the foveation is obtained by saccadic eye movements. We can conclude that, in general, the estimation of velocity does depend on contrast. Poor signal quality at contrast levels around perceptual threshold makes it difficult for the pursuit system to reliably estimate velocity. In other words: A correct judgement of target direction and velocity does not necessarily imply that the stimulus can be pursued properly.

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Visual Perception: Motion

Influence of the Spoke Luminance and Spoke Width on the Reverse Spoke illusion—Model and Experiments

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Purpose: We investigate the illusory rotation of stationary spokes in a wheel of rotating segments filled with different luminance values [1]. We analyze the influence of luminance and spatial width of the spokes with a simple model of local motion estimation. Model predictions were confirmed in psychophysical experiments.

Modeling: The spatial phase is computed from Gabor filter responses in circular direction at spoke locations in each frame of the investigated image sequences [2]. We then analyze the temporal course of the detected phase. The computed temporal phase changes for variations of spoke luminance were most uniform (corresponding with continuous illusory motion) for spokes with the mean luminance of the filled segments. Spoke luminance at extreme values (white/black) yield high variations of the temporal phase change, thus leading to a percept of pulsating movement. Further, the variation of spoke width (spokes at mean luminance) leads to simulation results indicating that thinner spokes should yield stronger and more coherent illusory motion cues than broader spokes. In order to quantify these effects we propose a scalar measure for the strength of the motion which compares the detected phase against a shifted linear phase.

Psychophysics: Computational model predictions were verified in psychophysical experiments. Stimuli were generated dynamically with OpenGL (using anti-aliasing) and were presented using a standard computer monitor. We use a nulling paradigm to measure the strength of the illusion (thresholds were obtained with Best PEST [3]). Results for varying the spoke luminance confirm the predictions derived from the model simulations: the effect is maximized for a mean spoke luminance and decreases for higher and lower luminance values leading to an inverted-U function. Observers also confirmed that stimuli with white or black spokes seem to pulsate. The variation of the spoke width reveals that motion induced by wheels with thinner spokes is stronger than for broader spokes, as suggested by the model. Furthermore, we investigated modifications of the illusion concerning geometrical and contrast variations of the original stimuli. Experiments could again confirm model predictions.

Conclusions: The findings reveal stimulus configurations that maximize the effect of the reverse spoke illusion. We demonstrate that the continuous phase extracted from cells with Gabor-like V1 receptive fields contains sufficient visual motion information. Our experiments falsify Anstis' & Rogers' [1] conjecture that the luminance value of the spokes has to be equal to one of the sector luminances to induce an illusory effect. We show that the observed illusory motion is similar to the principle introduced by Freeman et al. [4] for computer graphics visualization.

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Multiple Motions in the Projective Plane

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Motion selectivity is a key feature of biological visual processing and multiple transparent motions have been widely used to probe vision. Of particular interest is how human observers resolve ambiguities that are inherent to certain types of motion patterns. A simple example is the motion of a pattern that is spatially 1D and can be seen as moving in different directions depending on its physical motion parameters and the boundary conditions. However, when a number of 1D and 2D patterns that move differently are superimposed, the categorization of the resulting patterns becomes more interesting. We present (i) a new theoretical framework for categorizing multiple motions, and (ii) an JAVA-based tool that can be used to generate multiple transparent-motion patterns in an intuitive and interactive way.

In a recently developed theory of multiple motions [1] the confidence for a certain motion model is assessed in terms of the ranks of the generalized structure tensors. To resolve the correspondence between the ranks of the tensors and the motion patterns, we introduced the projective plane as a new way of describing motion patterns. The projective plane is the set of all directions in the three-dimensional Euclidean space. The correspondence is such that 2D moving patterns correspond to points and 1D moving patterns correspond to lines in the projective plane. This representation has a number of benefits. For example, the motion of two overlaid 1D patterns (e.g. two gratings) can be distinguished from the motion of one 2D pattern. Such patterns remain equivalent within traditional theories of only one motion.

The interactive tool lets the user draw points and lines on a board that represents the projective plane and the corresponding motions are shown in a second panel. The superposition can be chosen to be transparent or translucent. Single lines in the projective plane are synthesized as moving gratings. When we draw two lines that intersect, we see the motion of the plaid that corresponds to the intersection of the two lines. When we draw three lines that intersect in one point, we see the motion of the intersection. However, when the three lines intersect in three points, there is no consistent motion percept and this difference, that is perceptually very strong, is elegantly captured by the representation in the projective plane.

[1] http://www.inb.uni-luebeck.de/locomotor/

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Electrophysiological Evidence for Independent Speed Channels in Human Motion Processing

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Purpose: A variety of psychophysical studies suggests that motion perception in humans is mediated by at least two speed-tuned channels. To study the neurophysiological underpinnings of these channels in the human visual cortex, we recorded visual evoked potentials (VEPs) to motion onset. Methods: We applied an adaptation paradigm that allowed us (a) to isolate and extract direction-specific cortical responses and (b) to assess cross-adaptation in the speed domain. VEPs resulting from the onset of left- or rightward motion at either low (3.5°/s) or high speeds (32°/s) were recorded from three occipital recording sites in 11 subjects. For each of these test stimuli, responses were collected after adaptation to one of five different conditions: a static adaptation pattern (baseline), adaptation to low-speed motion either in the same or in the opposite direction as the test, or adaptation to high-speed motion either in the same or in the opposite direction as the test. Results: We report considerable direction-specific adaptation for same adaptation and test speeds (by 28–37% of baseline response; $P<0.002$), while there was no direction-specific adaptation across speeds. We supplement these electrophysiological data with corresponding psychophysical results. Conlusion: The lack of direction-specific cross-adaptation in the speed domain demonstrated with physiological and psychophysical techniques supports models of at least two speed channels in the human motion system.

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Recognizing Friends from Different Viewpoints: Biological Motion as Cue for Identity

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The human visual system is very sensitive to the detection of animate motion patterns. We can efficiently recognize human action patterns and attribute many features of psychological, biological and social relevance to other persons. An experimental approach for studying information from biological motion (BM) with reduced interference from non dynamic cues is to represent the main joints of a person's body with bright dots against a dark background. In the present study we investigated the influence of viewing angle on recognition performance of walking patterns from well familiar individuals such as friends or colleagues represented as point-light displays (PLD). Previous work on individual recognition [1, 2] provided empirical evidence that cues from BM contain information enabling recognition of familiar persons and identification of one's own walking pattern when represented as PLD. We tested viewpoint-dependent recognition performance in two groups of twelve persons respectively knowing each other very well. Motion data of the participants were acquired by recording their walking patterns in 3D space using a motion capture system. The locations of the major joints were computed from the trajectories of the original markers. Size normalized PLDs of these walking patterns were presented to the same group members on a computer screen in three different orientations (frontal view, half profile view and profile view). Before the experiment observers were shown a list of all occurring names, including their own. Observers were requested to press a button if they had recognized the person's gait pattern and to indicate afterwards the person's name by clicking on the corresponding name button in a list containing all names. Observers did not receive feedback on their response. Analysis revealed a significant effect of viewing angle on recognition performance. Displays presented in frontal view and in half profile view were significantly more often correctly identified than displays presented in profile view. Whereas recognition performance was found to be significantly above chance level, BM failed to provide a highly reliable cue for individual identification if walking patterns of familiar persons had not been seen before as PLD. We conclude that individual features of gait dynamics can be more efficiently extracted when seen in frontal or half profile view. This viewpoint dependent recognition effect might be due to the fact that the attention towards another person is triggered if this person is approaching us resulting in increased exposure to frontal views of gait patterns.

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Direction Perception of Visual Stimulus Motion is Modulated by Cognitive Demands

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While in many studies the precision for direction discrimination has been investigated, only few studies investigated the accuracy, i.e. the absolute judgement of the perceived direction of motion. In addition, all studies performed so far employed only linear trajectories in their stimulus set. Accordingly, we measured how direction perception is modulated by the frontoparallel stimulus direction itself and whether this performance is influenced by different motion trajectories or additional cognitive demands. In the first series of experiments, we measured psychophysically in fixating human subjects their perceived direction of motion (PDM) of a random dot pattern (RDP), using a modified version of the Simple Up Down method (Levitt 1971). Computer generated visual stimuli were presented on a monitor within a 25 degree aperture at a viewing distance of 57 cm. Subjects viewed two RDPs in sequential order. The first RDP moved either on a linear or on a circular pathway, the second RDP always moved on a linear pathway. Subjects had to indicate whether the movement direction of the second stimulus was rotated clockwise or counterclockwise compared to the final movement direction of the first stimulus (2 AFC). Each subject's (n=9) performance was tested at 24 different directions (0°, 15°, 30°, ,345°). In a second experiment we presented an auditory stimulus simultaneously with the RDP (moving on a circular pathway) in the first stimulus interval. As auditory stimulus we used a series of clicks whose frequency was modulated sinusoidally. Subjects had to indicate whether the movement direction of the second stimulus (linear translation) was rotated clockwise or counterclockwise compared to that of the first RDP at the moment of the peak-frequency of the auditory stimulus (i.e. direction discrimination with an additional cognitive demand). For translational motion all subjects' mean PDM did not differ significantly from the reference direction (mean difference: 0,49 deg). For circular motion the mean PDM was –14.62 deg, i.e. the PDM was shifted 14.62 deg against the circular motion direction. In addition, a strong modulation of the shift across the different reference directions was observed. For the simultaneous visual and auditory stimulation the mean PDM was shifted 30.55 deg against the circular motion direction. This larger difference is probably due to the visual-auditory task resulting in a higher cognitive demand. Our results indicate that the ability to discriminate the direction of a moving visual stimulus is strongly influenced by the motion direction, trajectory and additional cognitive demands.

Motion from Form from Asynchronous Motion

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Motion from form from asynchronous motion

Figure-ground segregation can rely on purely temporal information, that is, on short temporal delays between motion events of elements in figure and ground [1]. We assume that the figure in these stimuli is perceived by a two-stage mechanism, consisting of local motion detectors on a first stage and a segregation mechanism on a second stage. In a recent experiment [2], we found a benefit for binocular presentation but also that the motion detectors on the first-stage are monocular, leaving open the question where the benefit of binocular presentation should result from—the segregation mechanism of the second stage or higher (unitary) cognitions. In this follow-up study, I present psychophysical evidence showing that the second-stage mechanism is not monocular but binocular (i.e. 'post-fusional'), and that its activation can be read out by binocular motion detectors. Tracking of these motion-from-time-based-figure-ground-segregation stimuli requires attention and succeeds up to a speed of approx. 2 cycles per second, which is in accordance with previous findings [3, 4]. The speed of the grid motion seems to be limited by the time required to obtain a single reliable stationary representation of the grid. Taking together, the results suggest a sequence of (1) monocular motion detectors, (2) binocular segregation mechanisms, and (3) binocular motion detectors. Moreover, the study reveals two temporal thresholds for these tasks. Whereas a minimum time delay between motions in figure and ground of approx. 20 ms suffices for subjects to reliably separate figure from ground in stationary localisation tasks, delays of 60 to 80 ms are required in order to obtain a percept strong enough to allow for subsequent motion processing.

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Seeing Biological Motion in the Visual Periphery

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The human visual system is remarkably good at perceiving human movements from only a few points attached to the body. It is generally assumed that this ability depends largely on the grouping of consistently moving points into a segmented body [1], [2]. In central vision such a mechanism is conceivable, because there grouping mechanisms are well developed. In the visual periphery however, we are well at detecting motion, but not at grouping. This implies that people should be bad at perceiving biological motion stimuli in the visual periphery. We present data of an experiment in which observers had to judge whether they saw a person walking forwards or reversed. The observers performed just as good on biological motion in the visual centre as in the periphery, provided that the individual points moved. If the points did not move (i.e. were relocated to a different position on the body each frame), peripheral vision was much worse. This makes a mechanism that relies entirely on grouping unlikely. Instead, a template based mechanism, such as proposed by [3], [4], would be consistent with our results.

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Attention-Demanding Biological Motion Processing: Recruitment of Periventricular Parietal Regions

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Recent findings point to the existence of cortico-subcortical parietal network that drives visual attention-related feature integration [1–3]. Here, continuing the line of research on biological motion processing in patients with early periventricular lesions [4], we ask whether the functioning of this network might be modulated by periventricular lesions. To this end, adolescents who were born preterm with different severity of bilateral periventricular leukomalacia (PVL), fullterms and preterms without PVL were shown a set of impoverished point-light stimuli. Observers had to detect a point-light walker embedded in an array of distractors mimicking the motion of targets dots [5]. Patients exhibited higher susceptibility to distortions caused by distractors. In patients only, sensitivity to point-light figure highly correlates not just with performance on additionally administered perceptual organization tasks but also on visual attention IQ tasks. Moreover, the sensitivity index, as well as the values of the both IQ factors, decreases with increases in the extent of parieto-occipital PVL. No relationship was found between these variables and the lesion extent in the frontal or temporal region. Irrespective of the severity of parieto-occipital PVL, patients had no difficulties performing effortful tasks requiring non-visual attention. The data suggest that feature integration and visual attention in processing of cluttered biological motion are intimately tied. Most importantly, periventricular parieto-occipital regions might be a part of distributed network recruited in deployment of the posterior visual attentional system. To clarify this issue, we analyse functional brain activity in patients with PVL, and compare the time course and dynamic topography of the gamma MEG response to biological motion with the findings in healthy adults [6]. We also discuss the findings in relation to the recent report on biological motion perception after long-term visual deprivation [7].

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Smooth Pursuit Eye Movements in Response to the Motion after Effect

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We studied the relationship between pursuit eye movements and the perception of motion. Motion can be perceived even when there is no stimulus translating on the retina. One such situation is the motion after effect (MAE) After prolonged exposure to a stimulus moving in one direction, a subsequently presented stationary grating is perceived to be moving in the opposite direction.

We used a nulling paradigm to measure the magnitude of the MAE. A moving sinewave grating of 0.25 cycle per degree, 8 degree per second, and 40 per cent contrast was presented for 30 seconds. The subjects were instructed to keep their eyes on a central fixation spot. The moving grating was followed by a test grating that was either stationary or would slowly move in the adapting or the opposite directions. At the same time eye movements were monitored during the adapting and the testing phase. At the end of the trial, the subject had to give a rating whether the grating was stationary, moving in the adapting direction, or in the opposite direction.

Typically, a stationary test grating was perceived to be moving in the opposite direction. The test grating was perceived to be stationary when it moved in the adapting direction at a speed of about 0.5 degree per second. At the same physical speed of the test grating, the average eye movement speed at the start of the testing phase was 0, despite the retinal motion signal. For physically stationary test gratings, which were most often perceived to be moving in the opposite direction, smooth pursuit eye movements were observed that coincided with the percept.

We conclude that smooth pursuit eye movements are possible without retinal image motion. Smooth pursuit and perception seem to share the same neural pathways for the analysis of motion.

Cerebellar Gamma-Band Activity Correlates with the Size of the Visual Motion Aftereffect

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Patients suffering from cerebellar disease are consistently impaired in tasks requiring the perception of visual motion. While this finding is robust and has been replicated independently by several laboratories, attempts to narrow the specific role of the cerebellum in motion perception down by studying deficits in patients have failed. Anatomical studies have suggested that large parts of cerebral cortex, including the parietooccipital areas involved in the processing of visual motion and spatial orientation maintain reciprocal connections with the cerebellum. In order to test if information processing in parietocciptal cortex indeed involves an interaction with the cerebellum, we resorted to whole-head magnetoencephalography (MEG). This approach allowed us to analyze the interplay of cerebral and cerebellar cortex at high temporal resolution, while subjects perceived visual motion. Specifically, we determined the topography and strength of gamma-band activity (GBA), while subjects experienced a motion aftereffect (MAE). The MAE was elicited by a dynamic random dot pattern which was presented after a 5s adaptation period, differing for two conditions compared and centered right of the fixation spot in the first experiment. In condition 1, the subjects (n=8) were adapted to a stimulus with all dots moving coherently in an upward direction (20°/s), while in condition 2, motion coherence was set zero. The individual differences of the MAE perceived between condition 1 and 2 varied from 0.1 to 2.9°/s (mean=1.3; $p<0.01$). A significant difference in GBA between the two perceptually different but physically identical conditions was observed over parietal cortex contralateral to the stimulus in the range of 69–71Hz. In addition, a strong linear relationship between individual differences in the MAE and GBA (93–94Hz) was observed over the ipsilateral cerebellum ($r=0.965$, $p<0.0001$). In order to test the reliability of the pattern of cerebro-cerebellar activity revealed in this first experiment, we carried out a control experiment, in which the position of the motion stimuli was shifted to the opposite (=left) side, a shift which should result in mirroring of the MEG pattern obtained in the first experiment. In fact, this was the case. Finally, in both experiments a significant increase in coherence between GBA recorded from parietooccipital cortex and the cerebellum suggests that the perception of the MAE is a function based on synchronous activity in a cerebro-cerebellar network, rather than being a pure cerebrocortical phenomenon.

Person Identification from Biological Motion: Viewpoint Dependencies

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With rigid objects, the visual system shows some degree of viewpoint invariance. Information obtained about an object from one view can be used to identify the object from a novel view. Little is known whether we can also generalize to new views of non-rigid objects, such as human bodies. Here, we examine this question using biological motion. Stimuli were Fourier represented point-light walkers decomposed into an average posture and the first five harmonics. We investigated the role of these harmonics for person identification from biological motion, and measured performance when viewing angles were varied between learning and test. Three groups of observers were trained to identify seven male walkers, previously unknown to them, shown from different views: 0 deg (frontal view), 30 deg, or 90 deg. Non-reinforced test stimuli were generated by first computing an average walker and then replacing either only its first, second, or third to fifth harmonics with the respective harmonics of the individual walkers. In the test session these walkers were shown either from the same viewing angle as in the training sessions, or from one of the two other viewpoints. Results show that walkers can be identified best if shown from the same view as during training. There was also a significant transfer to other angles, but performance declined with increasing difference between learning view and test view. There was a marginal effect of test view, with the 30 deg view producing best performance. The first harmonic contributes most information to the identification of the walkers. The second harmonic alone is still sufficient for recognition, but this is not the case for the higher order harmonics. There were no significant interactions between the type of harmonic and the training view or the test viewpoint, respectively. We conclude that there is a clear viewpoint effect for recognition of biological motion. Still, the visual system is able to generalize to a considerable degree across viewpoints.

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Visual Perception: Spatial Vision

Collinear Suppression

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Introduction: Stimuli surrounding a target can modulate behavioral as well as neural responses to that target. For example, iso-oriented surrounds usually diminish target perception while collinear contextual elements facilitate target processing— following the Gestalt law of good continuation. Using the recently discovered shine-through effect, we show, to the best of our knowledge, the first counter-example to the Gestalt law of good continuation: collinear elements can exert dramatic contextual suppression.

Materials and Methods: In the shine-through effect, a vernier precedes a grating comprising more than seven aligned elements. The vernier shines through this grating appearing brighter, wider, even longer, and superimposed on the grating though it is not.

Stimuli were displayed on an analog monitor (HP 1334 A) controlled by a Power Macintosh computer via fast 16$\sim$bit D/A converters (1MHz pixel rate). In all experiments a vertical vernier preceded a grating comprising 25 aligned vertical verniers. Except for offset, all spatial parameters of grating elements were the same as those of the foregoing vernier. Segments were 600" long and separated by a small vertical gap of $\sim$ 60". Horizontal spacing between grating elements was 200". The preceding vernier and the middle element of the grating appeared in the center of the screen. With this set-up the vernier shines through the grating. In most experiments, contextual lines or gratings accompanied the standard grating. Single contextual lines were 400" long and had no vertical gap. The vertical gap between the contextual lines and the grating had a width of 200". Contextual gratings consisted of 25 single contextual elements. The grating and the contextual elements were always presented simultaneously.

Subjects were asked to discriminate the offset direction (left versus right) of the shine through element by pressing the corresponding one of two push buttons. Incorrect responses were followed by an error signal produced by the computer. We determined thresholds of 75% correct responses with an adaptive staircase method.

Results:

1. Single collinear contextual elements can exert dramatic contextual suppression.
2. Embedding the collinear contextual elements in contextual gratings yields no suppression.

We suggest that contextual suppression vanishes if the context is a coherent object. For this reason collinear elements might loose their suppressive power if they are part of the contextual gratings that are coherent objects.

Conclusions: For masked stimuli the Gestalt law of good continuation is not valid. However, other Gestalt principles, such as object coherence, might be on work.

SFB 517 “Neurocognition”

Selective Luminance Induction on Bright and Dark Regions in Textures

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It is thought that the "ON" and "OFF" channels, used for detecting luminance increments and decrements, are perceptually inseparable when we process complex textures. Here we show that this is not the case. Methods: a 256 grey-levels texture patch (0.5 x 0.5 deg.), with the characteristic second order statistics of natural images, was surrounded by a uniform luminance region of various sizes (up to 4.0 x 4.0 deg.). We have modulated the luminance of the surrounding region sinusoidally in time (at 0.6Hz) either above or below the mean luminance of the central texture. We found that this modulation induced changes in the perceived contrast of the central patch. Subjects were asked to null this induction by adjusting the depth of modulation of either the bright or the dark regions of the central texture. Results: when uniform surround luminance was modulated above the mean luminance of the central patch, subjects chose to null the perceived induction by primarily altering the modulation of the bright regions of the texture. Conversely, when uniform surround luminance was less than the mean of the central patch, subjects chose to null the induction by primarily altering the modulation of the dark regions of the texture. This implies that, in contradiction to previous reports, our perception of bright and dark regions in complex textures is mediated by perceptually segregated ON- and OFF-channels.

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Effects of Visual Grouping in Spatial Grating Patch Arrangements

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Long range connections among early visual filters localized in space, spatial frequency and orientation have been shown to be effective over spatial distances up to about 12 wavelenght units of the filter's tuning wavelength [1]. Here the effects of collinearity and spatial frequency homogeneity on the contrast detection threshold of grating patch configurations consisting of four elements were investigated. Control measurements assured that the single grating patches, which differed in orientation and spatial frequency, were equally detectable when presented individually at each possible position. Further control measurements with an adaptation paradigm assured that the distances between the patch positions of each spatial arrangement were large enough to preclude any direct adaptation transfer. It is shown that the effects of collinearity are small and not distinguished from probability summation if the four grating patches of each arrangement are heterogeneous with regard to spatial frequency. But if all four grating patches agree in spatial frequency, strong detection facilitation occurs. Interestingly, the facilitation effect is strongest for long distances, outside the range of the contextual effects, as determined by Polat and Sagi (1993). Inside this range inhibition is observed for most of the configurations tested. It is argued that visual grouping, as encountered in higher level object vision, is already effective in basic visual tasks such as contrast detection. Object based grouping is apparently capable of integrating information beyond the spatial scope of the classical long range contextual effects.

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The Trial Context Determines Adjusted Localization of Stimuli: Reconciling the Fröhlich and Onset Repulsion Effects

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It has long been known that observers make localization errors in the direction of motion when asked to localize the onset position of a moving target (Fröhlich effect; e.g. [1]). However, recent studies also revealed the opposite: In the so-called onset repulsion effect, mislocalization was opposite to target motion when observers pointed to the initial position [2]. We demonstrate in two experiments that the conflict between these findings is resolved by considering the trial context: When the stimuli appeared at predictable positions to the left or right of fixation, pointing responses to the onset position were displaced in movement direction. In contrast, when the stimuli appeared at unpredictable positions in the visual field, pointing responses were displaced opposite to motion. Thus, localization errors vary with stimulus context. The theoretical implications of these findings are discussed.

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Wavelength Dependence of Visual Acuity in Man and Goldfish

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In goldfish the four different cone types are evenly distributed over the entire retina and arranged in a hexagonal pattern. The relative number of L-, M- and S-cones is about 0.45, 0.35 and 0.20, that of UV-cones even smaller. Therefore, we assumed that visual acuity may be best in the long-wavelength range of the spectrum. In humans visual acuity is determined by the density of M- and L-cones in the fovea (in different ratios depending on the subject). To compare the contribution of the different cone types to spatial resolution in man and goldfish we measured the action spectrum of visual acuity using high contrast transparencies (square wave gratings; MIT, Infant Vision Lab). For each of 20 wavelengths spatial resolution was determined as a function of intensity. In goldfish (Neumeyer, C. (2003) J. Comp. Physiol. A 189: 811–821) maximal values of spatial resolution of $\sim$2 cycles/deg were found between 440 and 680 nm. In humans high values of 50–60 cycles/deg were measured between 530 and 630 nm only. Plotting the amount of quanta/cms required to obtain this maximal resolution provides a spectral sensitivity function with three pronounced maxima at 460, 530, and 650 nm in goldfish, and a function with two maxima at 530 and 630 nm in human subjects. In goldfish the function corresponds to the spectral sensitivity function reflecting the detection of "color". This was confirmed in experiments under the influence of Ethambutol and under a reduced room light. In humans the action spectrum is similar to the increment threshold function, however, without the third peak at short wavelengths. To obtain a high resolution of 40 cycles/deg in the short wavelength range at $\sim$ 450 nm as well, 2 log units more photons are necessary than at 530 or 620 nm. This indicates that M- or L-cones, but not S-cones are responsible for this performance. Using low intensities of 450 nm light, spatial resolution was less than 10 cycles/deg. The results can be explained by the density of cones and small ganglion cells in both species, and indicate the same type of parallel processing of "color" and high contrast "form"on the one hand, and "brightness" and "motion" on the other.

Retinal Image Motion Abolishes Pattern-Reversal but not Pattern-Onset Visual Evoked Potentials

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Purpose: In patients with nystagmus the functional assessment with visual evoked potentials (VEPs) is severely impeded. Specifically, pattern-reversal responses are strongly reduced or absent in nystagmus patients, while pattern-onset responses can often still be obtained [1]. To quantitatively assess the differential effect of retinal image slip on pattern-reversal and pattern-onset responses we simulated different degrees of nystagmus in normal subjects. Methods: In eight subjects we monitored eye-movements and recorded pattern-reversal and pattern-onset VEPs from occipital electrodes. Subjects viewed the stimulus monocularly via a mirror, which was placed close to the eye and driven by a scanner at four different amplitudes (0°, 1°, 2°, and 3°) of a 4Hz sawtooth waveform. Results: Retinal image motion nearly abolished the pattern-reversal VEPs (by up to 85%; $P<0.001$), while there was no significant effect on pattern-onset VEPs. No oculomotor activity was induced by nystagmus-like retinal image slip at 4 Hz. Conclusion: The strong differential effect of simulated nystagmus on pattern-reversal and pattern-onset VEPs indicates that the spatio-temporal properties of the pattern-reversal stimulus are sufficient to explain its low efficacy in patients with nystagmus. For clinical applications, it follows that pattern-onset is the preferred stimulation-mode in patients with oculomotor instabilities. Of the various possible explanations we quantitatively argue for a mechanism based on motion adaptation.

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