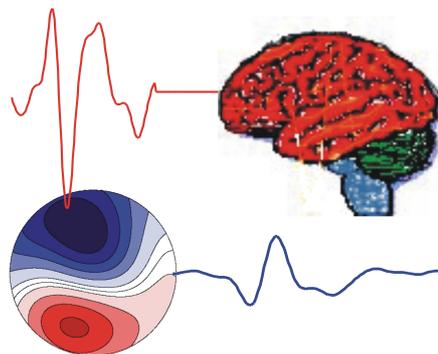


KOGNITIVE NEUROPHYSIOLOGIE DES MENSCHEN

HUMAN COGNITIVE NEUROPHYSIOLOGY



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Abstract

B. Kopp & T. Fingscheidt (Hannover & Braunschweig, Germany) — Electrophysiological Correlates of Orientation Asymmetry in Visual Search

Orientation asymmetry refers to more efficient visual search for vertically than for horizontally oriented objects. We manipulated the visual context of shape-from-shading objects (number of objects, orientation of targets, and rotation between targets and distractors), and measured visual search efficiency and event-related brain potentials. Performance measures indicated that visual search was substantially less efficient when observers searched for horizontal targets amongst horizontal distractors. Vertically oriented stimuli elicited slightly more negative N1 amplitudes than did horizontally oriented stimuli. P3 amplitudes were specifically reduced when observers searched for horizontally oriented targets amongst horizontally oriented distractors, suggesting that the P3 reflects neuronal states which predispose observers for behavioral orientation asymmetry in visual search. The behavioral and electrophysiological data are discussed from the viewpoint of three models of orientation asymmetry in visual search: the light-from-above model according to which search efficiency is influenced by a-priori knowledge about the source of light, a similarity-based model of visual search, and a context model which rests on cortical normalization computations. The similarity model and the context model of visual search fitted nicely with the data, while the light-from-above model fails to account for the P3 suppression effect. However, the context model offers the advantage of providing a computational approach towards orientation asymmetry in visual search.

Keywords: Event-related brain potentials (ERPs); Visual search; Orientation anisotropy; Light-from-above prior; Context model; Visual saliency

Electrophysiological Correlates of Orientation Asymmetry in Visual Search

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Introduction

Investigating the efficiency of visual search (VS) is a popular method for examining cog-

nitive processes related to visual perception (Wolfe, 1998; Eckstein, 2011). Stimulus orientation is among the clearly established basic (preattentive) features supporting very efficient VS (Wolfe & Horowitz, 2004). However, essentially all VS experiments on preattentive processing of orientation have been conducted with simple line segments (Wolfe, Klempen, & Shulman, 1999). A notable exception has been the class of studies on shape-from-shading (Ramachandran, 1988; Aks & Enns, 1992; Kleffner & Ramachandran, 1992; Ramachandran & Rogers-Ramachandran, 2008). Typical stimuli are depicted in Figure 1. Here, smooth shading gradients, i.e., continuous

changes in luminance, provide the visual system with information concerning the surface shape of objects, i.e., the concavity and convexity of surfaces with respect to a particular single point source of light. These shape-from-shading objects should be considered being polar objects, in the sense of (Wolfe et al., 2004). Polar objects have an orientation axis and a polarity if they appear different from a 180° rotation of themselves, such that possible orientations range from 0° to 360°. In contrast, simple line segments solely have an axis of orientation, and their possible orientations range from 0° to 180°.

A number of studies examined the effects of manipulating the orientation axis of shape-from-shading objects on the efficiency of VS (Kleffner & Ramachandran, 1992; Sun & Perona, 1998; Wolfe et al., 1999; Adams, 2007; Thornton & Gilden, 2007). In these studies, empirical evidence for *orientation* asymmetry was repeatedly found: VS is more efficient when the axes of target objects and distractor objects are vertically oriented whereas VS becomes more difficult when their axes are oriented horizontally. The existence of orientation asymmetry in VS has been attributed to the effects of a-priori knowledge on visual perception. Specifically, one of the best-known examples of a prior belief in visual perception is the assumption that light is coming from above (Kersten et al., 2004). This *light-from-above prior* is used to recover shape from otherwise ambiguous shading (Ramachandran, 1988; Ramachandran & Rogers-Ramachandran, 2008). According to the light-from-above account, orientation asymmetry in VS arises because the implicit assumption of overhead lighting aids to per-

ceive three-dimensional shape more vividly in case of vertically compared to horizontally oriented shape-from-shading objects (Adams et al., 2004). Thus, implementing a-priori knowledge provides visual perception with additional cues (i.e., concavity, convexity) when objects are vertically oriented in contrast to when they are oriented horizontally.

However, previous research demonstrated that orientation asymmetry appears not just with shape-from-shading objects, but in similar strength with various sorts of polar objects, such as diverse objects that are not interpretable as three-dimensional surfaces (van Zoest et al., Exps. 1–3) and black-white edges (Kopp et al., 2010, Exp. 2). These data clearly challenge the validity of the light-from-above model of orientation asymmetry in VS. There are two main alternative accounts of orientation asymmetry in VS: First, van Zoest et al. (2006) interpreted their findings in terms of item similarity. Specifically, they conjectured that targets and distractors are perceived as being more similar to each other when objects are horizontally oriented as compared to when they are vertically oriented, thereby decreasing search efficiency (Duncan & Humphreys, 1989). Second, we proposed a context model of orientation asymmetry in VS which has its roots in normalization theories of cortical neuronal computation (Kopp et al., 2010; Kopp et al., 2011; Carandini & Heeger, 2012). Basically, normalization equations compute ratios between the response of individual neurons and the summed activity of neuron pools. Normalization theory was originally developed to explain characteristics of neuronal responses in the primary visual cortex (V1), yet normalization is now thought to operate throughout

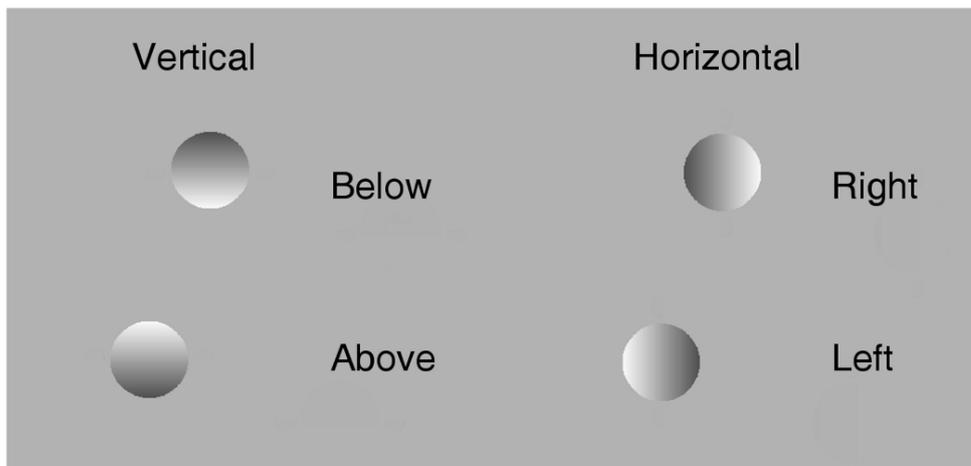


Figure 1: The shape-from-shading objects which were used in the present study. The left panel shows the two vertically oriented objects, whereas the right panel shows the two horizontally oriented objects. *Upper left:* The white-below object. *Lower left:* The white-above object. *Upper right:* The white-right object. *Lower right:* The white-left object. Note that orientation axis and direction of the luminance contrast are perpendicular to each other. Thus, the luminance contrast proceeds in the horizontal direction for vertically oriented objects, whereas the luminance contrast proceeds in the vertical direction for horizontally oriented objects.

the visual system as well as throughout non-visual brain regions (Albrecht & Geisler, 1991; Heeger, 1992; Wainwright et al., 2002; Wilson & Humanski, 1993; Carandini & Heeger, 2012). Our context model attributed orientation asymmetry in VS to more intense normalization, and hence less efficient VS, when objects are horizontally oriented as compared to when they are vertically oriented, as further detailed in the Discussion of this article.

Further, the neurophysiological phenomenon of surround suppression is key to understanding the logic of the current experiment (Seriès, Lorenceau, & Frégnac, 2003; Carandini et al., 2005; Angelucci & Bressloff, 2006). Responding of V1 neurons to stimuli inside their receptive fields can be suppressed by placing additional stimuli in their surrounding region. Take neuronal orientation responses as an example: Surround suppression is maximal when stimuli in the receptive field and those in the surround region are oriented into the same direction, whereas surround suppression is negligible when receptive field and surround region stimuli are perpendicular to each other. Surround suppression led us to design the current experiment which is outlined in Table 1 and illustrated in Figure 2.

We varied the influence of surrounding stimuli by manipulating the context in which shape-from-shading objects are embedded. Specifically, we manipulated three experimental factors: the number of objects in the stimulus array, the orientation of target stimuli, and the rotation of surrounding stimuli (relative to target orientation). As in our earlier study (Kopp et al., 2010, Exp. 2), the number of objects factor had two levels (one object, i.e., a stimu-

lus identification task vs. four objects, i.e., a VS task), and the orientation of target stimuli factor had two levels (i.e., vertical orientation axis vs. horizontal orientation axis). In addition to that, we introduced the rotation factor which had two levels (iso-oriented surrounding stimuli, i.e., distractors are rotated 180° from targets, vs. ortho-oriented surrounding stimuli, i.e., distractors are rotated 90° from targets). Note that Wolfe et al. (1999, Exps. 1 and 4) had already shown that search for a polar target rotated 90° from polar distractors is more efficient than search for a polar target rotated 180° from polar distractors.

We assessed event-related brain potentials (ERPs; Luck, 2005) in addition to behavioral performance measures. First, we recorded visual evoked potentials (VEPs; Hillyard et al., 1998). The first VEP component that we measured was a positivity termed P1. The P1 is usually measured at parieto-occipital electrodes and it reflects activity of extrastriate areas in the 80–200 ms range (Di Russo et al., 2002; Di Russo et al., 2007). The second VEP component that we measured was the posterior N1 (140–240 ms at parieto-occipital electrodes) component with its known influence of visual context (Di Russo et al., 2007; Machilsen et al., 2011). We also recorded the P3 (or P300; Kopp, 2008; Kolossa et al., 2013). Most importantly for the present discussion, it is well known that the P3 component of the ERP must be generated after an observer has categorized the eliciting stimulus according to the rules of the task (Luck, 2005). Kok (2001) reported as the main finding emerging from P3 studies in VS tasks that the number of objects in a stimulus array affects P3 amplitude (the more items in an array, the smaller the P3 am-

Table 1: The experimental design.

There were three experimental factors: number of objects in the stimulus array (one object, four objects), orientation of target stimuli (vertical = “ver or”, horizontal = “hor or”), and rotation of surrounding stimuli relative to target orientation (iso-oriented surround = “iso”, ortho-oriented surround = “ortho”). Target presence/absence constitutes a fourth analytical factor (present = “tp”, absent = “ta”). Note that target polarity represents yet another, nested factor (vertical orientation: above = “a”, below = “b”; horizontal orientation: left = “l”, right = “r”). The “above”, “below”, “left”, and “right” notation equals the notation in Figure 1).

The “ver” and “hor” columns count the number of vertical and horizontal objects across target present and target absent trials of each condition. Note that condition labels and numbers of vertical and horizontal objects diverge from each other in the four objects, ortho-oriented surround rotation condition (i.e., there is a majority of horizontal objects in conditions labeled “vertical”, and vice versa).

Condition label		One object				Four objects			
		tp	ta	ver	hor	tp	ta	ver	hor
iso	ver or	above	below	2	0	$1 \times a, 3 \times b$	$4 \times b$	8	0
iso	ver or	below	above	2	0	$1 \times b, 3 \times a$	$4 \times a$	8	0
iso	hor or	left	right	0	2	$1 \times l, 3 \times r$	$4 \times r$	0	8
iso	hor or	right	left	0	2	$1 \times r, 3 \times l$	$4 \times l$	0	8
ortho	ver or	above	left	1	1	$1 \times a, 3 \times l$	$4 \times l$	1	7
ortho	ver or	below	right	1	1	$1 \times b, 3 \times r$	$4 \times r$	1	7
ortho	hor or	left	below	1	1	$1 \times l, 3 \times b$	$4 \times b$	7	1
ortho	hor or	right	above	1	1	$1 \times r, 3 \times a$	$4 \times a$	7	1

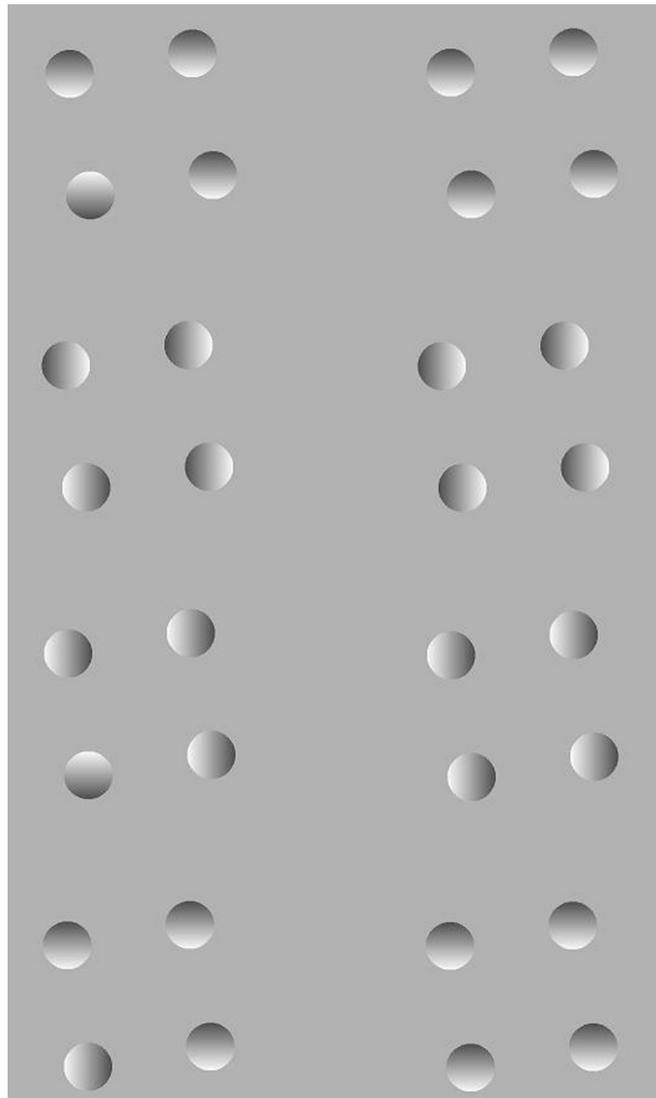


Figure 2: Eight exemplary search arrays, each with four stimuli. *Left panels:* Target present arrays, with the target always being depicted in the lower left corner. *Right panels:* Target absent arrays. *Upper two panels:* Iso-oriented spatial stimulus context, i.e. targets rotated 180° from distractors. *Uppermost panel:* Vertically iso-oriented arrays (for sake of simplicity, only a target with white-above polarity is shown). *Upper-mid panel:* Horizontally iso-oriented arrays (only a target with white-left polarity is shown). *Lower two panels:* Ortho-oriented spatial stimulus context, i.e. targets rotated 90° (clockwise) from distractors. *Lower-mid panel:* Vertically ortho-oriented arrays (only a target with white-above polarity is shown). Note that, only the target is vertically oriented, whereas all distractors are horizontally oriented. *Lowermost panel:* Horizontally ortho-oriented arrays (only a target with white-left polarity is shown). Note that, only the target is horizontally oriented, whereas all distractors are vertically oriented.

plitude; but see Luck & Hillyard (1990) for divergent findings). We basically had made two ERP observations in our earlier study (Kopp et al., 2010, Exps. 1–2). First, VEP amplitudes in the P1 and in the N1 latency ranges were slightly more negative in response to vertically, compared to horizontally, oriented stimuli, regardless of the number of objects that were presented in the stimulus arrays. Second, P3 amplitudes were suppressed in response to stimulus arrays comprising multiple horizontally oriented objects when compared with P3 amplitudes in response to multiple vertically oriented objects, whereas no P3 amplitude differences were discernible in response to single horizontally vs. vertically oriented objects.

Given the described experimental manipulation of the context in which shape-from-shading objects were embedded, the light-from-above model of orientation asymmetry in VS predicts that orientation asymmetry occurs irrespective of the number of objects in the stimulus array (one, four) and irrespective of the rotation angle between surrounding stimuli and target stimuli (90°, 180°). In contrast, the similarity model and the context model both predict that orientation asymmetry occurs specifically on iso-oriented (180°) multiple objects conditions. Further, the light-from-above model predicts that vertically oriented objects evoke more intense neuronal activities, irrespective of the number of objects in the stimulus array (one, four) and irrespective of the rotation angle between surrounding stimuli and target stimuli (90°, 180°). In contrast, the similarity model and the context model both predict that the presentation of horizontal iso-oriented (180°) multiple objects is associated

with a specific suppression of neuronal activities.

In the present study, we took advantage of the high temporal resolution of electroencephalography (EEG) to investigate how the neuronal correlates of orientation asymmetry are modulated by the specific context in which shape-from-shading objects are embedded. Most importantly, we measured EEG activity in response to displays in which objects were embedded in a context of iso-oriented or ortho-oriented shape-from-shading elements. Specifically, we measured behavioral efficiency as well as N1 and P3 amplitudes in order to investigate cognitive and neuronal processes related to orientation asymmetry in VS.

Materials and Methods

Participants

Sixteen healthy undergraduate students of the Technische Universität Braunschweig participated in the experiment (2 male; age 19 to 29 years, mean 22.1 years). They volunteered to participate in return for course credit. 14 of them were right-handed (Oldfield handedness scores -75 to $+100$, mean 65.4; Oldfield, 1971). All participants had normal or corrected-to-normal visual acuity. They were naive with regard to the issues in the study.

Ethics statement

The authors confirm that the research has been conducted according to all ethical standards imposed by their Ethics Committee at the Technische Universität Braunschweig, who approved the study. Written informed consent

was obtained by all participants, according to the procedures imposed and approved by the above Ethics Committee

Stimuli, Display and Apparatus

Circular disks, illustrated in Figure 1, subtended 1.5° of visual angle. Some of these shaded disks convey an impression of depth, based exclusively on subtle variations (gradients) in luminance. Orientation of the shaded discs was defined by shading gradients, as further explicated in Figure 1. There were two orientations of the shaded discs: vertical and horizontal (orientation factor). When shaded discs appear vertically oriented, the shading gradient ran either from top to bottom (white-above), perceived as convex surface bumps, or it had opposite polarity (white-below), perceived as concave surface dimples. When shaded discs appear horizontally oriented, the shading gradient ran either from left to right (white-left), or it had opposite polarity (white-right). Note that the polarity of the shaded discs represents a nested factor (white-above and white-below as two levels in the vertical direction, white-left and white-right as two levels in the horizontal direction) which is of importance for evaluating surface asymmetry.

The shaded disks were configured around a central fixation point along a virtual circle with a radius which subtended 2° of visual angle. Disks were drawn at canonical locations along the virtual circle (45° , -45° , 135° , -135°). Items were distributed randomly to one of these four positions in case that only one item was presented. The entire stimulus array was rotated about fixation to remove configural effects by choosing a uniform deviate from the interval $\pm 25^\circ$. Disks were presented against a gray

background (RGB color code: 178, 178, 178). The contrast relation between disks and background was such that some regions of the disks were brighter than the background and others were darker than the background (Aks & Enns, 1992).

Stimulus arrays contained either one or four disks (number of objects factor). Both types of arrays consisted either exclusively of distractors (target-absent trials), or they included one single target (target-present trials) which could occur at any location along the virtual circle. The rotation of distractors relative to targets constituted another factor: distractors were rotated 180° from targets in iso-oriented surround conditions, such that solely polarity differed between distractors and targets, whereas their orientation remained aligned. In ortho-oriented surround conditions, distractors were rotated 90° from targets (clockwise), such that both, orientation (perpendicularly) and polarity, differed between distractors and targets.

Stimuli were displayed on a 19" CRT monitor with a high refresh rate (100 Hz at a resolution of 1280×1024 pixels). The experimental protocol was carried out by a Presentation® (Neurobehavioral Systems, Albany, CA) program written on a personal computer (PC). Manual responses were executed on both Ctrl buttons of a wireless keyboard (Logitech®, Romanel-sur-Morges, Switzerland) and recorded by the Presentation® program. The left Ctrl button was pressed by the index finger of the left hand, whereas the index finger of the right hand was used to press the right Ctrl button. Stimulus arrays were preceded by a small fixation cross (250 ms duration of presentation; 1,000 ms stimulus

onset asynchrony). Stimulus arrays remained present until response. Response-stimulus intervals were fixed at 1,000 ms.

Task and Procedure

Observers conducted simple stimulus identification (in case of a single object) or speeded VS (in case that the array consisted of four objects) to indicate whether a target was identified or not. The assignment of response buttons to “target present” and “target absent” decisions was counterbalanced across participants.

Each participant completed eight blocks of trials (see Table 1; 208 trials each, totaling to 1,664 trials per participant). Within each trial block, one object and four object trials as well as target present and target absent trials were randomly intermingled, with equal probability of occurrence (i.e., four times 52 trials per block). Four blocks of trials comprised iso-oriented surround conditions, two blocks in which vertically oriented stimuli were presented (target = white-above, distractors = white-below and target = white-below, distractors = white-above, respectively) and two blocks in which horizontally oriented stimuli were presented (target = white-left, distractors = white-right and target = white-right, distractors = white-left, respectively). The remaining four blocks comprised ortho-oriented surround conditions, two blocks in which vertically oriented targets were presented (target = white-above, distractors = white-left and target = white-below, distractors = white-right, respectively) and two blocks in which horizontally oriented targets were presented (target = white-left, distractors = white-below and target = white-right, distractors = white-above, re-

spectively).

The sequence of trial blocks was counterbalanced across participants in such a way that eight participants performed the four iso-oriented blocks before the four ortho-oriented blocks, whereas the remaining eight participants started with the ortho-oriented blocks and finished the experiment with the iso-oriented blocks. Vertical and horizontal tasks were presented in alternating blocks of trials in a Latin square design (i.e., vertical-above, horizontal-left, vertical-below, horizontal-right; horizontal-left, vertical-above, horizontal-right, vertical-below; vertical-below, horizontal-right, vertical-above, horizontal-left; horizontal-right, vertical-below, horizontal-left, vertical-above).

Performing one block of trials lasted about ten minutes. Short breaks of about five minutes separated the blocks. The experiment was carried out in a dimly-lit room in which the participants sat 1 m away from the CRT. In order to familiarize the participants with the demands of the task, a few practice trials were administered before each block of trials.

Electrophysiology

Continuous EEG was recorded by means of another PC, a QuickAmps-72 amplifier (Brain Products, Gilching, Germany) and the BrainVision Recorder® Version 1.02 software (Brain Products, Gilching, Germany) from frontal (F7, F3, Fz, F4, F8), central (T7, C3, Cz, C4, T8), parietal (P7, P3, Pz, P4, P8), occipital (O1, O2), and mastoid (M1, M2) sites. Ag-AgCl EEG electrodes were used. They were mounted on an EasyCap (EasyCap, Herrsching-Breitbrunn, Germany). Electrode impedance was kept below 10 k Ω (mean impedance: 4 k Ω). All EEG electrodes

were referenced to average reference. Participants were informed about the problem of non-cerebral artifacts and they were encouraged to reduce their occurrence (Picton et al., 2000). Ocular artifacts were monitored by means of bipolar pairs of electrodes positioned at the sub- and supraorbital ridges (vertical electrooculogram, vEOG) and at the external ocular canthi (horizontal electrooculogram, hEOG). The EEG and EOG channels were amplified with a bandpass of 0.01 to 30 Hz and digitized at 250 Hz.

Off-line analysis was performed by means of the BrainVision Analyzer® Version 1.05 software (Brain Products, Gilching, Germany). Manual artifact rejection was performed before averaging to discard trials during which an eye movement or any other non-cerebral artifact occurred. Semi-automatic blink detection and the application of an established method for ocular artifact removal were employed for ocular correction (Gratton, Coles, & Donchin, 1983). A digital high-pass filter was applied to the data (0.75 Hz, 48 dB/oct) in order to eliminate low-frequency variations in the EEG signal which were associated with the occasional occurrence of electrodermal artifacts.

The EEG was then divided into epochs of 1,000 ms duration, starting 100 ms before onset of the stimulus array. The pre-stimulus baseline of 100 ms was subtracted from the sampling points. The EEG was averaged off-line. Error trials (misses, false alarms) were excluded from averaging. Deflections in the averaged EOG waveforms were small indicating that fixation was well maintained.

Analysis

Behavioral performance

Behavioral task performance was quantified in two ways: First, the median of the response speed for each cell of the design matrix (Table 1) was computed for each individual participant, and these median individual response times (RTs) were subjected to statistical analysis (Table 2). Trials in which an incorrect response was emitted were excluded from this analysis. Second, for each individual participant, the accuracy of the behavioral responses was computed for each cell of the design matrix (Table 1). Percentage of misses was computed for target-present trials. Percentage of false alarms was computed for target-absent trials. All percentages were transferred into the arcsin transformation prior to statistical analysis.

ERPs

P1 and N1 peak amplitudes were measured in the intervals from 80 ms to 200 ms (P1) and 140 ms to 240 ms (N1) at two parietal (P7, P8) and two occipital (O1, O2) electrodes. These measures were derived from stimulus-locked averages. Individual amplitudes were determined for each electrode. Amplitudes were measured as the difference between peak amplitude and the mean voltage during the 100 ms pre-stimulus baseline. Prior to statistical analysis, P1 and N1 amplitude measures were averaged across the four electrodes over the occipito-parietal region of interest (P7, P8, O1, O2).

P3 amplitudes were measured at electrode Pz. An area rather than a peak measure was used for P3 amplitudes because the latency

Table 2: Number of trials, separately for Set size (one, four), Target (present, absent) and Stimulus conditions (Context (iso-oriented, ortho-oriented), Orientation (vertical, horizontal) and Polarity (above, below; left, right) of the Target).

	Stimulus condition								
	Iso-oriented Context				Ortho-oriented Context				Σ
	Vertical		Horizontal		Vertical		Horizontal		
	Above	Below	Left	Right	Above	Below	Left	Right	
Set size 1									
Present	52	52	52	52	52	52	52	52	416
Absent	52	52	52	52	52	52	52	52	416
Set size 4									
Present	52	52	52	52	52	52	52	52	416
Absent	52	52	52	52	52	52	52	52	416
Σ	208	208	208	208	208	208	208	208	1664

variation that was expected for multiple object conditions could greatly distort peak amplitude measures (Kopp et al., 2010). When single objects were presented, peak latencies in the grand-average waveforms differed between vertical (364 ms latency) and horizontal (392 ms latency) target orientation conditions (cf. Figure 5). Hence, P3 amplitudes were measured as the area under the curve within the latency range ± 50 ms around these condition-specific peak latencies. When four objects were presented, grand-average waveforms showed the expected multiple peak structure (cf. Figure 5; see also Kopp et al., 2010). We chose the latency of the central peak in the grand-average waveforms (436 ms latency), and we analyzed P3 amplitudes in those conditions in which four objects had been presented as the area under the curve within the latency range 436 ± 50 ms.

Statistical analyses

Behavioral and electrophysiological measures were analyzed with repeated-measures analyses of variance (ANOVAs), carried out at the .05 significance level. The results of univariate tests and a measure of effect size, η_p^2 (partial eta squared), are provided. Behavioral measures (RTs, response accuracy) as well as P1, N1 and P3 measures were analyzed separately for the two levels of the number of objects factor, mainly because the type of task differed between one object and four objects conditions (a stimulus identification task vs. a VS task, respectively). All ANOVAs thus comprised four within-subjects factors: orientation of target stimuli (vertical vs. horizontal orientation axis), rotation between targets and distractors (iso-oriented vs. ortho-oriented surround conditions), nested polarity of the target orientation axis (white-above and white-left targets were combined and con-

trusted against white-below and white-right targets; cf. (Kleffner & Ramachandran, 1992; Sun & Perona, 1998; Mamassian et al., 2003), and finally target absence vs. presence. To conserve space, we focus primarily on results (a) which provide evidence for the validity of the measures by replicating principal findings in the literature and those (b) which are relevant for the evaluation of the predictions that were derived from the three competing hypotheses. SPSS 13.0 served for statistical analyses (IBM, Armonk, NY; <http://www-01.ibm.com/software/analytics/spss>).

Results

Behavioral performance

The ANOVA on the RTs for one object conditions revealed a significant target presence/absence effect (present mean reaction time $M=525$ ms, absent $M=572$ ms; $F(1,15)=37.72$, $p<.001$, $\eta_p^2=.72$), but also a significant target orientation effect (vertical $M=536$ ms, horizontal $M=561$ ms; $F(1,15)=6.25$, $p<.05$, $\eta_p^2=.29$). Based on the literature on VS (Wolfe & Horowitz, 2004), target presence/absence effects must certainly be expected. The target orientation effect indicates an efficiency advantage for vertically compared to horizontally oriented objects in the absence of surrounding stimuli, contradicting both hypotheses in which the origin of orientation asymmetry in VS is attributed to mechanisms of target-distractor interaction. Note that we had already reported a similar finding in our earlier study (Kopp et al., 2010, Exp. 2).

The ANOVA on the RTs for four object conditions revealed a significant three-way

interaction between target orientation, surround rotation, and target presence/absence, $F(1,15)=19.34$, $p<.01$, $\eta_p^2=.56$. When separate ANOVAs were performed on each surround rotation condition, a significant two-way interaction of target orientation by target presence/absence emerged for iso-oriented conditions, $F(1,15)=13.69$, $p<.01$, $\eta_p^2=.48$, indicating the existence of orientation asymmetry which was more pronounced when no target was present in the stimulus arrays (cf. Figure 3). However, the interaction was not significant for ortho-oriented conditions, $F(1,15)=4.29$, $p=.06$, $\eta_p^2=.22$, where solely a significant target effect was discernible, $F(1,15)=10.69$, $p<.01$, $\eta_p^2=.42$. These results suggest that orientation asymmetry in VS occurs in iso-oriented, but not in ortho-oriented, conditions. These findings are clearly compatible with both target-distractor interaction hypotheses of orientation asymmetry in VS.

The ANOVA on the error rates for one object conditions revealed no significant effects. The ANOVA on the error rates for four object conditions revealed a two-way interaction between target orientation and surround rotation, $F(1,15)=8.50$, $p<.05$, $\eta_p^2=.36$, indicating orientation asymmetry which occurred in iso-oriented, but not in ortho-oriented, surround rotation conditions, as seen in Figure 3. Importantly, speed and accuracy performance measures converge in suggesting that VS efficiency specifically decreased in conditions comprising multiple horizontally oriented objects (see Figure 3) which usually presents itself as orientation asymmetry in typical VS studies.

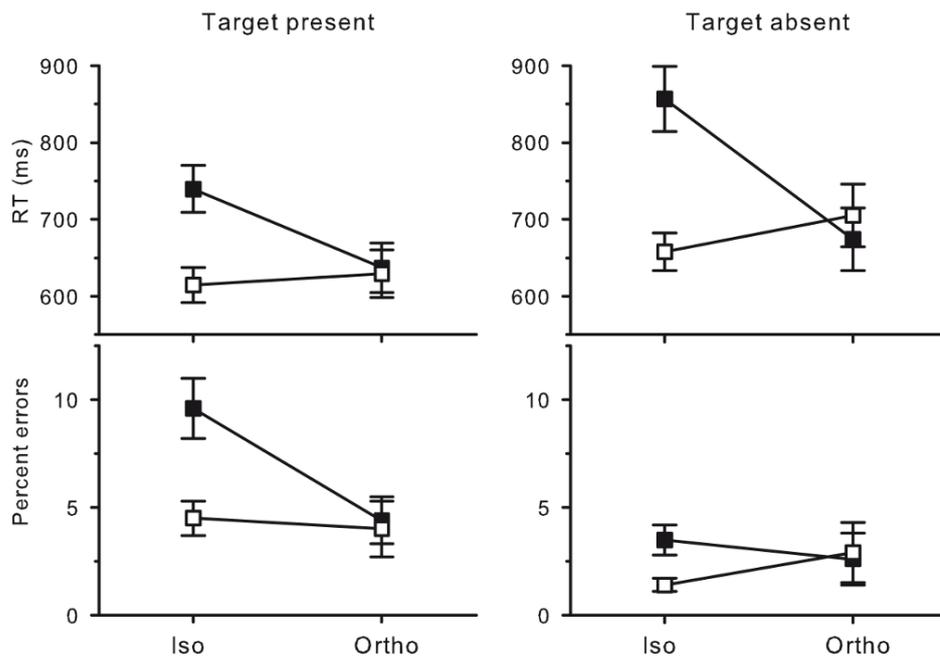


Figure 3: Behavioral results ($M \pm SE$) obtained in multiple object conditions of the present study (response times in ms (RT (ms), upper panels) and percent errors, lower panels), separately for target present (left panels) and target absent (right panels) trials. Left to right on the x-axis is from iso-oriented surround conditions to ortho-oriented surround conditions. White symbols represent vertical target orientation, black symbols indicate horizontal target orientation.

ERP

P1/N1 amplitude measures

The grand average VEP waveforms obtained at four posterior electrodes (collapsed into a single region of interest waveform) from the number of objects conditions (single object four objects) are presented in Figure 4. Note that one of these waveforms, labeled *horizontal object(s)* was produced by averaging iso-oriented horizontal and ortho-oriented vertical waveforms, whereas the other waveform, labeled *vertical object(s)*, was produced by averaging iso-oriented vertical and ortho-oriented horizontal waveforms. These labels convey information about the orientation axis of the majority of objects in the stimulus arrays that evoked these VEP responses. This is of particular importance when four objects were presented because, as further explained in Table 1, arrays within vertical ortho-oriented orientation conditions contained horizontally oriented objects, with the sole exception of the potential eponymous vertical target. In contrast, arrays within horizontal ortho-oriented orientation conditions contained vertically oriented objects, with the sole exception of the potential eponymous horizontal target.

Visual inspection of Figure 4 suggests that P1 and N1 amplitudes tended to be slightly more positive in response to arrays that were mainly composed of horizontally oriented objects compared to arrays that mainly comprised vertically oriented objects, irrespective of the number of objects that were present in the evoking stimulus array. For P1 amplitudes, these observations were not confirmed statistically by a corresponding target orientation by surround rotation interaction, $F(1,15)=3.29$,

$p=.09$, $\eta_p^2=.18$ ($F(1,15)=2.77$, $p=.12$, $\eta_p^2=.16$), for the subset of data obtained from the one (four) object condition. In contrast, these observations were confirmed for N1 amplitudes by significant target orientation by surround rotation interactions, $F(1,15)=10.77$, $p<.01$, $\eta_p^2=.42$ ($F(1,15)=8.95$, $p<.01$, $\eta_p^2=.37$) in the one (four) object condition. Note that these results replicate our earlier findings with regard to N1 amplitudes, but not with regard to P1 amplitudes (Kopp et al., 2010, Exps. 1–2). By and large, these findings suggest that N1 responses differ between vertically and horizontally oriented objects, irrespective of the number of objects in the stimulus array.

P3 amplitude measures

The grand average P3 waveforms at electrode Pz are depicted in Figure 5, separately for single object (left panel) and four object (right panel) conditions. In the first place, strong amplitude reduction as a function the number of objects in the stimulus array is immediately apparent (Kok, 2001; Kopp et al., 2010). When focusing on the subset of data obtained from single object stimulus arrays, P3 waveforms seemed to reflect a neuronal popout response to vertically oriented stimuli that were presented in iso-oriented surround rotation conditions. However, this impression was not confirmed by the corresponding result from statistical analysis, i.e. by the interaction between target orientation and surround rotation, $F(1,15)=0.89$, $p=.36$, $\eta_p^2=.06$. Statistical significance was likewise not found when P3 responses to vertically and horizontally oriented stimuli were compared for the iso-oriented surround rotation conditions solely, $t(15)=1.771$, $p=.097$.

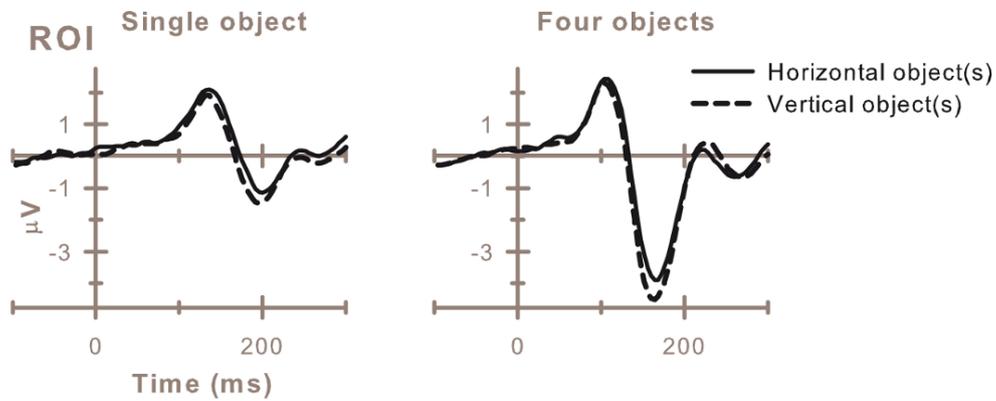


Figure 4: Grand average VEPs at the parieto-occipital region of interest (ROI; the waveforms depict the average over the P7, P8, O1, and O2 electrodes) for vertically and horizontally oriented stimuli, separately for single object (left panel) and four object (right panel) conditions. See text for more details.

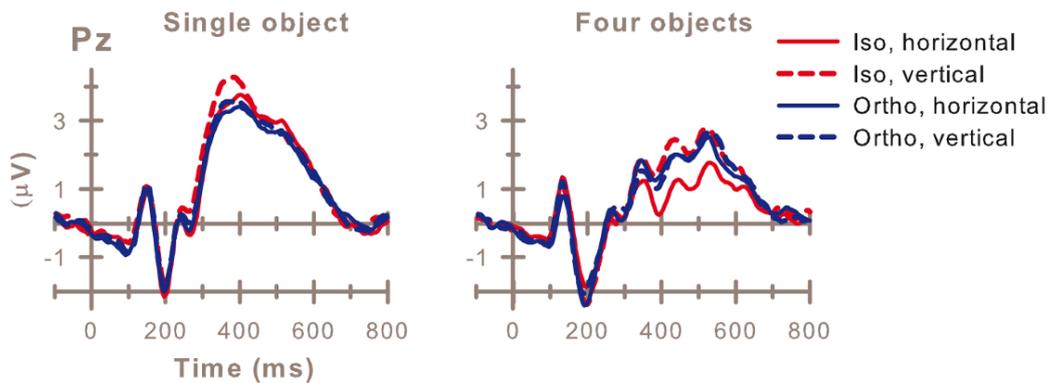


Figure 5: Grand average stimulus ERP waveforms at electrode Pz, separately for single object (left panel) and four object (right panel) conditions. Surround conditions are represented by line color (iso-oriented = red lines, ortho-oriented = blue lines) and target orientation is indicated by line style (horizontal = solid lines, vertical = dashed lines).

When focusing on the subset of data obtained from four object stimulus arrays, P3 waveforms seemed to follow a common pattern, with the sole exception of those waveforms that were obtained from iso-oriented surround rotation conditions when stimuli were horizontally oriented. Note that these are exactly the conditions in which multiple horizontally oriented objects are present in the stimulus arrays. These impressions which were obtained from visual inspection of the waveforms were confirmed by corresponding results from statistical analysis, i.e. by the interaction between target orientation and surround rotation, $F(1,15)=5.10$, $p<.05$, $\eta_p^2=.25$. Statistical significance was also found when P3 responses to vertically and horizontally oriented targets were compared for the iso-oriented surround rotation conditions, $t(15)=4.359$, $p<.01$, but not when they were compared for the ortho-oriented surround rotation conditions, $t(15)=0.434$, $p=.671$. Thus, the interaction effect reflects the fact that P3 amplitude decrements in response to horizontally oriented targets occurs conditional upon the presence of horizontally oriented distractors within the stimulus array. Note also that this result not only replicates our earlier findings (Kopp et al., 2010, Exps. 1–2), but importantly that it confirms a major prediction that was derived from our context model of orientation asymmetry in VS (Kopp et al., 2010; 2011).

Discussion

In this study, we investigated the effects of manipulating the context of shape-from-shading objects on the efficiency of VS. Behavioral performance revealed the typical vertical-over-

horizontal advantage in VS (i.e., orientation asymmetry). We observed that ERP amplitudes in the N1 latency range were augmented (i.e., more negative) in response to vertically oriented objects compared to horizontally oriented objects. Importantly, P3 amplitudes were specifically reduced on conditions comprising multiple horizontally oriented objects. The P3 suppression effect becomes apparent when comparing P3 amplitudes evoked by ortho-oriented and by iso-oriented vertical surround conditions with those elicited by iso-oriented horizontal surround conditions. We discuss below why the P3 suppression effect might reflect neuronal states which predispose observers for behavioral orientation asymmetry in VS.

The P3 suppression effect occurred on multiple horizontal object conditions. Targets have luminance contrasts which are oriented 90 degree away from that of the distractors when observers search for targets on ortho-oriented multiple objects conditions. This might make the targets contrast orientation singletons, possibly to pop out by low level saliency mechanisms. This low level saliency may be strong enough to dominate task decision, making RT short such that there is no orientation asymmetry, nor P3 attenuation. In contrast, the direction of the contrast orientation is equal in target and distractors on iso-oriented multiple objects conditions. Given this situation, targets cannot pop out by low level saliency, and higher level mechanisms, hinging upon polarity decisions rather than orientation decisions, need to play a larger role in this situation (Zhaoping & Gyader, 2007). Thus, the P3 suppression effect seems to be conditional upon VS being conducted at higher levels of

cortical processing, in line with what is known about the P3 ERP component (Kok, 2001; Luck, 2005; Kopp, 2008).

Apart from behavioral orientation asymmetry in VS on conditions comprising multiple horizontally oriented objects, RT analyses unexpectedly revealed that observers could identify vertically oriented single objects faster than horizontally oriented single objects. This result is certainly consistent with the view that vision is influenced by a-priori knowledge about the source of light (Ramachandran, 1988; Kersten et al., 2004; Ramachandran & Rogers-Ramachandran, 2008). According to this model, the bias for overhead lighting enables three-dimensional perception of vertically, but of not horizontally, oriented stimuli, thereby aiding visual analysis (Kleffner & Ramachandran, 1992; Sun & Perona, 1998; Wolfe et al., 1999; Adams et al., 2004; Adams, 2007; Thornton & Gilden, 2007). However, the light-from-above model leads one to expect more efficient visual processing, and enhanced neuronal responses, to vertically than to horizontally oriented shape-from-shading objects, irrespective of surround conditions. The behavioral data partially confirmed this expectation (i.e., on single object conditions and on iso-oriented multiple object conditions), whereas other behavioral data (i.e., on ortho-oriented multiple object conditions) conflicted with the light-from-above model. The N1 enhancement by vertically oriented objects is also in agreement with the light-from-above model. However, the P3 suppression effect contradicts the light-from-above model since it demonstrates neuronal attenuation by multiple horizontally oriented objects. Further, it should be kept in mind that the light-from-

above model fails with regard to some of the already known facts about behavioral orientation asymmetry in VS (van Zoest et al., 2006, Exps. 1–3; Kopp et al., 2010, Exp. 2).

The behavioral data on multiple object conditions were in agreement with the similarity model of orientation asymmetry in VS (van Zoest et al., 2006). This model conjectures that targets and distractors are perceived as being more similar to each other when objects are horizontally oriented as compared to when they are vertically oriented, thereby decreasing search efficiency and increasing task difficulty (Duncan & Humphreys, 1989). However, behavioral data on single object conditions conflicted with the similarity model. The observed N1 enhancement by vertically oriented single objects cannot be explained by the similarity model, whereas the N1 enhancement effect by vertically oriented multiple objects and the P3 suppression effect by horizontally oriented multiple objects were both in agreement with the similarity model. In particular, it is known from an extensive literature that increases in task difficulty are related to decreases in P3 amplitudes (Kok, 2001). The similarity model basically postulates that item similarity is dependent of item orientation. However, this essential conjecture of the similarity model needs to be tested empirically since there is no independent evidence available to date for determining its correctness.

As outlined above, the existing models of orientation symmetry in VS do not fully explain the behavioral and/or neuronal findings from the current study. Next, we introduce the context model of orientation asymmetry in VS, and we examine its performance in predicting our findings. Some fundamentals of the context

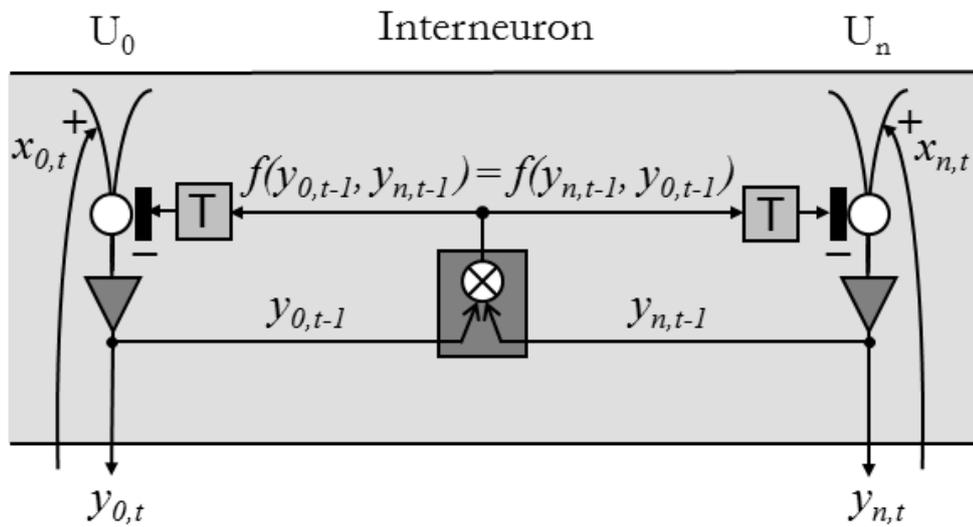


Figure 6: An illustration of contextual filtering. Afferent and efferent fibres of two feature extraction units (U_0 , U_n) and of one interneuron are depicted. Block “T” symbolizes the inhibitory loop delay which is the difference in time between $t-1$ and t . Excitatory connections are indicated by open arrows, inhibitory connections are shown as vertical bars

model are illustrated in Figure 6. The figure describes how signal processing within a local cortical network modulates signals in a particular unit, termed unit number “0”, at a particular point in discrete time, t (Kopp et al., 2011). Specifically, $f(\cdot)$, the filtering function, contributes to convert the input to unit 0, $x_{0,t}$ ($x_{0,t} \geq 0$), to its output $y_{0,t}$ ($y_{0,t} \geq 0$). Two general assumptions about the architecture of this locally interconnected system of neurons form the basis of our context model. First, at time instant $t - 1$, corollaries of output signals from each unit are sent to cortical interneurons along axonal collaterals, exemplified by $y_{0,t-1}$ and $y_{n,t-1}$ with $y_{0,t-1} \geq 0$ and $y_{n,t-1} \geq 0$. Second, if two corollaries excite the interneurons concurrently, suppression at time instant t is exhibited to the units which have been the origin of the corollaries, exemplified by $f(y_{0,t-1}, y_{n,t-1}) \geq 0$. Substantial suppression of the input signal to unit 0 will result in case of simultaneous input signals to the interneuron, thereby providing a mechanism for powerful contextual filtering suppressing locally homogeneous information.

The computational implementation of contextual filtering (Kopp et al., 2011) within this system of locally interconnected units consists of divisive normalization (Albrecht & Geisler, 1991; Heeger, 1992; Wainwright, Schwartz, & Simoncelli, 2002; Wilson & Humanski, 1993). Normalization equations compute ratios between the response of individual neurons and the summed activity of neuron pools (Carandini & Heeger, 2012). That is, if $y_{0,t}$ describes the output of unit 0 at time t , it can be computed as

$$y_{0,t} = \frac{A \cdot x_{0,t}}{B + C \cdot \sum_{n=1}^N f(y_{0,t-1}, y_{n,t-1})}, \quad (1)$$

with $A, B, C \geq 0$ being parameters to be chosen, and $x_{0,t}$ representing the input signal at time t , $f(y_{0,t-1}, y_{n,t-1}) \geq 0$ being the inhibitory influence of unit n on unit 0 at time t , and N denoting the number of connected units that may impose a suppressive effect on unit 0. Equation 1 can be interpreted as a contextual filtering function, parameterized via $f(\cdot)$ by corollaries of the outputs, $y_{0,t-1}$ and $y_{n,t-1}$, respectively, at time $t - 1$. Without loss of generality, the number of free parameters can be reduced as follows:

$$y_{0,t} = \frac{x_{0,t}}{B/A + C/A \cdot \sum_{n=1}^N f(y_{0,t-1}, y_{n,t-1})}. \quad (2)$$

We further suggest a specific parameterization $f(\cdot)$, and thereby a specific contextual filtering function. Specifically, the inhibitory loop between neighbouring units can be described as multiplicative:

$$f(y_{0,t-1}, y_{n,t-1}) = y_{0,t-1} \cdot y_{n,t-1}. \quad (3)$$

If $y_{0,t-1} = y_{n,t-1} = y$, we simply have $f(y_{0,t-1}, y_{n,t-1}) = y^2$. Interestingly, quadratic contextual filtering by divisive normalization has been advocated earlier in an attempt to account for non-linear properties of visual neurons (Schwartz & Simoncelli, 2001). On the other hand, if $y_{n,t-1} = 0$, then $f(y_{0,t-1}, y_{n,t-1}) = 0$ which means that unit n does not impose an inhibitory effect on unit 0. Contextual filtering therefore seems to possess at least two major characteristics: Firstly, the strength of the inhibitory effect on unit 0 depends in a multiplicative manner on the

outputs of the unit itself and of each of its connected neighbours. In essence, then, this locally interconnected system of neurons can be identified as a non-linear system (Wu, David, & Gallant, 2006) Secondly, in case that there are no output signals of neighbouring units, the inhibitory influence features conditionality because its minimum is simply zero according to $f(y_{0,t-1}, y_{n,t-1} = 0) = 0$. The contextual filtering function eq. 2 is then transparent, i.e., $y_{0,t} = x_{0,t}$, if $B/A = 1$. This analysis leads to the final formulation of the contextual filtering function.

$$y_{0,t} = \frac{x_{0,t}}{1 + \beta \cdot \sum_{n=1}^N (y_{0,t-1} \cdot y_{n,t-1})}, \quad (4)$$

with parameter $\beta = C/A \geq 0$ to be determined empirically.

To summarize, the context model of orientation asymmetry in VS rests on divisive normalization (Albrecht & Geisler, 1991; Heeger, 1992; Wainwright et al., 2002; Wilson & Humanski, 1993; Carandini & Heeger, 2012), described as contextual cortical filtering. Specifically, a multiplicative filtering function was specified (Schwartz & Simoncelli, 2001). Thus, if x denotes the input signal to a unit, the filtered output signal, y , is proportional to x divided by $n \times x^2$ in case of concordant signals to n neighboring units. An important implication of multiplicative filtering functions lies in the emergent asymmetry of output signals from two otherwise comparable units (e.g., output $y_1 < \text{output } y_2$) in case of asymmetric input signals (e.g., if input $x_1 > \text{input } x_2$). Note the reversal of the ordinal relationship between x_1 and x_2 on one hand, and y_1 and y_2 on the other hand, when comparing the input to and the output from the two units.

Figure 7 presents how the context model accounts for behavioral and neuronal orientation asymmetry in VS. In order to do so, one needs to distinguish between primary visual, secondary visual, visual associative as well as multimodal levels along the cortical hierarchy. Orientation sensitivity is a dominant property of V1 neurons. Further, V1 neurons responding to stimuli inside their receptive fields can be suppressed by placing additional stimuli in their surrounding regions (Seriès et al., 2003; Carandini et al., 2005; Angelucci & Bressloff, 2006). Surround suppression occurs with vertical and horizontal orientations, yet there are more V1 neurons with horizontal orientation preference than there are neurons with preference for vertical or oblique orientations (Li, Peterson, & Freeman, 2003); this might be ecologically justified (Simoncelli & Olshausen, 2001; Geisler, 2008). Let x denote the input signal to a V1 neuron, then its filtered output signal, y , will be proportional to x divided by $n \times x^2$, as discussed above. Thus, although horizontal and vertical V1 input signals should not differ (i.e., $x_{\text{horizontal}} = x_{\text{vertical}}$), horizontal and vertical V1 output signals should be different (i.e., $y_{\text{horizontal}} < y_{\text{vertical}}$) because $n_{\text{horizontal}}$ should exceed n_{vertical} . According to the context model, the inequality of horizontal and vertical V1 output signals provides the seed for further orientation asymmetries along the cortical hierarchy. As detailed in Figure 7, the inequalities between horizontal and vertical signals are maintained at higher cortical levels, due to the fact that unequal input signals are associated with opposite-signed unequal output signals, as discussed above (i.e., $y_{\text{horizontal}} < y_{\text{vertical}}$ if $x_{\text{horizontal}} > x_{\text{vertical}}$, and vice versa).

Figure 7 also shows that there are two

		vertical axis		horizontal axis			
level		orientation axis	luminance contrast	luminance contrast	orientation axis	center surround	ERP correlate
V1	input		X:h	=	X:v	intra-object	
	output		Y:h	<	Y:v		
Ve	input	X:v		<	X:h	intra-object	
	output	Y:v		>	Y:h		→ N1
Va	input	X:v		>	X:h	inter-object	
	output	Y:v		<	Y:h		
sm	input	X:v		<	X:h	inter-object	
	output	Y:v		>	Y:h		→ P3

Figure 7: The context model of orientation asymmetry in VS, applied to our shape-from-shading objects (see Figure 1). V1 processing should result in an advantage for vertical luminance contrasts compared to horizontal luminance contrasts. At higher levels of processing, unequal input signals will be associated with unequal output signals, but with opposite signs (i.e., $y_{horizontal} < y_{vertical}$ if $x_{horizontal} > x_{vertical}$, and vice versa), as explained in the text. V1: primary (striate) visual cortex; Ve: extrastriate visual cortex; Va: visual association cortex; sm: supramodal association cortex. See text for details.

auxiliary assumptions of the context model. First, the orientation sensitivity of V1 neurons refers to the direction of the luminance contrast, rather than to the orientation axis of the shape-from-shading objects (Figure 1). In contrast, the orientation sensitivity of neurons at higher levels of the cortical hierarchy refers to the orientation axis of the shape-from-shading objects. Second, center-surround interactions of striate and extrastriate neurons are supposed to occur within single shape-from-shading objects, whereas center-surround interactions at higher levels of the cortical hierarchy are related to interactions between shape-from-shading objects. Both auxiliary assumptions are commensurable with the knowns in the literature (Hess & Field, 1993; Lamme & Roelfsema, 2000; Nassi & Callaway, 2009). The context model and its auxiliary assumptions predict most of the behavioral phenomena that we observed in the current study, except that observers identified vertically oriented single objects faster than horizontally oriented single objects. Further, both ERP correlates of orientation asymmetry in VS were consistent with the context model. Specifically, the enhanced N1 in response to vertically oriented objects can, *pari passu*, be interpreted as N1 attenuation in response to horizontally oriented objects. Its independence from the number of objects suggests that it might originate from intra-object center-surround interactions. In contrast, the P3 suppression effect which occurred on multiple horizontal object conditions seems to be associated with center-surround interactions between iso-oriented objects. Importantly, the context model provides a neurocognitive explanation why the interactions along the

horizontal axis differ in intensity from those along the vertical axis.

This context model predicts behavioral orientation asymmetry in VS; it is therefore compatible with the earlier body of work on orientation asymmetry in VS (Kleffner & Ramachandran, 1992; Sun & Perona, 1998; Wolfe et al., 1999; van Zoest et al., 2006; Adams, 2007; Thornton & Gilden, 2007; Kopp et al., 2010). The context model is furthermore compatible with the present and earlier P3 findings (Kopp et al., 2010). Additional evidence that cortical visual processing is strongly modulated by contextual interaction comes from psychophysical studies in which observers had to discriminate the orientation of lines. When tested with simple stimuli, these studies yielded that performance is best for horizontal and vertical orientations and worst for oblique orientations (the ‘oblique effect’; Essock, DeFord, Hansen, & Sinai, 2003; Hansen & Essock, 2004). However, these authors showed that – when tested with more complex images consisting of naturalistic content – performance is best for oblique and vertical orientations and worst for horizontal orientations (the ‘horizontal effect’). They interpreted this horizontal effect as being the consequence of minimizing the visual saliency of the horizontal content under more naturalistic conditions.

Contextual filtering, mediated by local cortical processing, may possess crucial modulatory functions such as redundancy reduction (Barlow, 2001). Specifically, contextual filtering attenuates the saliency of isomorphic input signals, whereas the saliency of non-isomorphic input signals, such as edges and contours, is much less modified. Accentuating discontinu-

ous input signals might facilitate figure-ground separation. Ultimately, this analysis leads to a center-surround hypothesis of visual saliency (Nothdurft, 1991; Li, 1999; 2002; Gao, Mahadevan, & Vasconcelos, 2008).

Conclusions

The origin of orientation asymmetry in VS is an unresolved issue. On one hand, the light-from-above model assumes that search efficiency is influenced by a-priori knowledge about the source of light. On the other hand, both the similarity model and the context model ascribe the phenomenon to different inter-object interaction mechanisms. Whereas item similarity is dependent of item orientation in the similarity model, the context model attributes orientation asymmetry in VS to divisive normalization, mediated by local networks along the cortical hierarchy. The P3 suppression effect was in agreement with the similarity model and with the context model, but it contradicted the light-from-above model, suggesting that interactions between multiple iso-oriented objects play an essential role for neuronal mechanisms of orientation asymmetry in VS. The context model is based explicitly on neuronal computations, whereas the similarity model represents a purely cognitive model, without implementing its principles at the neurocomputational level.

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Testing an adapted fMRI paradigm for simultaneous EEG measurements S. Baumeister (1), S. Hohmann (1), I. Wolf (1), N. Holz (1), R. Boecker (1), M. Plichta (2), S. Rechtsteiner (1), B. Palma (3), M. Ruf (4), P. Kirsch (5), H. Flor (6), A. Meyer-Lindenberg (2), T. Banaschewski (1), D. Brandeis (1,7) (1) *Klinik für Psychiatrie and Psychotherapie des Kindes- und Jugendalters, Zentralinstitut für Seelische Gesundheit, Medizinische Fakultät Mannheim / Universität Heidelberg*; (2) *Klinik für Psychiatrie and Psychotherapie, Zentralinstitut für Seelische Gesundheit, Medizinische Fakultät Mannheim / Universität Heidelberg*; (3) *Neurowissenschaftliches Labor, Pontificia Universidad Católica de Chile*; (4) *Abteilung Neuroimaging, Zentralinstitut für Seelische Gesundheit, Medizinische Fakultät Mannheim / Universität Heidelberg*; (5) *Abteilung Klinische Psychologie, Zentralinstitut für Seelische Gesundheit, Medizinische Fakultät Mannheim / Universität Heidelberg*; (6) *Institut für Neuropsychologie und Klinische Psychologie, Zentralinstitut für Seelische Gesundheit, Medizinische Fakultät Mannheim / Universität Heidelberg*; (7) *Zentrum für Kinder- und Jugendpsychiatrie, Universität Zürich* Inhibitionskontrolle ist eine im Alltag bedeutsame Fähigkeit, die bei psychischen Erkrankungen wie beispielsweise der Aufmerksamkeitsdefizits /-Hyperaktivitätsstörung beeinträchtigt ist.

Diverse Studien haben diese Fähigkeit bereits mit bildgebenden (fMRT) oder elektrophysiologischen (EEG) Verfahren untersucht, jedoch existieren bisher nur wenige Versuche, diese Methoden miteinander zu kombinieren. Daher wurde ein fMRT-erprobtes Flanker/NoGo Paradigma (Meyer-Lindenberg et al., 2006) für die Nutzung als EEG-Paradigma adaptiert und aus der Messung im Kernspintomografen resultierende Effekte untersucht. 17 gesunde junge Erwachsene (Alter 20–35, M=24.71, SD=4.15) führten eine Flanker/NoGo Aufgabe in einem 3T-Kernspintomografen durch, während 10 ebenfalls gesunde junge Probanden (Alter 20–29, M=24.5, SD=3.09) die Aufgabe ohne simultane fMRT-Messung durchführten. In beiden Stichproben wurde das EEG anhand eines 64-Kanal MRT-kompatiblen Systems aufgezeichnet. Die Aufgabe erfordert einen linken oder rechten Tastendruck entsprechend der Richtung eines mittleren Pfeils, wenn die seitlichen Objekte entweder andere Pfeile oder Quadrate sind. Die Antwort muss jedoch unterdrückt werden, wenn die seitlichen Objekte "XX" sind. Nach Gradienten-, Kardioballistogramm- und ICA-Korrektur für die simultan erhobenen Daten, sowie ICA-Korrektur für die EEG-Daten zeigen sich in beiden Datensätzen signifikante NoGo Effekte bezüglich der P3. Dabei weist die NoGo-P3 aus dem Simultan-Datensatz eine signifikant geringere Amplitude an Cz auf als in den EEG-Daten (470–574 ms, $p < .05$). Die Topografie zeigt eine weniger zentral lokalisierte NoGo-P3 als erwartet, verhält sich jedoch in beiden Datensätzen vergleichbar. Die Adaption eines fMRT-Paradigmas für das EEG führte zu den erwarteten NoGo-P3 Effekten. Hierbei zeigte sich ein signifikanter Amplitudenunter-

schied zwischen der Erhebung innerhalb und außerhalb des Kernspintomografen. Die Vergleichbarkeit der ungewöhnlichen Topografie der NoGo-P3 in beiden Datensätzen lässt jedoch den Schluss zu, dass diese keine Folge der simultanen Messung, sondern aufgabenspezifisch ist. Folglich lässt sich die Aufgabe erfolgreich für die EEG-Messung und simultane EEG-Messung verwenden. Um die Effekte der simultanen Messung noch verlässlicher zu untersuchen, sollten zukünftige Studien die Aufgabe anhand identischer Stichproben vergleichen.

Neuronal activity of the reward system: first results of a combined EEG-fMRI study in the context of a longitudinal study

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The reward system of the brain is associated with various psychiatric diseases like depression, addiction or ADHD, and shows considerable overlap with the stress system. On the one hand, reward may mitigate the effect of stress on the hypothalamic-pituitary-adrenocortical (HPA) axis; on the other hand, early chronic stress may lead to reduced

reward anticipation and reward outcome processing. Therefore the functional analysis of the reward system may have a significant impact on the prevention of psychiatric diseases. Especially combined electroencephalography (EEG) and functional magnetic-resonance-imaging (fMRI) should optimally measure brain activity induced by reward related behavior. 100 healthy right-handed adults aged 24 to 25 years from a longitudinal study participated in a monetary incentive delay (MID) task, based on previous work of Kirsch et al. (2003) and adapted for simultaneous EEG-fMRI. The MID task required a button press to receive either a monetary or a verbal reward. Data were recorded via a 64-channel MRI-compatible EEG system and a 3T Siemens Trio scanner. In the fMRI analysis, activation within areas related to reward anticipation (nucleus accumbens) and reward delivery (caudate, putamen) proved to be significantly higher for the monetary reward as compared to verbal reward ($p=0.0001$; FWE corrected). The EEG analysis revealed several reward related event-related potential components after gradient, ballistocardiogram and independent component analysis (ICA) correction. Following a significantly higher P3b, a significantly stronger CNV could be observed in the monetary reward condition as compared to verbal reward. The present results underline the validity of simultaneous EEG-fMRI measurements by replicating core effects from separate fMRI and EEG studies. The integration of both methods as a next step will combine their advantages concerning time and space resolution. Future analyses will focus on the consequences of gene-environment interactions related to anticipation and delivery of

reward.

Neurofeedback in ADHD - new developments

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Recent controlled EEG neurofeedback studies indicate sizeable clinical effects on ADHD (Attention-deficit/hyperactivity disorder) symptoms. However, unspecific effects are often underestimated due to the study designs, and usually it remains unclear which specific neurophysiological networks and processes are regulated and altered with training.

New studies and meta-analyses are briefly reviewed, and neurophysiologically and topographically specific results and approaches like tomographic EEG-based neurofeedback, or MR-based neurofeedback are presented. The first results using these new approaches suggest that increased spatial resolution may be more effective because of targeting circumscribed brain functions and networks, but also due to better control conditions. The approaches are still under development, however, and assumptions regarding the better trainability of regional activity with specific clinical effects must be critically evaluated, especially for clinical groups.

The effects of rTMS on prefrontal activation patterns in patients with panic disorder

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With a life-time prevalence of about 3.5 percent, Panic disorder (PD) belongs to the most common anxiety disorder which can often chronify if not treated adequately. Characterized by the sudden onset of unexpected panic attacks it is associated with a significant loss of quality of life. As in other anxiety disorders, an inadequate top-down regulation of subcortical structures (e.g., the amygdala) by the prefrontal cortex (PFC) is assumed to be a core feature. Even though fMRI studies could show that Cognitive Behavioral Therapy (CBT) is an effective treatment method that can normalize this prefrontal hypoactivity, the onset of its effect is delayed. Moreover, recent neuroscientific studies indicated a beneficial effect of repetitive transcranial magnetic stimulation (rTMS), which has been shown to modulate neural activity by depolarization of cortical neurons. The goal of this study was, therefore, to investigate the application of a sham (placebo) controlled activating rTMS protocol during CBT. To do so, forty PD patients were assessed with the optical imaging method near infrared spectroscopy (NIRS) while performing emotional paradigms (emotional Stroop, Westphal-Paradigm) as well as a cognitive task (Verbal Fluency Task) before and after receiving 15 sessions of rTMS. Preliminary results show a significant increase in prefrontal activation in the active rTMS group as compared to the placebo group.

Music therapy modulates fronto-temporal activity in rest-EEG in depressed clients

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Fronto-temporal areas process shared elements of speech and music. Improvisational psychodynamic music therapy (MT) utilizes verbal and musical reflection on emotions and images arising from clinical improvisation. Music listening is shifting frontal alpha asymmetries (FAA) in depression, and increases frontal midline theta (FMT). In a two-armed randomized controlled trial (RCT) with 79 depressed clients (with comorbid anxiety), we compared standard care (SC) versus MT added to SC at intake and after 3 months. We found that MT significantly reduced depression and anxiety symptoms. The purpose of this study is to test whether or not MT has an impact on anterior fronto-temporal resting state alpha and theta oscillations. Correlations between anterior EEG, Montgomery-Åsberg Depression Rating Scale (MADRS) and the Hospital Anxiety and Depression Scale - Anxiety Subscale (HADS-A), power spectral analysis (topography, means, asymmetry) and normative EEG database comparisons were explored. After 3 months of MT, lasting changes in resting EEG were observed, i.e., significant absolute power increases at left fronto-temporal alpha, but most distinct for theta (also at left fronto-central and right temporoparietal leads). MT differed to SC at F7-F8 (z-scored FAA, $p < .03$) and T3-T4 (theta, $p < .005$) asymmetry scores, pointing towards decreased relative left-sided brain activity after MT; pre/post increased FMT and decreased HADS-A scores ($r = .42$, $p < .05$) indicate reduced anxiety after MT. Verbal reflection and improvising on emotions in MT may induce

neural reorganization in fronto-temporal areas. Alpha and theta changes in fronto-temporal and temporoparietal areas indicate MT action and treatment effects on cortical activity in depression, suggesting an impact of MT on anxiety reduction.

Cognitive ageing and event-related potentials M. Falkenstein, P. Gajewski *IfADo, Ardeystr. 67, D-44139 Dortmund*

Even though healthy aging affects various sensory, cognitive and motor functions, such changes are not unequivocally reflected in behavior. Event-related potentials (ERP) which are derived from the electroencephalogram (EEG) are well suited to specify the source of age-related behavioral changes, to detect subliminal changes of functions and to unveil compensatory activity. In the first part of the talk, several examples for each of those aspects will be given. Moreover ERPs can be used to assess the impact of interventions aiming at the improvement of cognitive functions. In the second part of the talk, some results of a large training study with healthy seniors will be presented, and the impact of different training regimes (cognitive, physical, relaxation) on different sensory and cognitive functions and their ERP correlates will be outlined. The results show specific changes of ERPs due to cognitive but not physical or relaxation training, while behavioral effects were found for both interventions. The implications of those findings will be discussed.

Solving mathematical problems: effects of learning on evoked EEG frequencies

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We investigated the change of evoked EEG frequencies induced by learning to solve mathematical tasks by divisibility rules. In a behavioral study on 51 adults we found that there is a significant increase in performance from 42% to 93% correct responses induced by learning. A total of 34 subjects participated in an EEG experiment which consisted of two parts. First, subjects had to solve 200 tasks without knowing the rules, followed by learning the divisibility rules. A time limit of 3 seconds was used. The EEG was measured simultaneously in 30 channels, artifacts were removed offline, and the data before and after learning were compared. For analysis the wavelet transformation with the Morlet Wavelet was used, and the scalp topography of the maximal frequency and its occurrence time was compared. Frequencies between about 7 and 13 Hz were observed, and after successful learning the maximal frequencies were significantly smaller over left frontal areas. Similar changes were observed over right parietal regions. In addition, we observed lower frequencies for easy than for hard tasks. In summary, our data illustrate a significant relation between successful learning and changes in the frequency content of the task-related EEG.

Representation of Task-related Responses in Near-Infrared Spectroscopy (NIRS) Time Series by State Space Modelling

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We study the application of Independent Component Analysis (ICA) and of linear state space (LSS) modelling to several time series recorded by near-infrared spectroscopy (NIRS), for the purpose of extracting task-related responses, resulting from a finger-tapping motor task. We employ a particular type of state space models (IC-LSS) that was recently proposed as an alternative to ICA. We find that among the resulting set of components, the task-related responses are essentially focussed into a small number of components, while other components represent high-frequency noise. As a consequence, task-related responses can be extracted with better quality than it has previously been possible by ICA. For a time series where the responses have strong triangular components (believed to arise from tissue outside the skull), we find that IC-LSS modelling retrieves a rectangular response that ICA was unable to find.

Auditory distraction of goal-directed behaviour in young adults and high- and low-performing healthy elderly: evidence from EEG S. Getzmann, P. D. Gajewski, M. Falkenstein *IfADo Leibniz-Institut für Arbeitsforschung, Ardeystr. 67, D-44139 Dortmund*

Aging usually affects the ability to focus attention on a given task and to ignore distractors. However, aging is also associated with increased between-subject variability, raising the issue in what features of processing older high-performing and low-performing humans may differ in goal-directed behaviour. Employing an auditory distraction task, in which listeners discriminated between equiprobable short and long sound stimuli, involuntary shifts

in attention to task-irrelevant frequency deviations and subsequent reorientation were studied. Behavioral data and event-related potential (ERP) measures were analyzed in 35 younger, 35 older high-performing, and 35 older low-performing listeners. When responding to the regular standard stimuli younger listeners produced more correct responses than the older low-performing group, but less than the older high-performing group. High performance of the older listeners came along with a pronounced frontal activation (P2) that was absent in the younger, and reduced in the older low-performing group. The rare deviant stimuli elicited a sequence of mismatch negativity (MMN), frontal P3a and reorienting negativity (RON). Here, older high-performing listeners performed as well as younger listeners, while showing a less pronounced MMN and P3a than the younger listeners. In contrast, the older low-performing listeners showed a stronger and later P3a, and a delayed RON, relative to their high-performing counterparts. This pattern of results suggests that stronger involuntary attention capture by task-irrelevant features and delayed reorienting to the primary features could cause poor performance in the elderly. High performance in target processing, on the other hand, could be due to intensified attentional shifting toward the target features.

Influence of individual head anatomy on the analysis and interpretation of neural activation as measured by optical imaging

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We have conducted a simulation study in which we found a strong connection between fNIRS sensitivity and scalp-cortex distance

(SCD). By simulating NIR light scattering and absorption in human head tissue models it could be shown that a high SCD leads to a decreased volume of light absorbing gray matter and therefore the sensitivity of fNIRS to measure hemodynamic changes in the cortex is decreased, while it is increased in the scalp. The head circumference, an easily assessable parameter, was positively correlated with SCD. We used the simulated volumes of light absorbing scalp (V_{scalp}) and gray brain matter (V_{gray}) to examine the feasibility of fNIRS to measure low frequency oscillations usually observed within resting state paradigms. We found the signal-to-noise ratio of fNIRS within a frequency window of 0.01–0.02 Hz to be significantly correlated with V_{scalp} and within 0.02–0.05 Hz to be significantly correlated with V_{gray} . These findings suggest that fNIRS is feasible for resting state paradigms, but also that not the whole range of the low frequency window is accessible. We also conducted a simultaneous fNIRS-fMRI study in which participants performed a working memory paradigm. We found the SCD to decrease the amplitude of hemodynamic responses to stimuli as measured by fNIRS. Beyond that, we observed a different impact of extracranial hemodynamics (as measured by fMRI) on fNIRS-signals. The signal that maps concentration changes of oxygenated hemoglobin (oxy-signal), was severely impacted by skin blood flow, whereas the deoxy-signal was hardly affected. By conducting a simultaneous fNIRS-fMRI session during an inter-temporal choice paradigm, we found an interesting correlation between brain activation as measured by fMRI and a personality trait of the participating subjects. In contrast, this correlation

could not be found with fNIRS. The influence of task-evoked extracranial signals impairing especially the oxy-signal may have been the limiting factor.

Neural correlates of the mirror neuron system and social interaction in humans

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Das Prinzip der Spiegelneuronen, das von Giacomo Rizzolatti erstmals beschrieben wurde, ermöglicht uns scheinbar, andere Menschen intuitiv zu verstehen, und ihre Freude und Schmerz nachzufühlen. Dieses Prinzip könnte somit als neurobiologische Basis für "Lernen am Modell", für Empathie und soziale Interaktion betrachtet werden. In einer ersten Untersuchung konnten wir mittels einer Untersuchung mit der Nahinfrarotspektroskopie (NIRS) zeigen, dass Aktivierungsmuster sowohl beim Ausführen als auch beim Betrachten einfacher Handlungen in parieto-temporalen Regionen nachzuweisen sind (Kriterium für das Spiegelneuronensystem). In einer weiteren Studie nutzten wir den Vorteil der hohen Bewegungsfreiheit bei NIRS-Messungen, und untersuchten die neuronalen Korrelate sozialer Interaktion zweier Personen in Realität. Wie erwartet zeigte sich hierbei eine signifikante Beteiligung des parietalen Spiegelneuronenareals, mit höherer Aktivierung bei interaktiver im Vergleich zur alleinigen Ausführung einer einfachen Handlung. Eine letzte Studie erweitert dieses Ergebniss um einen differentiellen Aspekt. Aus anderen, molekularbiologischen Untersuchungen wissen wir um die Bedeutung des serotonergen Systems für emotionale Prozesse im Allge-

meinen. Eine besondere Bedeutung hat hier eine Variation im Serotonintransportergen, die in der kurzen Ausprägung mit Ängstlichkeit aber auch mit höherer sozialer Verträglichkeit in Verbindung gebracht wurde. Wir konnten in unserer Untersuchung erstmals zeigen, dass genau diese kurze Variante des Serotonintransportgens zu einer stärkeren Aktivierung im parietalen Kortex während der sozialen Interaktion führt. Zusammenfassend stellt NIRS eine einzigartige Methode dar, neuronale Korrelate sozialer Interaktion zu untersuchen.

Pre- and post-movement oscillatory characteristics of the primary motor cortex in a whole-body sensorimotor task

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The currently available literature on movement related cortical processes is limited to simple movements with small muscular activity. Considering the motor requirements of daily life activities as well as those in sports, these movements are not representative and control processes may differ significantly in more complex movements which usually involve a larger muscle mass and are more dynamic. The present study analyzed cortical activity as measured by electroencephalography (EEG) during a whole body sensorimotor movement task. 12 subjects performed 30 counter-movement jumps. EEG was recorded over the sensorimotor areas of the cortex and analyzed using band-pass-Filters. Alpha, beta and gamma frequency bands were defined based on individual frequency characteristics for four segments containing the

pre- and post-movement period, respectively. For statistical analysis log-transformed electrical power values were calculated for the electrodes overlying the functional leg/foot region of the primary motor cortex. We found a desynchronisation (ERD) in the alpha and beta frequency bands before movement while power values in all gamma frequency bands remained unchanged. Immediately after landing, beta power returned to baseline values while alpha power was still reduced for about two seconds. Electrical power in all gamma frequency bands was elevated for about two seconds. Moreover, we found broad band effects for all frequency bands rather than narrow reactive frequencies. The results of the present study suggest common processes in the primary motor cortex preceding simple (small muscle mass) and complex (large muscle mass) movements that are associated with power changes in the alpha, beta and gamma frequency bands. These results were interpreted related to movement preparation as well as to information transfer of proprioceptive feedback.

Turn-anticipation in dialogue: an EEG-study S. Jansen, H. Wesselmeier and H.M. Müller *Experimentelle Neurolinguistik, Linguistik und Literaturwissenschaft, Universität Bielefeld, 33501 Bielefeld, Germany*

Anticipation is an essential process in conversation, which allows the listener to catch the precise moment of the current speaker's end of utterance and which avoids gaps and overlaps in dialogue (Magyari & De Ruiter 2008; Sacks Schegloff, Jefferson 1974). There are numerous experiments used to analyze the exact semantic, syntactic, and prosodic information source that listeners use. It has already been

pointed out that anticipation of turn-ending is based more on semantic and syntactic information than on prosodic information (Magyari & de Ruiter 2008). However, it is still unclear how precisely this lexico-syntactic information supports anticipation. Previous spectral analysis identified the neuronal processes accompanying anticipation of turn-ending by using beta-power analysis. The brain areas involved in anticipating turn-ending are part of the same functional network that supports sentence and discourse-level comprehension processes and control (Magyari et al., 2011). To analyze turn-anticipation related ERPs, 30 healthy, right-handed participants (16 women, 14 men; age 21–35) volunteered in our EEG experiment. The first part of this study was composed of 35 auditory questions and 20 declarative sentences. For each sentence, participants were asked for a short verbal cue ("Ja") to mark the moment at which they thought it would end. In contrast to this, in the second part of the experiment, consisting of 24 declarative sentences, of which $\frac{1}{3}$ were syntactically and $\frac{1}{3}$ semantically violated, we asked for a button-press when the participants predicted the end of turns. The readiness potential (RP) of the verbal responses was identified in order to be compared to the RP of the button-press responses. For analysis, we compared ERPs during the syntactic/semantic violations, sentence endings and responses. Contrary to the expectation with semantic/syntactic violations, where we presume reduced or at least delayed RPs for responses. We expect comparable RPs for the button-press and verbal cue condition.

When spoken and written words meet in the brain L. B. Jost, A.K. Moscicka, Ch. Frisch,

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Integrating visual and auditory language information is critical for reading. Suppression and congruency effects in audiovisual paradigms with letters and speech sounds provided information about low-level mechanisms of grapheme-phoneme integration during reading. However, the central question about how such processes relate to reading entire words remains unexplored. Here, we investigate (1) when audiovisual integration occurs for words and pseudowords and (2) whether this integration is reduced in poor readers. A 128-channel EEG was recorded while 60 monolingual (Swiss)-German speaking first-graders performed an oddball detection task. Word and pseudoword stimuli were presented in blocks either auditorily (A), visually (V) or audiovisually (matching: AVM; non-matching: AVN). Corresponding ERP's were computed, and unimodal ERPs were summed (sumAV). We then applied a TANOVA ($p < 0.01$) across all subjects (separately for words/pseudowords) to test for integration effects: suppression (sumAV-AVM) and congruency (AVN-AVM). Mean voltages of the difference ERPs across the resulting time windows were calculated. We then computed ANOVAs on GFP with the factor reading group (poor, intermediate, good). Significant audiovisual suppression effects were observed for words (496–756 ms) and pseudowords (460–736 ms). As such, pronounced integration effects for words and pseudowords occurred in a similar time window, possibly in agreement with previous studies on letters and speech

sounds. In addition, an earlier short segment was found for pseudowords (336–364 ms), which approached significance for words in adjacent time frames. Significant congruency effects were found only for words (164–200 ms), but not for pseudowords. This suggests early integration processes of written and spoken language which may be specific for words. The GFP analyses revealed no significant group effects suggesting that integration processes are not reduced in poor readers. Further topographic analyses will test whether these processes are altered in poor readers. These analyses will also test the specificity of the early congruency effect by comparing words and pseudowords directly.

In the blink of an eye—How to quickly detect and correct eye artefacts A. Klein *Physiologisches Institut der Justus-Liebig-Universität, Gießen*

Blinks and other movements of the eyes are one of the commonest sources of artefacts in EEG-recordings, and there are only very limited means to minimise them beforehand by appropriate experimental design. EOG artefacts can be corrected very effectively by a number of different methods, for example template subtractions, wavelet-based filters, or the suppression of appropriately selected principal or independent components. The situation worsens, however, in the absence of usable EOG-recordings. Firstly, there are only a few remaining criteria for the detection of contaminated EEG-segments in this case, and secondly, it becomes very difficult to track the course of EOG without an appropriate reference. Correction of EOG-artefacts with wavelets might still be possible in this case, but would be very expensive computationally,

thus making correction based on principal or independent components much more appealing, even though possible problems with the suppression of frontal EEG tend to worsen in this setting. We present an approach for EP-experiments providing good performance with respect to the detection of contaminated epochs on the one hand, and with respect to the correction of artefacts by means of principal or independent components on the other.

Electrophysiological correlates of auditory verbal self-monitoring in healthy subjects

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Auditory verbal hallucinations in schizophrenia have been hypothesized to result from inefficient self-monitoring of inner speech. Neurophysiological experiments in this domain are however still sparse, because the processes of speech generation, speech perception and self-monitoring overlap and are difficult to disentangle. The aim of this project was to develop and test a paradigm to isolate and quantify self-monitoring processes with ERPs. We visually presented single words that subjects read aloud while auditory feedback was delivered through a headphone. Feedback consisted of the subject's voice, a foreign voice saying the same word, a mute condition, or the delayed subject's voice. In addition, self and foreign words were heard without visual stimulation. 13 healthy subjects performed the experiment while 76-channel ERPs were recorded. ERP contrasts were built for the effects of agency (own vs. foreign voice) and expectancy (with vs. without simultaneous feedback). We found in the N100 main ef-

fects of agency and expectancy, but no interaction, and t-maps of the effects pointed at different sources accounting for the effects. Later, the effects of agency and expectancy seemed to be rather additive. Agency monitoring processes can be isolated from motor activity, language-motor production, auditory sensory processing and expectancy. This is particularly interesting for the investigation of schizophrenia patients with auditory verbal hallucinations.

Randomization based microstate statistics, introduction of the methodology and comparison with existing procedures

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ERP microstate analysis is a particularly sensitive tool to assess the dynamics of neurocognitive networks. For statistics on ERP microstates, so far, topographic patterns obtained from grand mean data (microstate prototypes) were fitted back to individual data. This has the disadvantage that the goodness of fit is typically reduced by individual noise. Our aim was to improve statistical power of microstate statistics using procedures that avoid fitting microstate prototypes to individual data. In addition, we propose a new criterion to select the optimal number of microstate prototypes based on cross-validation across subjects. The developed procedure is based on randomization: The effect of interest, e.g. the on- or offset of a particular microstate, is quantified in the grand mean data of the groups

and/or conditions. Next, the group/condition assignments of the individual ERPs are randomized, the grand means are recomputed, and the effect of interest is re-extracted. Sufficient repetitions of this randomization procedure then yield the random distribution of the effect, against which the real data can be tested. In a sample analysis, the newly developed microstate statistics yielded robust, easily interpretable statistical results with very few assumptions and a-priori choices. In a first comparison with previously employed statistical procedures, the new method was more sensitive, especially for more subtle effects. The proposed microstate analysis is a sensitive tool to assess differences in multichannel ERP dynamics. The increased statistical power allows identifying more subtle effects, which is particularly important in difficult patient populations.

Task switching, cognitive control, and the P300 B. Kopp, F. Lange *Cognitive Neurology, Technische Universität Braunschweig, Department of Neurology, Braunschweig Hospital, Germany*

A frontally distributed, P3a-like component of the event-related brain potential (ERP) has repeatedly been observed in various task switching studies. However, the exact nature of the events which elicit the P3a in task switching paradigms remains to be delineated. Here, we tested the hypothesis that the P3a is linked to neural mechanisms of cognitive control, required to monitor the appropriateness of chosen attention sets in the context of given task rules. Specifically, we predicted that the P3a occurs in response to those events which eliminate uncertainties about the currently correct task rule. In order to examine our hypothesis

experimentally, we measured the EEG while 16 healthy young participants performed task switching paradigms closely modeled to the Wisconsin Card Sorting Test. We applied a $2 \times 2 \times 2$ factorial design, with number of task rules (two vs. three rules), cue explicitness (task vs. transition cueing), and cue timing (prospective vs. retrospective cueing) as independent variables. Switch cues elicited sustained positivities with parietal topography, irrespective of the experimental condition on which the ERP was recorded. However, the P3a appeared only on conditions in which transition cues did not explicitly signal which one of three possible rules was currently effective. On the prospective cueing condition, we observed a notable P3a in response to feedback-stimuli which were presented in switch trials. On the retrospective cueing condition, the P3a occurred in response to cues in the trials which followed switch trials. Thus, both types of P3a-eliciting events eliminated uncertainties about the currently correct task rule. These results support the hypothesis that P3a responses in task switching paradigms reflect neural mechanisms of cognitive control.

The influence of visual alcoholic stimuli on error processing depending on alcohol consumption patterns in healthy subjects: A combined NIRS-EEG measurement. A. Kroczeck, F. Häußinger, A.J. Fallgatter, A.-C. Ehlis *Klinik für Psychiatrie und Psychotherapie, Calwerstraße 14. 72076 Tübingen*

In this study error processing was assessed by EEG recordings of event-related potentials (ERP) simultaneously to the measurement of the hemodynamic response using Near-Infrared Spectroscopy (NIRS). The si-

multaneous measurement combines the high temporal resolution provided through EEG with the enhanced spatial resolution of cortical structures gained by NIRS. The evaluation of own performance (action monitoring) and especially error-processing is fundamental to decision making processes. Deficiencies in decision making are prominent for substance abuse disorders like alcoholism. The error related negativity (ERN) and the error-positivity (Pe) are ERPs associated with error processing altered in alcoholic patients. This study revealed differences in error processing even in a healthy population depending on the alcohol consumption patterns. A modified Eriksen Flanker Task was used to prompt error commission while alcoholic and nonalcoholic beverages were depicted in order to examine the influence of alcohol-associated cues on error processing. Compared to light social drinkers, heavy social drinkers exhibited diminished ERN amplitudes. This difference was even more pronounced in trials where a visual alcoholic cue preceded error commission. Differences with the same tendency were reported in studies investigating error monitoring in alcoholics compared to healthy controls. This preliminary data indicates alterations in neural activation patterns during error processing as a possible marker for a higher risk to develop a substance abuse disorder.

Neurophysiological correlates of auditory motion perception in the blind J. Lewald (1), S. Getzmann (2) (1) *Department of Cognitive Psychology, Ruhr University Bochum, Bochum, Germany;* (2) *Leibniz Research Centre for Working Environment and Human Factors, Dortmund, Germany*
Blindness is traditionally associated with the

view that compensation for the visual loss by increased use of auditory spatial information may result in related supra-normal abilities. However, a more important question in this context is how blind persons develop and maintain an internal concept of the topography of the auditory space when any sustained calibration by visuospatial information is absent. Recently, it has been demonstrated that both early and late blind subjects exhibit a much more substantial superiority in spatial perception of dynamic, rather than static, information compared with sighted controls (Lewald, submitted). This finding is compatible with the hypothesis that in the absence of visual input the calibration of the auditory space is performed by audiomotor feedback, that is, by the evaluation of systematic changes of auditory spatial cues resulting from head/body movements. On this basis, we further hypothesized that the cortical processing of auditory motion is enhanced in blind, compared to sighted, subjects. To test this latter hypothesis, here we investigated the so called motion onset response, a prominent auditory evoked potential elicited by the onset of motion in an otherwise continuous sound, using high-density electroencephalography in combination with standardized low-resolution brain electromagnetic tomography (sLORETA). Blind subjects and matched sighted controls heard free-field sound stimuli that moved from a central position to the left or right in total darkness. Blind subjects, as contrasted with sighted controls, showed a stronger cN1 component of the MOR, and more intense activation in right extrastriate occipital and posterior cingulate areas as well as in inferior parietal lobule which is known to be specifically involved in au-

ditory motion processing in sighted people. Thus, blind persons may more intensely use the same cortical areas that subserve auditory motion analysis in sighted persons, and may additionally recruit parts of the "visual" cortex to perform these functions.

Primary motor cortex gamma activity is related to sensorimotor performance

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Athletes can achieve striking sensorimotor skills after years of extensive training. So far, only little is known about the neurophysiological processes underlying such skilled performance. Previous electroencephalographic (EEG) studies used the expert-novice paradigm to study inter and intrasubject oscillatory differences related to sensorimotor performance. It has been shown that significant group differences in behavioral outcomes were accompanied by significant power differences in the alpha (7–12 Hz), beta (13–30 Hz) and frontal midline theta (4–7 Hz) frequency bands (e.g. Del Percio et al. 2009; Doppelmayr et al. 2008). The present study aimed to extend previous research by further considering higher frequency bands in the gamma range (35–40 Hz) which have been shown to reflect motor processes (Pfurtscheller et al. 1999). For this reason, we analyzed the alpha, beta and gamma power over the primary motor cortex contralateral to the aiming arm/hand during air pistol shooting in experts and novices for high and low scores, respectively. As expected, experts had significantly higher shooting scores than novices. In the last 3 s prior to trigger pull alpha power grad-

ually increased and beta power decreased with no difference between groups. However, gamma power was significantly lower in experts vs. novices. Although the novices showed a gradual decrease in gamma power towards the trigger pull, they did not nearly reach the power values of experts. Gamma power was also significantly reduced in high compared to low scores 1 s prior to the trigger pull. Moreover, there was a significant negative correlation between gamma power and shooting score. Our findings suggest that gamma power over the primary motor cortex is related to performance in a visuomotor aiming task.

References: Del Percio et al. (2009): *Hum Brain Mapp* 30.11: 3527-40. Doppelmayr et al. (2008): *Neuropsychologia* 46.5: 1463-7. Pfurtscheller et al. (1999): *Clin Neurophysiol* 110.11: 1842-57.

Increased EEG beta activity during mania compared to depression - an inter-individual source localization study.

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Bipolar disorder (BPD) is a chronic illness with a relapsing and remitting course. Relapses are manic or depressive in nature. Neuroimaging findings propose that the emotional dysregulation of mood disorders are mediated by various brain regions and neural circuits. We investigated brain electric differences between manic and depressive BPD episodes using standardized Low Resolution Electromagnetic Tomography (sLORETA). Vigilance-controlled resting EEG was obtained from BPD patients during a manic episode (26 patients: 6 males, 20 females, mean age=35.96±11.21) or

a depressive episode (55 patients: 25 males, 30 females, mean age=40.25±9.94). For the two patient groups, EEG data were recomputed into intracerebral sLORETA current densities in 6239 voxels for each of eight EEG frequency bands (delta through gamma). T-tests compared sLORETA current densities between groups. Testing revealed significant differences ($p < 0.05$ corrected for multiple testing) between groups. The patients recorded during a manic episode showed higher current density in the three EEG beta frequency bands from 12.5 to 30.0 Hz (beta-1: 2140 voxels, beta-2: 3 voxels, beta-3: 842 voxels) which represent excitatory activity. This higher current density was observed in the superior frontal lobe (Brodmann Area [BA] 4, BA 6, BA 8), the anterior cingulate cortex (ACC) (BA 24) and the parietal lobe (BA 3, BA 7, BA 40). Thus, increased activation in the fronto-parietal sensorimotor region and limbic region was observed during manic compared to depressive mood states of BPD patients. These results support previous neuroimaging studies that reported hyperactivity of superior frontal, parietal regions as well as the ACC during BPD mania. It is hypothesized that increased beta power may reflect a state feature of BPD mania.

NIRS - Grundlagen und Anwendungen in der Neurophysiologie des Menschen M. Plichta *Klinik für Psychiatrie und Psychotherapie, Zentralinstitut für Seelische Gesundheit, Mannheim*

Die Nah-Infrarot Spektroskopie (NIRS) misst Hirnaktivität mittels Licht und hat sich als reliables und kosteneffizientes Verfahren im Forschungskontext etabliert. NIRS weist wichtige Vorteile gegenüber Standardverfahren der funktionellen Bildgebung (fMRT, PET) auf: Es sind keine radioaktiven Substanzen wie bei der PET-Messung nötig, und das völlige Fehlen von Lärm während der Messung ist für die Versuchsperson angenehm und erlaubt es beispielsweise, auch Experimente mit akustischer Stimulation durchzuführen. NIRS hat sich bei der Untersuchung von frühkindlicher Sprachverarbei-

tung sehr bewährt, da die Messungen einfach und gefahrlos bereits bei Neugeborenen durchgeführt werden können. Die wenig restriktive Messsituation (keine Fixierung des Kopfes notwendig; entspannte Sitzposition) wird von Menschen, die zur Klaustrophobie neigen als angenehm empfunden. Auch Menschen bei denen Kontraindikationen für eine fMRT-Messung vorliegen (Tätowierungen im Kopf/Halsbereich; Patienten mit Herzschrittmacher etc.) lassen sich problemlos mit NIRS untersuchen. Schlussendlich erlaubt es die Mobilität des NIRS-Gerätes, Probandengruppen zu untersuchen, die ansonsten nur schlecht mit Bildgebungsverfahren untersucht werden können (Gefängnisinsassen; Schulkinder im Klassenraum). Eine weitere Besonderheit ist, dass sich NIRS mit anderen Techniken (EEG, fMRT) nahezu interferenzfrei kombinieren lässt. Wie bei jeder Technik gibt es auch bei NIRS einige Nachteile, wie zum Beispiel die limitierte Messstiefe, welche bei der Planung von Untersuchungen berücksichtigt werden müssen. Diese und weitere Aspekte von NIRS werden innerhalb des Workshops anhand von Studien aus unterschiedlichen Forschungsbereichen vorgestellt.

Introspection: What can we know about ourselves? M. Ruchow *Christophsbad, Faurndauer Str. 6–28, 73035 Göppingen*

Nach ihrer Verbannung aus den Naturwissenschaften Anfang des 20. Jahrhunderts erfährt die Methode der Introspektion durch die modernern bildgebenden Verfahren eine Art Renaissance. Viele kognitionswissenschaftliche Studien rekurren eher unkritisch auf subjektive Angaben von Probanden, um diese dann mit neuronalen Prozessen oder Strukturen zu korrelieren. Auch in der neuzeitlichen Philosophie ist die Vorstellung privater, introspektiv zugänglicher mentaler Ereignisse von zentraler Bedeutung. So vertrat Descartes z.B. die Auffassung, dass ich mich zwar hinsichtlich der Existenz von Gegenständen der Außenwelt irren kann, jedoch nicht hinsichtlich der Existenz meiner Sinnesempfindungen, die mir introspektiv unmittelbar zugäng-

lich sind. Mit diesem besonderen Status der Sinnesempfindungen verbanden sowohl Empiristen als auch Rationalisten die Hoffnung, ein fundamentum inconcussum für die (Natur-)wissenschaften gefunden zu haben und den Herausforderungen des Skeptizismus ein für alle Mal entgangen zu sein. Anhand der Überlegungen von Sellars, Hegel und Wittgenstein soll gezeigt werden, dass der Begriff der Introspektion widersprüchlich ist und sich damit auch die Idee einer Fundierung der Wissenschaften in privaten mentalen Ereignissen nicht durchführen lässt. Dementsprechend wird anstelle eines korrespondenztheoretischen Wahrheits- und Wissenschaftsbegriffs ein kohärenztheoretischer vorgeschlagen.

The really fast wavelet transform T. Sauer *Lehrstuhl für Mathematik mit Schwerpunkt Digitale Bildverarbeitung, Universität Passau, 94030 Passau* Die kontinuierliche Wavelettransformation hat sich gerade bei der Verarbeitung neurophysiologischer Daten als ein sehr hilfreiches Werkzeug etabliert. Ein großes Problem ist allerdings immer noch der hohe Rechenaufwand. Neue Technologien, insbesondere die Rechenkapazitäten von Grafikkarten, erlauben es aber, diese Berechnung massiv zu parallelisieren und so deutlich schneller auszuführen.

Spatio-temporal EEG dynamics of an in/outgroup implicit association test B. Schiller (1), L.R.R. Gianotti (1), T. Baumgartner (1), T. Koenig (2), D. Knoch (1) (1) *Social and Affective Neuroscience, Department of Psychology, University of Basel*; (2) *Department of Psychiatric Neurophysiology, University Hospital of Psychiatry Bern*

In certain socially sensitive domains (e.g., intergroup relations), implicit attitude measures predict variance in behavior not captured by explicit measures. The reason presumably is that people are not able or willing to explicitly report their true intergroup attitudes. One commonly used measure of

implicit attitudes is the implicit association test (IAT) (Greenwald et al., *J Pers Soc Psychol*, 1998). In recent years our knowledge about the core brain regions involved in the IAT has increased considerably (Knutson et al., *Hum Brain Mapp*, 2007; Beer et al., *Neuroimage*, 2008). The temporal dynamics of underlying neuronal processes associated with the IAT, however, are still poorly understood. The present study measured 64-channel event-related potentials (ERPs) of 83 healthy subjects while completing an in/outgroup IAT. ERPs were recomputed into map series. Microstate segmentation of the two grandmean map series (incongruent vs. congruent conditions) during IAT presentation parsed the ERP map sequence into 8 microstates. Using simple randomization procedures, we identified a late microstate that showed longer duration in the incongruent compared to the congruent condition (292 vs. 230 ms, bootstrapping: $p < .01$), despite similar onset latencies (454 vs. 450 ms). Moreover, duration differences of this microstate between the incongruent and congruent condition were positively correlated with subjects' IAT bias ($r = .21$, $p = .05$). During this microstate sLORETA (Pascual-Marqui, *Exp Clin Pharmacol*, 2002) distributed source inverse solution revealed activation in the cingulate cortex, pre- and post-central gyrus, and in the superior frontal cortex. We speculate that the longer duration of this microstate in the incongruent condition is due to more difficult word classification because subjects have to overcome their automatic tendency to associate positive with ingroup and negative with outgroup words.

Investigation of weighted complete networks for the analysis of effective connectivity in a photic driving experiment C. Schmidt *Institut für med. Statistik und Informatik, Universitätsklinikum Jena*

Recently, effective connectivity data is being increasingly analyzed from a graph theory perspective, as the intricate topology of the respective networks offers essential information about underlying neural processes. This information is generally

not obvious, because subtle structural features are overlaid by a dense pattern of directed interactions between vertices. We investigate the direct use of connectivity measures in the construction of effective connectivity networks to circumvent the very time-consuming computation of significance thresholds for those interactions. However, the resulting networks pose new challenges as they are complete, weighted graphs that have pairwise different vertex labels. We describe these networks using several measures that are defined for weighted networks. In particular, we introduce a decomposition of samples of such networks into their weighted structural building blocks. We apply this methodology to samples of networks that are derived from EEG recordings in a photic driving experiment, in which 10 healthy volunteers underwent visual stimulation by repetitive flashes that can lead to an entrainment of the alpha rhythm. For the first time such a photic driving approach was employed by utilizing the individual alpha rhythm of each volunteer. The visual stimulation was performed using a high density of stimulation frequencies adjusted to specific ratios of this individual alpha causing different entrainment effects. Network measures that are sensitive to the stimuli and/or correlate with the flicker ratio can be subsequently identified by using general linear models.

Uni- and multimodal optical imaging using near-infrared spectroscopy in current psychiatric research

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Die optisch-basierte Methode der Nahinfrarot-Spektroskopie (NIRS) hat in den vergangenen zwei Jahrzehnten das Feld neurophysiologischer Forschungsmethoden erweitert und bietet eine Alternative zu anderen, zum Teil stärker artefaktanfälligen oder nebenwirkungsassoziierten Messmethoden. Gleichzeitig eignet sich die NIRS auch besonders für die kombinierte Anwendung mit

anderen Bildgebungsverfahren (z.B. EEG, MEG, fMRT), da es sich weder um ein elektrisch- noch magnetisch-basiertes Verfahren handelt. Trotz der nachteiligen geringen räumlichen, insbesondere Tiefen-Auflösung und der damit verbundenen Beschränkung auf kortikale Zielregionen hat sich die Methode insbesondere auf dem Gebiet psychiatrischer Neurowissenschaften bewährt. Der aktuelle Beitrag gibt einen Einblick in einige aktuelle Forschungsprojekte der psychiatrischen Universitätsklinik Tübingen, in denen NIRS sowohl uni- als auch multimodal in Kombination mit EEG sowie in besonderen experimentellen Settings (z.B. auf einem Laufband) bei Gesunden und verschiedenen Gruppen von Patienten mit psychischen Erkrankungen (Schizophrenie, Angsterkrankungen) zur Anwendung kommt. Die bisherigen Befunde weisen darauf hin, dass NIRS in diesem Kontext eine vorteilhafte und geeignete Methode darstellt, um neurophysiologische Korrelate verschiedener Wahrnehmungs-, Kognitions- und Gedächtnisprozesse abzubilden und pathologische Mechanismen zu identifizieren. Signifikante Zusammenhänge zwischen NIRS- und EEG-Daten belegen zudem den Nutzen einer multimodalen Anwendung der Methode, mit deren Hilfe topographische Aktivierungsmuster funktionell interpretiert werden können.

Comparison of the rhythmicity of quadratic phase couplings in the tracé discontinue EEG pattern of premature newborn and in the tracé alternant EEG pattern of full-term newborn

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The aim of this study was to compare rhythmicities in the quadratic phase coupling (QPC) in the tracé discontinue EEG patterns (TD) of premature newborns and the tracé alternant EEG patterns (TA) of full-term newborns by means of time-variant bispectral analysis. Both pattern occur during quiet sleep and are characterized by an ongoing sequence of

interburst and burst patterns. The courses of time-variant bispectral measures during the EEG burst most likely indicate specific interrelations between cortical and thalamocortical brain structures. The EEG of a group of premature (n=5) and of full-term (n=5) newborns was analysed. For each newborn, four different bipolar recordings were used for analysis. In a preprocessing step, interval-based time-variant linear phase locking, n:m synchronization and direct bi-amplitude/bi-coherence analyses were performed to find the region-of-interest (ROI) for the investigation of the time-variant QPC. Time-variant QPC was investigated by means of time-variant parametric bispectral analysis. The frequency plane [0.5 Hz, 1.5 Hz] × [3 Hz, 6 Hz] was used as the ROI. QPC rhythms with a frequency of 0.1 Hz (8–11 s) were found in all full-term newborns at all electrodes. The effect was most pronounced at fronto-temporal positions. For the premature newborns the QPC rhythms were less stable and slower (<0.1 Hz, 11–17 s) at all electrodes and showed a higher inter-individual variation than for the full-term newborns. Statistically, the adaptation of a linear mixed model revealed a difference of about 5 s between both groups of newborns. The comparison of the results of both groups of newborns indicates a development in the interaction between cortical, thalamocortical and possibly neurovegetative structures in the neonatal brain. Therefore, in a next step a combined approach will be performed by analyzing EEG as well as heart rate (HR) and near-infrared spectroscopy (NIRS) pattern.

Neuronal mechanisms of language perception in early infancy: evidence from combined NIRS and EEG measures S. Telkemeyer (1; 2), S. Rossi (3), H. Obrig (3), I. Wartenburger (2) (1) *Languages of Emotion Cluster, FU Berlin*; (2) *Department für Linguistik, Universität Potsdam*; (3) *Max-Planck-Institut für Kognitions- und Neurowissenschaften Leipzig*

Die Fähigkeit den kontinuierlichen Sprachstrom in einzelne Einheiten wie z.B. Wörter und Phrasen

zu segmentieren ist von großer Bedeutung für die Sprachentwicklung (Kuhl, 2004). Im Sprachstrom enthaltene akustische Hinweisreize unterstützen diesen Segmentierungsprozess. Wesentlich für das Entschlüsseln der sprachlichen Information sind dabei vor allem verschiedene zeitliche akustische Veränderungen im Sprachstrom: die Sprachmelodie (Prosodie) variiert eher langsam z.B. über eine Phrase oder einen Satz hinweg (zwischen ~150–300 ms), der Wechsel zwischen Phonemen oder Konsonanten und Vokalen erfolgt hingegen sehr schnell (zwischen ~20–50 ms). Welche neuronalen Korrelate liegen der Verarbeitung solch akustischer Informationen zugrunde? Erwachsenen-Studien zeigen einen Zusammenhang zwischen der lateralisierten Verarbeitung bestimmter Sprachreize und der Spezialisierung des auditorischen Kortex für die Verarbeitung bestimmter zeitlicher Variationen im akustischen Sprachsignal (Boemio et al., 2005; Poeppel et al., 2008). Darauf aufbauend präsentierten wir Neugeborenen und Kleinkindern nicht-sprachliche akustische Reize, deren zeitliche Struktur so variierte, dass sie den im Sprachsignal vorhandenen zeitlichen Frequenzmustern (schnellen im Vergleich zu langsamen akustischen Variationen) entsprachen. Die Hirnaktivität wurde simultan mittels EEG und Nahinfrarot-Spektroskopie gemessen. Die zeitlichen akustischen Modulationen führten zu differenzierten und lateralisierten Verarbeitungsmustern, die den Erwachsenen-Befunden sehr ähnlich waren (Boemio et al., 2005): schnelle akustische Variationen (wie sie z.B. im Wechsel zwischen Phonemen vorhanden sind) wurden von den Neugeborenen und Kleinkindern in bilateralen auditorischen Kortexregionen verarbeitet, langsame Variationen (wie z.B. in der Prosodie) führten zu einer rechts-lateralisierten Aktivierung dieser Areale. Die Ergebnisse unterstützen die Annahme, dass die lateralisierte Verarbeitung von Sprachreizen auf eine Spezialisierung des auditorischen Kortex für bestimmte zeitliche Frequenzmuster zurückzuführen ist (Hickok & Poeppel, 2007; Poeppel et al., 2008). Das Gehirn ist von Geburt auf die

Wahrnehmung der zeitlichen akustischen Variationen spezialisiert, die für die Entschlüsselung des Sprachsignals relevant sind.

Changes in Regional Blood Flow during Semantic Language Learning W. Skrandies (1), H. Shoji (2), H. Ozaki (2) (1) *Institute of Physiology, Justus Liebig University, Giessen, Germany;* (2) *Laboratory of Physiology, Faculty of Education, Ibaraki University, Mito, Japan*

We studied a group of 14 healthy Japanese adults who learned the meaning of German words. Twenty German words were presented on a monitor before and after a learning phase while brain activation was assessed with Near Infra-Red Spectroscopy (NIRS) in 24 channels located over the left and right hemisphere. A learning phase of 20 minutes was employed. Twenty Japanese words were presented as control stimuli. A mean rate of recall of 96.6% was observed in the group of subjects. NIRS showed a significant change of cerebral blood flow after learning reflected by an increase of blood flow with stimuli that were learned. Control stimuli yielded a significant decrease in blood flow indicating that habituation to the well known words occurred. These effects were widespread but strongest over central and frontal areas of the left hemisphere. These results suggest that semantic learning of word meaning correlates with changes of cortical blood flow not only in circumscribed language areas but also in other areas of the human cortex. The acquisition of new meaning yields increased brain activity while familiar or meaningless stimuli are followed by habituation. These results appear as a direct correlate of learning and cognitive processing of meaningful material.

Announcements — Ankündigungen

- **Fechner Day**

The 29th Meeting of the International Society for Psychophysics will be held in Freiburg, Germany from October 21 to 25, 2013.

Information and Registration at: <http://www.fechnerday.com/fd2013>

- **IOP World Congress**

The 17th World Congress of Psychophysiology (IOP2014) will take place in Hiroshima, Japan from September 23 to 27, 2014.

Information and Registration at: <http://www.iop2014.jp/>

- **23. Deutsches EEG/EP Mapping Meeting / 23rd German EEG/EP Mapping Meeting**

Conference language is German; English contributions will be accepted.

- 24. bis 26. Oktober 2014; Schloss Rauischholzhausen
- Anmeldeschluss ist der 15. Juli 2014.
- Information und Anmeldung unter: <http://www.med.uni-giessen.de/physio/>