

**Edmund Wascher and Christian Beste**

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# Tuning Perceptual Competition

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**Wascher E, Beste C.** Tuning perceptual competition. *J Neurophysiol* 103: 1057–1065, 2010. First published December 23, 2009; doi:10.1152/jn.00376.2009. The ability to notice relevant visual information has been assumed to be determined both by the relative saliency of relevant information compared with distracters within a given display and by voluntary allocation of attention toward intended goals. A dominance of either of these two mechanisms in stimulus processing has been claimed by different theories. A central question in this context is to what degree and how task irrelevant signals can influence processing of target information. In the present study, participants had to detect a luminance change in various conditions among others against an irrelevant orientation change. The saliency of the latter was systematically varied and was found to be predictive for the proportion of detected information when relevant and irrelevant information were spatially separated but not when they overlapped. Weighting and competition of incoming signals was reflected in the amplitude of the N1pc component of the event-related potential. Initial orientation of attention toward the irrelevant element had to be followed by a reallocation process, reflected in an N2pc. The control of conflicting information additionally evoked a fronto-central N2 that varied with the amount of competition induced. Thus the data support models that assume that attention is a dynamic interplay of bottom-up and top-down processes that may be mediated via a common dynamic neural network.

## INTRODUCTION

When processing a visual scene, we pay attention to some things at the expense of others (Duncan 2006). This selection mechanism, called attention, may be guided by salient signals in the visual field (attentional capture) or by the intention of the observer to look for a particular element in the scene. The “biased competition model” of attention (Desimone and Duncan 1995) postulates an interplay of these two mechanisms by assuming a competition of stimuli in multi-element displays for limited processing resources in sensory systems. This competition is exerted by an inhibitory effect on the processing of other stimuli (Desimone 1998; Kastner and Ungerleider 2001). Based on that mechanism, it is assumed that the organization of incoming information is initially driven by the interrelation of the saliency of all incoming signals. The function of voluntary attention toward a particular feature or location in the scene is to bias these competitive interactions in favor of the attended stimuli (Desimone and Duncan 1995). Thus attended stimuli are processed more effectively because they suffer less from the inhibitory effects of the stimuli that surround them; however, the initial allocation of attention is determined by stimulus saliency dominated by the bottom-up stream.

Core structures mediating the selection of visual stimuli encompass striate and extrastriate visual areas (e.g., Poghosyan et al. 2005). Sensory suppression among multiple, simultaneously presented visual stimuli has been found in several areas of the visual cortex, including areas V2, V4, the middle temporal (MT) and medial superior temporal (MST) areas, and the inferior temporal (IT) cortex (Miller et al. 1993; Moran and Desimone 1985; Reynolds et al. 1999). An important property of these structures is the dependence of neural firing on the saliency of stimuli (Koene and Zhaoping 2007). Due to multiple reciprocal inhibitory connections between striate and extrastriate visual areas, any visual stimulus may influence the processing of any other stimuli (e.g., Fahrenfort et al. 2007), forming the neuronal substrate of perceptual competition. These mechanisms can be characterized as a winner-take-all network with the most salient stimulus governing the initial allocation of attention (Knudsen 2007).

While perceptual competition is assigned to sensory areas, the top-down-induced bias has been assigned to frontal cortical structures that impinge on those structures (Knudsen 2007; Reynolds and Desimone 2003; Reynolds et al. 2000). A number of studies have shown that such a modulation of striate and extrastriate visual areas both by stimulus saliency and intention are central to visual attention (Deco and Rolls 2005; Sarter et al. 2006).

Evidence for this elementary model of visual processing has been repeatedly reported in studies that measured single-cell activity in monkeys as well as with functional imaging studies. In cognitive psychology, it appears to be closest related to the work of Theeuwes (Schreij et al. 2008; Theeuwes 2004). These studies showed how bottom-up saliency and top-down controlled intentional settings interact with each other, which is inconsistent with the concept of “contingent attentional capture” (Folk et al. 1992). This concept assumes that attentional capture by irrelevant signals can only occur when this stimulus is featurally similar (related) to a feature relevant for locating a target (Burnham 2007; Folk et al. 1992). The contingent capture model assumes that task-relevant features are placed in attentional sets that control the bottom-up stream (attentional capture) intentionally. Recent event-related potential (ERP) studies support both the contingent capture and the biased competition approach. While an ERP component assigned to the spatial allocation of attention (N2pc) was found to be reduced when a feature pop-out stimulus is not task relevant (Eimer and Kiss 2008; Kiss et al. 2008a; Lien et al. 2008), this component may reliably occur for an irrelevant feature (Hickey et al. 2006). Thus the ability to control irrelevant information via top-down control mechanisms may depend on the saliency of those stimuli.

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In the current study, we intend to investigate to what degree the saliency of task-irrelevant signals influences the processing of relevant information even if irrelevant signals are not featurally similar to the intended information and how this interaction is neurally implemented. It has been proposed by Theeuwes (Hickey et al. 2006; Schreij et al. 2008; Theeuwes 2004) that stimuli that are completely irrelevant for a given task may capture attention when they are sufficiently salient. We tried to scale this mechanism by modulating the saliency of irrelevant information. Because any competition is determined in the relative strength of the competitors involved, the ability to detect the target signal should be determined by its relative saliency in comparison to the irrelevant information in the scene.

To track the neural implementation of the mechanisms involved, event-related potentials (ERPs) of the electroencephalography (EEG) can be measured. Early components, such as the N1, are assumed to be generated in sensory areas, that is, for the visual domain in lateral extrastriate cortex with a contribution of dorsal parieto-occipital and ventral temporo-occipital structures (Gomez Gonzalez et al. 1994). In these early processing stages, attention has been assumed to act as gain control, modifying the magnitude of neural responses to incoming information (Hillyard et al. 1999; Mangun 1995; Posner and Dehaene 1994). However, already the N1 may be assigned to the generation of the spatial representation of signals relative to each other (Wascher et al. 2009). Moreover, several studies reported that asymmetries already in the N1 range may reflect stimulus driven allocation of attention (Shedden and Nordgaard 2001; Wascher and Beste 2009; Wolber and Wascher 2005).

An ERP component that is assumed to reflect top-down controlled visuo-spatial processing is the N2pc (Luck and Hillyard 1994a,b). This component has been assigned to an increase in negativity contralateral to a task relevant stimulus (however, see Hickey et al. 2009), typically peaking between 250 and 350 ms after stimulus onset. The cortical source of this component is assumed to be located in extrastriate visual areas with a possible contribution of posterior parietal cortex for the early part of this component (Hopf et al. 2000). Starting with studies on visual search (Luck and Hillyard 1994a,b), the N2pc has recently been used in the investigation of the attentional blink (Dell'Acqua et al. 2007), as a marker of the spatial locus of visual attention (Kiss et al. 2008b; Woodman and Luck 1999, 2003), but also as a correlate of attentional capture by salient singletons (Hickey et al. 2006). Of particular interest here is that the N2pc is assumed to be modulated by the relation of the target stimulus to its surroundings (Luck et al. 1997).

Finally, the control of conflicting information may be reflected by the fronto-central N2 (Folstein and van Petten 2008; van Veen and Carter 2002). It has repeatedly been shown that the N2 is sensitive to the degree of conflict and may be the source of top-down attentional control (Kehrer et al. 2009) occurring under conditions of visual distraction (Azizian et al. 2006; Beste et al. 2008; Forster and Pavone 2008).

Thus by inducing varying levels of perceptual conflicts and observing both sensory (occipital) and fronto-central cortical activation, we intended to contribute to the understanding of the processing of irrelevant information in visual scenes. The task used was designed to evoke perceptual conflicts based on

salient irrelevant signals. Stimuli were set up in a way that they were likely to maximize reciprocal inhibitory interaction within visual areas. This interaction is largest between functional units that are neuroanatomically closely located to each other. Within visual areas, functional columns (blobs and interblobs) may meet these requirements. They are located close to each other (Lu and Roe 2008) and are known to process qualitatively different aspects of stimuli. Blobs are sensitive to color and luminance of stimuli (e.g., De Valois et al. 2000), whereas interblobs are primarily sensitive to orientation of stimuli (Clifford et al. 2003; Livingstone and Hubel 1988). However, it should be noted that under particular conditions (equiluminant color patterns at high contrast), a subset of color-sensitive cells are also sensitive to orientation (Johnson et al. 2008).

Based on these neurophysiological and neuroanatomical prerequisites we induced perceptual competition using displays that are characterized by changes in luminance and orientation of the stimuli. The task of the subjects was to detect a luminance change in a fast sequence of two stimulus frames. In both pictures, two bars were presented left and right from fixation, either darker or brighter than the background, oriented either vertically or horizontally. Luminance or orientation could change at one bar. In half of the trials, both stimulus dimensions changed, either at one location or distributed across both positions. Of central interest for the competition account was the latter condition, where the luminance transient had to be detected against an irrelevant orientation change. In such a setting, competitive accounts of attention would predict influence of the task-irrelevant orientation change on target processing depending on its saliency. For the contingent capture account, the irrelevant orientation change should be negligible, irrespective of its saliency. With respect to the biased competition account, saliency-based modulations of processing should be visible in the EEG both over sensory areas and over fronto-central structures of executive control. Asymmetries in the N1 range should reflect the relation of saliency between the relevant and the irrelevant signal. They might indicate which element of the display is initially attended. The direction of this initial attentional shift should be determined by the relation of saliencies across simultaneously presented signals rather than by the top-down attentional settings that were to ignore the irrelevant orientation change. If the initial orientation of attention is driven by the distribution of saliency, top-down driven processes should be initiated predominantly in those cases where the initial shift led away from the relevant item. Both the N2pc as a correlate of intention based allocation of attention and the fronto-central N2 component should vary with the necessity to reallocate attention in a way that they increase when bottom-up processing is not sufficient to cope with the task.

## METHODS

### *Participants*

Twelve students (6 female) participated in the experiment (19–30 yr old; mean age: 23.9 yr). All participants took part in return for course credits or a payment of €8/h. None of the participants suffered from any known psychiatric or neurological disease. They had normal or corrected to normal vision. Participants provided informed written consent prior to entering the experiment. The study was approved by a local ethics committee.

### Stimuli and procedure

The stimulus material consisted of two vertically or horizontally oriented bars, presented  $1.1^\circ$  left and right from a fixation cross (see Fig. 1). The bars were either darker or brighter than the background ( $30 \text{ cd/m}^2$ ) with a Fechner contrast of 0.2 (i.e. 20 and  $45 \text{ cd/m}^2$ , respectively). Luminance and orientation were randomly intermixed in any possible combination for the first frame. In each trial, two frames of these stimuli were presented in rapid succession. Each frame was shown for 200 ms. Between the two frames a short break of 50 ms was set in which only the fixation cross was visible. Between the two frames, either the luminance (LUM) or the orientation (ORI) of one single bar, luminance and orientation of one bar (LOU = luminance-orientation unilateral), or luminance and orientation distributed across the two bars (LOB = luminance-orientation bilateral) could change. The latter condition will also be referred to as the "conflict" condition because in this condition, relevant and irrelevant information are spatially separated. The saliency of the orientation change was modulated by varying the length-to-width ratios of the bars (1:2.41, 1:1.7, and 1:1.35) while holding the area covered by the bars constant at  $0.76 \text{ cm}^2$ . With an observation distance of 120 cm, the bars with a length-to-width ratio of 1:2.41 had a size of  $0.56 \times 1.35^\circ$ .

The subjects had to detect changes in luminance and to ignore orientation changes. They had to press a button with the index finger of the left or the right hand at the side where the change had appeared. Trials in which only the orientation of one bar changed were no-go trials. Overall 1,920 trials were presented, 160 for each condition (4 change conditions and 3 levels of saliency), in random order. Breaks were set every 400 trials. The intertrial interval varied between 2,000 and 2,500 ms.

### Data analysis

**BEHAVIORAL DATA.** Responses were recorded from the onset of the first frame (to scan for premature responses) until 1,500 ms after the second frame. Response time was defined as the interval between the change and the button press. Responses faster than 150 ms were categorized as "fast guesses," slower than 1,000 ms as "too slow." Both of these categories hardly ever occurred (<1%). Substantial error categories were response errors (wrong button presses, respectively, false alarms

in the no-go condition) and misses (no response within 1,500 ms). Global accuracy was tested first in an ANOVA including the repeated-measurement factors Type of change (LUM, ORI, LOU, LOB) and saliency of the irrelevant orientation change (strong, middle, weak). This ANOVA was then additionally performed separately for response errors and misses. Post hoc tests were made if necessary. Analysis of response times was restricted to those conditions in which the subjects had to respond. Thus this ANOVA included only three types of change (LUM, LOU, LOB) and three levels of saliency.

**EEG DATA.** Electroencephalography (EEG) was recorded from 60 Ag/AgCl electrodes (common average served as on-line reference) affixed across the entire scalp according to the extended 10/20 System (Pivik et al. 1993). Eye movements were scanned continuously from two electrode pairs affixed above and below the left eye [vertical electrooculogram (EOG)] and at the outer canthi of each eye (horizontal EOG). EEG and EOG were sampled on-line with a frequency of 1 kHz by a Quickamp DC-amplifier with a band-pass filter of 0–200 Hz.

Data were referenced off-line to linked mastoids. Segments with a length of 1,500 ms (250 ms before the onset of the 1st frame to 1,000 ms after the 2nd frame) were defined for further processing. Baseline was set to 200 ms preceding the first frame. Only trials with correct responses were entered into analysis. These segments were checked off-line for artifacts (zero-lines, fast shifts, or drifts). Trials with horizontal eye movements (saccades) preceding the latency of the components of interest were excluded by manual inspection. The influence of remaining eye movements on electrocortical activity was corrected by the algorithm proposed by Gratton, Coles, and Donchin (1983).

Due to the fast sequence of the two frames, ERP responses of the two stimuli, in particular sensory components largely overlapped. Temporal jittering of the interstimulus intervals, to reduce this overlap would have essentially changed the task. Thus to address visuo-spatial processing, posterior (PO7/PO8) event-related lateralizations of the EEG were calculated (ERLs = contralateral minus ipsilateral activity with respect to the stimulus change; in case of conflict trials, the target element served as reference) just as a lateralized readiness potential is computed (Coles et al. 1988; Wascher and Wauschkuhn 1996). Bottom-up-driven activations of the sensory system as evoked by the changes was determined in the N1 range. These activations were

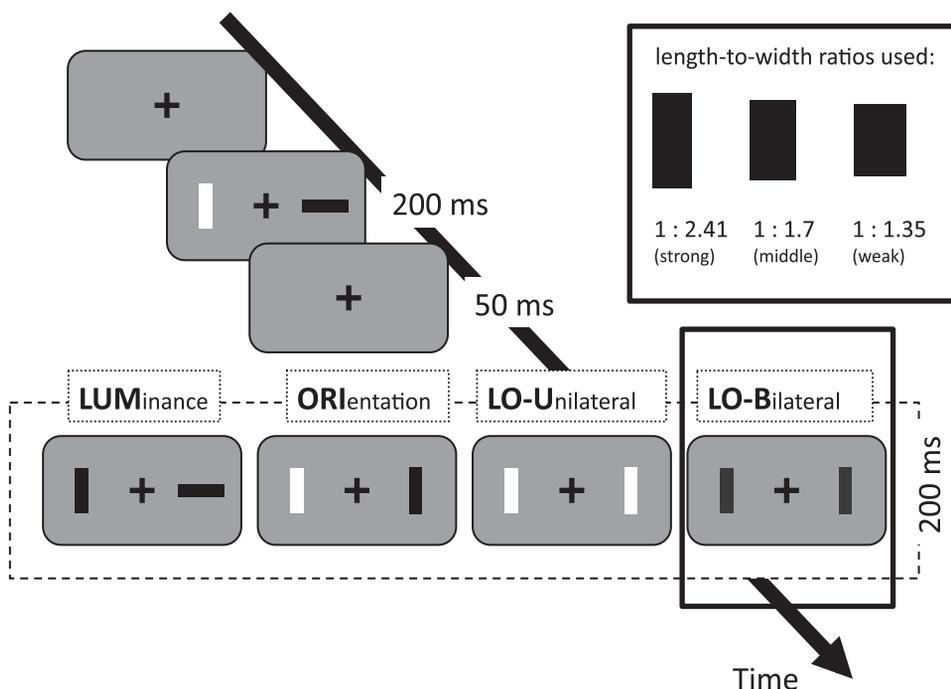


FIG. 1. Set-up and procedure. Participants had to detect luminance changes of a bar in a fast sequence of frames that could occur alone [luminance (LUM)], together with a change in orientation of the same bar [luminance-orientation unilateral (LOU)] or together with an orientation change at the opposite location [luminance-orientation bilateral (LOB)]. Trials in which only the orientation (ORI) changed at 1 bar were no-go trials. The length-to-width ratios of the bars were varied to manipulate the saliency of the orientation change.

measured as the maximum of asymmetry between 140 and 230 ms in the ERLs over posterior electrodes. This measure was restricted to the nonconflict conditions (LUM, ORI, LOU) because there was no reliable peak evoked in the conflict trials. This component was tested in an ANOVA including the factors type of change (3) and saliency (3). In the conflict condition (LOB), the asymmetry in the N1-range was measured as mean amplitudes of ERLs in the interval between 150 and 190 ms. This asymmetry was tested for effects of saliency in a separate ANOVA. As an equivalent of the N2pc, the asymmetry following that first response was measured in the conflict condition in a time window between 350 and 400 ms. All these components of lateralization were tested against zero to verify their reliable occurrence.

Because there was spatial overlap between stimulus and response location, all analyses were additionally performed for electrodes over the motor cortex (C1/C2) to control for possible confounds of the perceptual ERLs by movement-related ERLs.

In the regular (i.e., referred to mastoids) ERP, the maximal effect of conflict was observed at fronto-central site (FC<sub>2</sub>). There, a negative component around 360 ms appeared that was maximal when changes appeared at both locations. The ORI condition was not included in this analysis because a no-go-P3 overlapped the time window of the N2. Because no distinct peaks were measurable in those conditions in which no conflict appeared, the peaks were firstly measured as the mean amplitude between 330 and 390 ms at FCz. In the conflict trials, in which distinct peaks appeared within this interval, peaks were measured as local maxima in an interval between 280 and 480 ms over FCz and analyzed separately for latency and amplitude.

Factors with more than one degree of freedom in the numerator were Greenhouse-Geisser corrected (cf. Vasey and Thayer 1987). In that case,  $\epsilon$  values and  $P$  values derived from the corrected degrees of freedom will be reported.

## RESULTS

### Behavioral data

Error rates (see Fig. 2, left) varied across types of change,  $F(3,33) = 62.9$ ,  $\epsilon = 0.64$ ,  $P < 0.001$ , and increased overall with the saliency of the orientation change,  $F(2,22) = 38.2$ ,  $\epsilon = 0.74$ ,  $P < 0.001$ . However, the interaction between type of change and saliency,  $F(6,66) = 37.0$ ,  $\epsilon = 0.42$ ,  $P < 0.001$ , indicated substantial differences of saliency across conditions. While error rates did not differ with saliency of the irrelevant feature in the nonconflict trials,  $F(2,22) = 1.4$ ,  $\epsilon = 0.89$ ,  $P = 0.115$ , they did so when the luminance target had to be processed against a contralateral orientation change,  $F(2,22) = 56.4$ ,  $\epsilon = 0.71$ ,  $P < 0.001$ . Pair-wise  $t$ -test revealed that the error rates in this condition increased with the saliency of the

orientation change from 15.1 to 29.1%,  $t(11) = 6.19$ ,  $P < 0.001$ , and further to 34.9%,  $t(11) = 5.04$ ,  $P < 0.001$ .

More detailed analysis of the conflict condition revealed that about 2/3 of all errors were choice errors and 1/3 were misses. Both error types showed a reliable gradient with the saliency of the irrelevant feature. Choice errors,  $F(2,22) = 43.0$ ,  $\epsilon = 0.78$ ,  $P < 0.001$ , increased from 10.6 to 19.9%,  $t(11) = 5.40$ ,  $P < 0.001$ , and further to 23.8%,  $t(11) = 3.79$ ,  $P = 0.003$ . Misses,  $F(2,22) = 16.6$ ,  $\epsilon = 0.82$ ,  $P < 0.001$ , increased from 4.4 to 9.1%,  $t(11) = 4.33$ ,  $P = 0.001$ , and further to 11.0%,  $t(11) = 1.99$ ,  $P = 0.072$ . In the no-conflict conditions, choice errors and misses were equally distributed.

Response times (see Fig. 2, right) showed by and large the same effects as error rates. The main effects of type of change,  $F(2,22) = 30.4$ ,  $\epsilon = 0.52$ ,  $P < 0.001$ , and saliency,  $F(2,22) = 46.1$ ,  $\epsilon = 0.83$ ,  $P < 0.001$ , as well as the interaction of type of change by saliency,  $F(4,44) = 33.4$ ,  $\epsilon = 0.67$ ,  $P < 0.001$ , reached significance. Responses to single luminance changes were slower than responses to luminance changes of an element that changed orientation at the same time,  $F(1,11) = 25.6$ ,  $P < 0.001$ . Responses in the latter condition were faster than in conflict trials,  $F(1,11) = 33.0$ ,  $P < 0.001$ . Saliency did not affect response times when no conflict was involved,  $F(2,22) = 1.3$ ,  $P > 0.2$ . In the conflict condition, response times increased with saliency of the irrelevant transient,  $F(2,22) = 56.7$ ,  $\epsilon = 0.87$ ,  $P < 0.001$ , from 472 to 512 ms,  $t(11) = 5.81$ ,  $P < 0.001$ , and further on to 541 ms,  $t(11) = 5.65$ ,  $P < 0.001$ .

### EEG data

In the non-conflict trials (see Fig. 3, unshaded plots), in which the asymmetry in the N1 range could be measured as a distinct peak, the latency of this component did not vary with the type of change,  $F(2,22) = 2.0$ ,  $\epsilon = 0.68$ ,  $P = 0.172$ , but with the saliency of the orientation change,  $F(2,22) = 18.3$ ,  $\epsilon = 0.77$ ,  $P < 0.001$  with longest latencies for the weakest transient. The interaction between type of change and saliency,  $F(4,44) = 4.29$ ,  $\epsilon = 0.48$ ,  $P = 0.029$ , demonstrating that this effect of saliency was restricted to orientation changes [ $F(2,22) = 21.369$ ,  $\epsilon = 0.81$ ,  $P < 0.001$ ; LUM:  $F(2,22) = 1.778$ ,  $\epsilon = 0.69$ ,  $P > 0.2$ ; LOU:  $F(2,22) = 1.566$ ,  $\epsilon = 0.54$ ,  $P > 0.2$ ].

The amplitude of this peak varied with the type of change  $F(2,22) = 15.4$ ,  $\epsilon = 0.94$ ,  $P < 0.001$ . Largest amplitudes were observed when both stimulus dimensions changed at the same location (5.48  $\mu$ V). Single-dimension changes evoked asym-

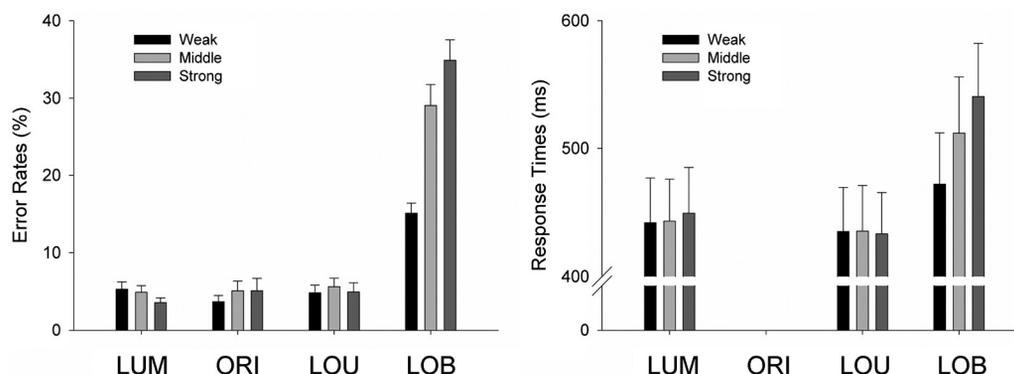


FIG. 2. Mean error rates (left) and response times (right; error bars depict the standard error). Both parameters varied with the saliency of the irrelevant orientation change, but only when target stimulus (luminance change) and distractor (orientation change) occurred at opposite locations.

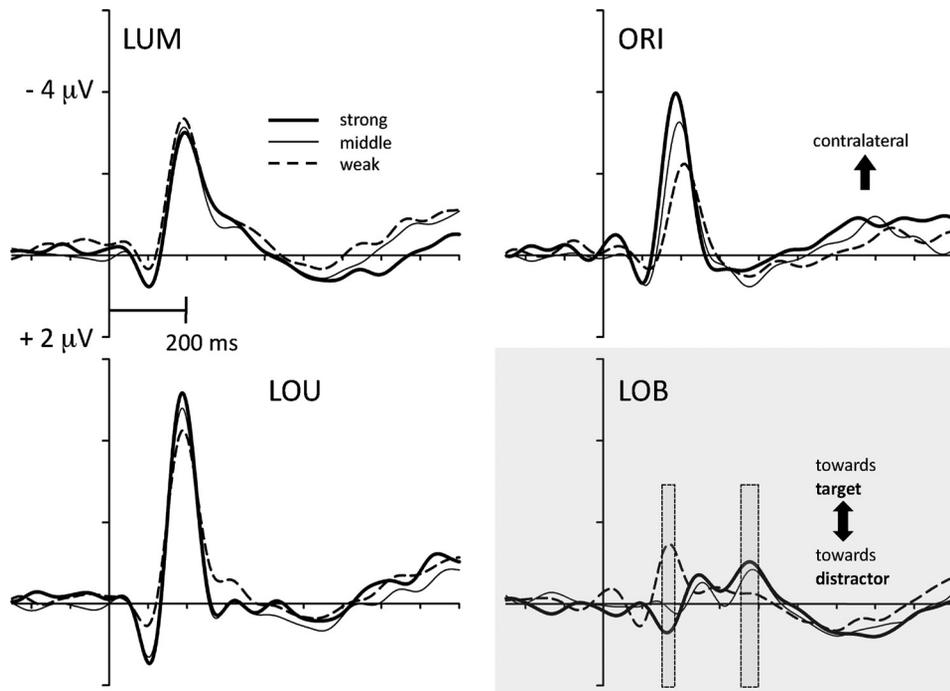


FIG. 3. Posterior (PO7/PO8) event-related lateralizations (ERLs) of the electroencephalography (EEG) separately for each type of change. Increase of negativity contralateral to an unilateral transient (LUM, ORI, LOU) is plotted upward. The gray-shaded plot indicates the ERLs in the central conflict condition (LOB; negativity contralateral to the target stimulus is plotted upward). In the time window of the N1, ERLs indicate the capture of attention toward the more salient element. Subsequent asymmetries in the N2 range (N2pc) were evoked only when the initial orientation of attention did not point toward the target element.

metries of comparable amplitudes (orientation:  $3.92 \mu\text{V}$ ; luminance  $3.85 \mu\text{V}$ ). Overall, amplitudes varied also with the saliency of the orientation change  $F(2,22) = 10.7$ ,  $\epsilon = 0.65$ ,  $P = 0.004$ , but this effect was qualified by its interaction with type of change,  $F(4,44) = 5.8$ ,  $\epsilon = 0.52$ ,  $P = 0.009$ , as follows. No modulation with saliency was observed in the luminance condition,  $F(2,22) = 2.3$ ,  $\epsilon = 0.61$ ,  $P = 0.147$ .<sup>1</sup> For single-orientation changes, asymmetries in the N1 range were larger when the transient was strong,  $F(2,22) = 24.4$ ,  $\epsilon = 0.85$ ,  $P < 0.001$ . An increase from  $2.90$  to  $4.18 \mu\text{V}$ ,  $t(11) = 4.15$ ,  $P = 0.002$ , and further on to  $4.67 \mu\text{V}$ ,  $t(11) = 2.06$ ,  $P = 0.064$ , was observed. When both dimensions changed on the same location, the modulation due to transient strength only marginally reached significance,  $F(2,22) = 3.4$ ,  $\epsilon = 0.69$ ,  $P = 0.074$ . In all these unilateral conditions analyzed in the preceding text, the peak amplitude of this early asymmetry differed reliably from zero, all  $t(11) > 6.5$  ( $P < 0.001$ ). Over the motor cortex, the LRP in this early time window marginally varied with the type of change,  $F(2,22) = 3.6$ ,  $\epsilon = 0.59$ ,  $P = 0.073$ , with smallest amplitudes for the orientation change, most probably reflecting that this condition was a no-go condition. More importantly, the LRP did not at all vary with saliency,  $F(2,22) = 0.7$ , NS.

The asymmetry in the N1 range for the conflict trials, measured as mean amplitude, varied with the strength of the orientation change,  $F(2,22) = 26.5$ ,  $\epsilon = 0.92$ ,  $P < 0.001$ . When the orientation change was weak, increased negativity was observed contralateral to the location of the luminance change ( $-1.80 \mu\text{V}$ ,  $t$ -test against 0:  $t(11) = 7.75$ ,  $P < 0.001$ ); when it was strong, the asymmetry was reversed ( $0.80 \mu\text{V}$ ,  $t(11) = 2.91$ ,  $P = 0.014$ ). For middle strength, no asymmetry was observed at all [ $-0.02 \mu\text{V}$ ,  $t(11) = 0.10$ ,  $P > 0.2$ ; pairwise comparisons: weak vs. middle:  $t(11) = 4.99$ ,  $P <$

$0.001$ ; middle vs. strong:  $t(11) = 2.56$ ,  $P < 0.001$ ]. Over the motor cortex, this modulation did not reach significance,  $F(2,22) = 3.0$ ,  $\epsilon = 0.65$ ,  $P = 0.100$ .

In this bilateral conflict condition, a second posterior asymmetry appeared in the N2 range, which varied marginally with the saliency of the irrelevant orientation change,  $F(2,22) = 3.3$ ,  $\epsilon = 0.99$ ,  $P = 0.054$ . This N2pc differed reliably from zero for strong,  $t(11) = 3.18$ ,  $P = 0.009$ , and medium orientation change,  $t(11) = 2.48$ ,  $P = 0.031$ , but not when the orientation change was weak,  $t(11) = 0.58$ ,  $P > 0.2$ . Pair-wise comparisons between adjacent conditions did not reach significance [weak vs. middle:  $t(11) = 1.68$ ,  $P = 0.120$ , middle vs. strong:  $t(11) = 0.80$ ,  $P > 0.2$ ]. Only the weak and the strong conditions differed reliably,  $t(11) = 2.54$ ,  $P = 0.028$ . Again, this effect was not mirrored in a modulation of the LRP,  $F(2,22) = 1.1$ ,  $\epsilon = 0.82$ ,  $P > 0.2$ .

ERPs recorded from PO7 and PO8 referred to linked mastoids, i.e., before the contra-ipsilateral subtraction, are displayed in Fig. 4 for the bilateral-conflict condition. The large P1/N1 complex evoked by the first frame did not differ between contralateral and ipsilateral sites, of course, because the change that defined laterality occurred with the second frame. The second frame evoked an N1 with reduced amplitude. With strong orientation changes, this N1 rose earlier ipsilateral to the attended luminance change, i.e., contralateral to the irrelevant orientation change. Around 400 ms, a phasic N2 was visible contralateral to the position of the attended luminance change. With weak orientation changes, the N1 effect was reversed with faster onset of the N1 contralateral to the attended luminance change. One might even argue that the N1 seems to be suppressed over the ipsilateral hemisphere, indicating top-down inhibition of the irrelevant luminance change. However, note that due to assumable high overlap of the ERPs evoked by the two subsequent frames, the ERPs evoked by the change in terms of known components has to be interpreted with caution.

<sup>1</sup> It is trivial that the variable "saliency" did not affect the asymmetries in the luminance condition because only the width-to-height ratio of the rectangles changed, but areas remained constant.

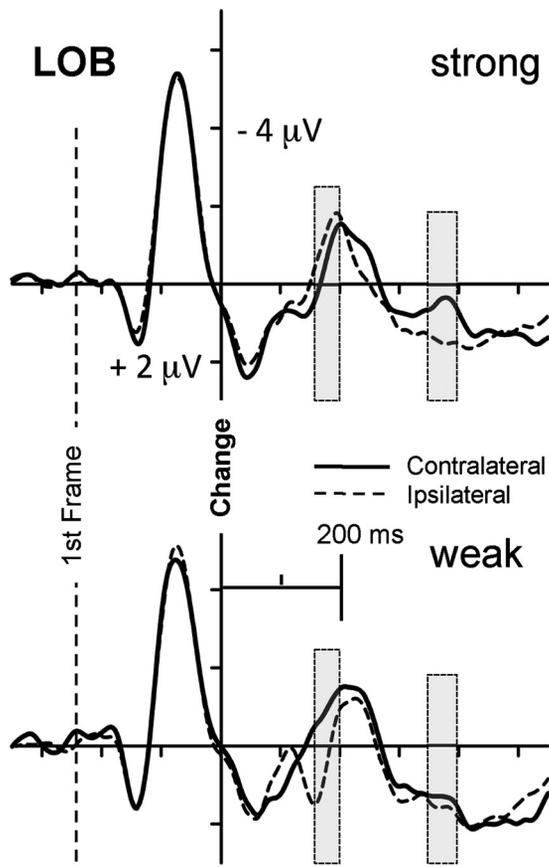


FIG. 4. Event-related potentials at PO7/PO8 referred to linked mastoids, for strong (top) and weak (bottom) orientation changes in the conflict condition. Activity contralateral to the attended luminance change (—) is superposed to ipsilateral activity (---). With strong orientation changes, a bilateral N1 is visible that rises earlier contralateral to the orientation change. With weak orientation changes, this effect is reversed. A subsequent N2pc is visible only for strong orientation changes.

In the regular ERPs at FCz (see Fig. 5), a negative component was observed that varied with the type of change,  $F(2,22) = 9.0$ ,  $\epsilon = 0.63$ ,  $P = 0.007$ . Largest amplitudes were observed for the conflict trials ( $-2.76 \mu\text{V}$ ) that differed reliably from luminance changes ( $-1.69 \mu\text{V}$ ),  $t(11) = 5.35$ ,  $P < 0.001$ , and marginally from those evoked by unilateral changes of both stimulus dimensions ( $-2.06 \mu\text{V}$ ),  $t(11) = 2.07$ ,  $P = 0.063$ . N2 amplitudes in the two conditions without a conflict differed marginally from each other,  $F(2,22) = 3.7$ ,  $P = 0.079$ , with slightly larger amplitudes when both dimensions changed at one location. Neither a main effect of saliency nor an interaction of condition by saliency was observed in these conditions ( $F$ 's  $< 1$ ). In the conflict trials, in which this component was measurable also as a distinct peak, the latency of the N2 decreased with increasing conflict,  $F(2,22) = 4.3$ ,  $\epsilon = 0.89$ ,  $P = 0.031$ , but amplitudes did not,  $F(2,22) = 0.7$ ,  $\epsilon = 0.80$ ,  $P > 0.2$ . Pair-wise comparisons of the N2 latency revealed that it appeared earlier for strong than for middle conflicts,  $t(11) = 2.22$ ,  $P = 0.049$ . The comparison of middle and weak conflicts did not become significant,  $t(11) = 0.82$ ,  $P > 0.2$ .

## DISCUSSION

In the current study, we examined the influence of the saliency of irrelevant information on competitive attentional

selection. Participants had to detect changes in the luminance of a rectangular bar (task-relevant stimulus) accompanied by changes in the orientation of the same bar or of the bar located at the contralateral side. The saliency of the orientation change was varied by using different length-to-width ratios of the bars. Behavioral results show that even though luminance was the only task-relevant feature of the stimuli, its detection was strongly influenced by the saliency of the orientation change, but only when luminance change and orientation changes were spatially separated. The saliency-based (bottom-up driven) processing of incoming information was reflected in posterior asymmetries in the N1 range. When orientation changes were presented in isolation, or when both luminance and orientation changed at one location in space, a well-defined asymmetric component was observed with a peak maximum around 180 ms that was modulated by saliency.

For orientation changes, the latency of the N1 asymmetry increased and its amplitude decreased with decreasing saliency of the orientation change. Such saliency dependent variations of the visual N1 have been previously reported and assigned to sensory evoked activity (Johannes et al. 1995). However,

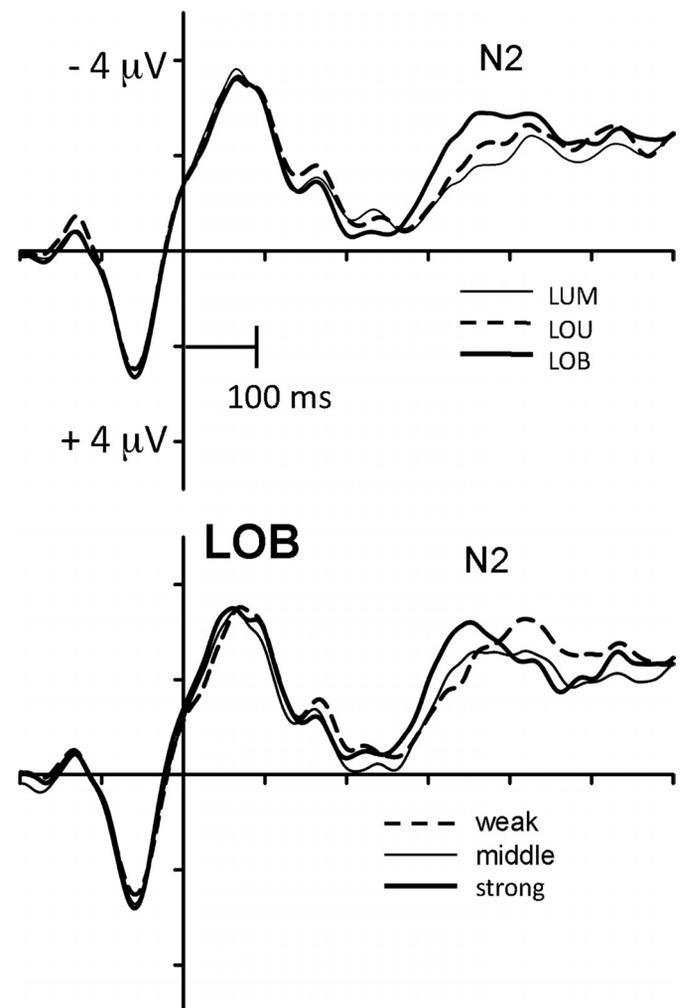


FIG. 5. Event-related potentials at FCz, referred to linked mastoids. Top: increased N2 amplitudes for trials in which the attended luminance change was accompanied by an orientation change. The largest amplitude was observed when these 2 signals were spatially separated (LOB). Within the latter condition (bottom), the N2 varied with the saliency of the distractor.

already in this early time window, activity can be controlled by top-down-driven attentional mechanisms (Hillyard et al. 1999; Johannes et al. 1995; Mangun 1995). In the present study, early top-down control might be reflected in the conflict condition when the orientation change was weak. In this condition, the N1 was attenuated or markedly delayed contralateral to the orientation change although the stimulation was bilateral. In contrast, when strong orientation changes were presented together with luminance changes, comparable N1 components were evoked over both hemispheres. Additionally, N1 amplitude varied less for orientation changes that were accompanied by a luminance change compared with single orientation changes, indicating an interaction of bottom-up saliency and target processing.

When luminance and orientation changed at opposite locations, the asymmetry in this early time window pointed either toward the location of the luminance change when the orientation change was weak or to the location of the orientation change when it was strong. This saliency-based distribution in the N1 range and the fronto-central N2 being largest in amplitude in the conflict condition indicated a perceptual conflict that was evoked by the confrontation of the two stimuli. This finding accords to the assumption that the fronto-central N2 may be a correlate of the degree of conflict, occurring under conditions of visual distraction (Azizian et al. 2006; Forster and Pavone 2008; Kehler et al. 2009).

Thus both behavioral and EEG data indicated that the impact of irrelevant distracting information was restricted to those trials in which this distracting information was spatially separated from the target stimulus. One might argue that the high error rates when luminance and orientation changes were presented simultaneously were due to an inability to discriminate one dimension from the other. However, orientation and luminance should per se be sufficiently different, and the luminance changes itself were huge (from almost black to almost white and reverse). Additionally, the amount of information that had to be processed was rather low (4 states that should be easily held in working memory). Finally, discrimination might be even harder when the two changes overlap in space. In this latter condition, however, error rates did not increase compared with single-feature changes. Thus the source of interference that led to these high error rates must be related to the spatial selection of relevant information. The occipito-parietal topography of the earliest EEG correlates of this interference (N1) additionally points toward a mechanism in visual areas. As pointed out in the INTRODUCTION, the differential sensitivity of blobs and interblobs for luminance and orientation changes (Clifford et al. 2003; De Valois et al. 2000; Johnson et al. 2008) and their proximity in the visual cortex (Lu and Roe 2008) may be the prerequisites for the strong competitive interaction between those two stimulus dimensions. Blobs and interblobs form a winner-take-all network via lateral reciprocal inhibitory connections (Itti and Koch 2000). This way, the saliency of the orientation change may modulate the firing of interblob columns. In case of the weak orientation change, the strength of blob-mediated processing may be higher than of interblobs-mediated processing, leading to a perceptual dominance of luminance changes. In case of increasing saliency, the influence of blob-mediated processing may be transiently suppressed by the processing of the orientation change within this network. The interference between

competing information might be amplified by the occurrence of a global transient evoked by multiple luminance changes in both hemifields due to the short blank (50 ms) between the two subsequent frames. The signal generated by this global transient might swamp the local motion signals that would normally draw attention to the location of the change (Rensink 2000) as it happens in change blindness paradigms.

Despite the fact that the processing of task-relevant information might have been disrupted in an initial processing stage, participants were able to perceive it far above chance level. Even if assumed that the interfering influence is transient, it is just attenuating but not canceling the processing of relevant information so that the system is able to reallocate attention to relevant information thereafter. In the EEG, such selection process of a target embedded in irrelevant information has been assigned to the N2pc. Based on studies examining visual search (Luck and Hillyard 1994b), the N2pc has been proposed to reflect filtering of irrelevant information and/or selection of relevant targets (Eimer 1996; Wolber and Wascher 2003, 2005). More recently, it has been nicely demonstrated that subcomponents of the N2pc might selectively reflect target and distracter processing (Hickey et al. 2009). With respect to the biased competition approach, extensive stimulus processing that controls for distracting information should only be necessary whenever the initial selection was insufficient to accomplish the task. This should be the case when an initial attempt to select the relevant item fails or when additional processing of the selected item (e.g., further discrimination) is necessary. Accordingly, in the present study, the N2pc is only observed in trials in which the asymmetry in the N1 range did not point toward the target element, namely those trials with strong or medium saliency of the irrelevant orientation change, indicating some functional similarity between asymmetries in the N1 and N2 range (see also Wascher and Beste 2009). Additionally, the increase of the frontocentral N2 indicated that increased cognitive control needs to be applied to obtain all relevant informations from a competitive display.

How can these results contribute to the discussion on the interplay of top-down and bottom-up controlled mechanisms in visual attention? The contingent capture theory of attention states that involuntary attentional capture is contingent on a salient event being featurally similar to a feature relevant to locate a target (Burnham 2007; Folk et al. 1992). However, some studies showed that also task-irrelevant singletons might capture attention when they are sufficiently salient (Remington et al. 1992; Schreij et al. 2008; Theeuwes 2004; Yantis 1993, 2005). The same contradiction can be found in ERP studies. While some studies report no N2pc for irrelevant distracters (Eimer and Kiss 2008; Hickey et al. 2008), others do (Hickey et al. 2006). Here a critical factor appears to be the design of the stimuli used (Lien et al. 2008). In those studies that report clear evidence for contingent capture, the irrelevant singleton was always presented in surrounding stimuli or was equiluminant to the background. In both cases, the contrast to the surrounding appears to be rather small. By already modulating sensory processing (Knudsen 2007), top-down control might be sufficient to suppress the irrelevant singleton in such stimulus arrangements. However, when the irrelevant stimulus is very salient, this control mechanism is prone to fail. The fact that strong irrelevant transients not only delayed response times, as would be expected when attention was only shortly

misguided, but led to huge error rates, indicate an early disruption of sensory processing.

In summary, we demonstrated basic mechanisms involved in spatial competitive selection and their neuronal implementation. We were able to show that it is possible to modulate perceptual competition by scaling the saliency of one stimulus in the bottom-up channel. Early, bottom-up-driven mechanisms were strongly determined by the saliency of the target element in relation to its surrounding. If the initial selection process was not capable to detect the task-relevant item, extended processing became necessary. It is noteworthy that not the existence of distracting information but its spatial separation from the target necessitated this step. Two processes seem to be evoked in such a situation: 1) the perceptual competition activates fronto-central instances of cognitive control (reflected in the fronto-central N2), most probably to allocate resources to resolve the conflict, and 2) an intention-based selection of the relevant target, reflected in the N2pc is initiated, which becomes only active when preceding processing mechanisms were not able to solve the task.

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