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Dimension-based attention modulates early visual processing

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Abstract

Target selection can be based on spatial or dimensional/featural mechanisms operating in a location-independent manner. We investigated whether dimension-based attention affects processing in early visual stages. Subjects searched for a singleton target among an 8-item array, with the search display preceded by an identical cue array with a dimensionally non-predictive, but spatially predictive singleton. Reaction times (RTs) were increased for changes in the target-defining dimension but not for featural changes within a dimension. This RT effect was mirrored by modulations of the P1 and anterior transition N2 (tN2). Current density reconstructions revealed increased activity in dorsal occipital cortex and decreased activity in left frontopolar cortex owing to repeated dimensional pop-out identities. These findings strengthen dimension-based theories of visual attention by indicating dimension-, rather than feature-, specific influences within the first 110 ms of visual processing.

Descriptors: Attention, EEG, P1, N2

Visual attention can be oriented to spatial locations without overt gaze shifts (Posner, 1980). Electrophysiologically, the covert orientation of spatial attention is reflected by early sensory evoked potentials (Eimer, 1994; Hillyard & Mangun, 1987; Mangun & Hillyard, 1988; Rugg, Milner, Lines, & Phalp, 1987), with the visual C1 component being the earliest marker (Kelly, Gomez-Ramirez, & Foxe, 2008). When observers are provided with prior information about the upcoming target location (e.g., by spatial pre-cueing), the amplitudes of the (visual C1 and the subsequent) P1 component are enhanced for targets occurring at the attended (as compared to unattended) location(s). Traditionally, P1 amplitude modulations have been taken to reflect a sensory 'gain control' mechanism that increases the signal gain at the attended location, thereby enhancing perceptual processing (Eimer, 1994; Hillyard, Vogel, & Luck, 1998; Luck, Woodman, & Vogel, 2000). More recently, however, it has been shown that attention can also be allocated to non-spatial features that define the target in a location-independent manner (Hopf, Boelmans, Schoenfeld, Luck, & Heinze, 2004; Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998). Moreover, feature-based attention has been found to influence early stages of processing, reflected in modulations of the visually evoked P1 (Han, Liu, Yund, & Woods, 2000; Mouchetant-Rostaing, Giard, Delpuech, Echallier, & Pernier, 2000; Taylor, 2002).

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Weighting of Visual Dimensions

Feature-based attention plays an important role in current theories of visual search, which assume that target-relevant feature information is encoded selectively in order to guide the allocation of focal attention to the target (Treisman & Sato, 1990; Wolfe, Cave, & Franzel, 1989). This emphasis on the *feature* specificity of attentional processes in the guidance of visual search has been challenged by Müller and colleagues (Found & Müller, 1996; Müller, Heller, & Ziegler, 1995), who instead proposed a *dimension*-based, or 'dimension-weighting,' account (DWA) of search guidance. This account assumes that target detection is influenced by a 'pre-attentive' mechanism of (spatially parallel) search guidance that modulates saliency coding by allocating limited 'selection weight' to the various dimensions that potentially define the target. Dimensions are assigned weight largely automatically, in bottom-up manner, with a larger weight allocated to the dimension defining the target on the current trial, implicitly 'predicting' that the next target will also be defined in this dimension. Thus, when the next target is indeed defined in this dimension, whether by the same or a different feature relative to the preceding target, target detection is expedited compared to when there is a dimension change (Found & Müller, 1996). Note that the absence of an effect of feature change/repetition within a repeated dimension is a strong criterion for the dimension specificity of this inter-trial 'priming' effect. Since this effect is observed when observers have no explicit knowledge of the target-defining dimension (Müller, Krummenacher, & Heller, 2004), it is mainly bottom-up driven. Interestingly, when the task requires observers to explicitly encode the target-defining dimension (or

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feature), the inter-trial effect is enhanced, suggesting that inter-trial priming is top-down modulable. To examine this possibility more directly, Müller, Reimann, and Krummenacher (2003) conducted a dimensional-cueing study in which the likely defining dimension of the upcoming target on a trial was pre-cued by symbolic (as well as direct) cues. The results revealed both a reliable cueing effect (i.e., faster reaction times [RTs] for valid compared to neutral and invalidly cued targets) and a modulation of the inter-trial effect by cue validity: the inter-trial effect was *reduced* on valid- and invalid-cue trials compared to neutral-cue trials. On valid-cue trials, this reduction was due to a reduced disadvantage for a change compared to a repetition of the target-defining dimension—due to observers being able to top-down set themselves to the new (cued) dimension in advance of target onset. That is, the dimensional set established by the end of a trial can be top-down adapted, at least to some extent, in response to the cue.[1]

Based on this evidence, the DWA assumes that one common 'attentional weight' resource is allocated to—and modulates the relative processing efficiency in—the various visual dimensions based on both bottom-up and top-down factors. This resource is 'attentional' in the sense that there is a limit to the total amount of weight available for allocation, so that, if the weight is increased for one dimension, it must be decreased for other dimensions. For this reason, the DWA is essentially an account of dimension '*weighting*,' rather than '*priming*' (passive priming is, in principle, cost-free).

Concerning the 'control' of the weight allocation, Pollmann, Weidner, Müller and von Cramon (2000), Pollmann, Weidner, Müller, Maertens, and von Cramon (2006), and Weidner, Pollman, Müller, and von Cramon (2002) have shown that the (re-) weighting of dimensions involves a whole fronto-posterior network of brain areas, including frontopolar and, respectively, fronto-median areas. Neuropsychological findings suggest that left frontopolar mechanisms are causally involved in dimension switching (e.g., Pollmann, Mahn, Reimann, Weidner, Tittgemeyer et al., 2007), though these mechanisms mediate only implicit switching processes; by contrast, fronto-median mechanisms come into play when weight switching requires more explicit, top-down control (Weidner at al., 2002). However, while the switch signals are likely to be generated by frontal brain mechanisms, the weighting itself modulates processing in posterior, dimension-specific brain areas. Thus, investigating cross-dimensional search for pop-out targets unpredictably defined by either color or motion, Pollmann et al. (2000, 2006) found increased activations in occipital areas depending on the dimensional identity of the target (V4 and, respectively, human MT; see also Schoenfeld, Hopf, Martinez, Mai, Sattler, et al., 2007). This pattern of hemodynamic activations is consistent with one fundamental postulate of the DWA, namely, that early (dimensionally organized) visual analyzer modules are modulated depending on the dimensional nature of the preceding target event. However, due to the sluggish nature of hemodynamic responses, imaging studies are inappropriate to further specify the time course of dimensional weighting mechanisms.

[1]These inter-trial effects demonstrated by Müller and colleagues are analogous to Maljkokic and Nakayama's (1994) demonstration of 'feature-based priming' in singleton search, except that they are dimension-specific in nature and subject to top-down modulation (Maljkovic & Nakayama characterized their feature-specific priming effect as being top-down impenetrable). Also, under comparable conditions, dimension-based effects are larger than feature-based effects (see Olivers & Meeter, 2006, for a systematic comparison).

Rationale of the Present Study

By means of event-related brain potentials, the present study was designed to test whether early visual processing can indeed be modulated dependent on the *dimensional* identity of the preceding sensory (pop-out) event. This was systematically assessed by introducing a visual search task in which the search display that contained the response-relevant target singleton was preceded by a response-irrelevant cue display, which also contained one singleton element (the cue) among the same number of homogeneous items. For instance, the cue could be an odd-colored (or an odd-shaped) item and the subsequent target singleton, to which observers had to respond, was also either a color (or a shape) singleton. Note that, although such cues are direct 'indicators' of the singleton dimension triggering an automatic dimensional orienting response, their effect is largely dimension-specific (Müller et al., 2003)[2] and may be top-down enhanced if the task requires the cues to be encoded explicitly (Müller et al., 2004). The latter was the case in the present study, because observers had to discern the dimension defining the target singleton in the subsequent target display. In addition, the (900-ms) SOA between the cue and target was so long that automatic-activation processes triggered by the cue would have largely subsided by the onset of the target display (see, e.g., Müller & Rabbitt, 1989). In the Experiment, the cue was non-predictive as to the defining dimension/feature of the upcoming target, but predictive as to its location. In order to capture dimension-based influences occurring at early sensory stages, we primarily focused on the P1 and N1 components. In addition, we expected the anterior transition N2 (tN2) to be modulated by the dimensional identity of the previous sensory event (Gramann, Töllner, Krummenacher, Eimer, & Müller, 2007), reflecting the control of dimensional weight setting (see also Pollmann et al., 2007).

To further specify the time course of dimensional weighting mechanism, the present investigation used a spatio-temporal coupled distributed source reconstruction algorithm (current density reconstruction, stCDR) (Darvas, Schmitt, Louis, Fuchs, Knoll, & Buchner, 2001) to reconstruct the cortical sources of activity associated with task-specific modulations of scalp potentials. In contrast to other reconstruction approaches (i.e., equivalent dipole reconstructions), this class of algorithms does not specify the number of active sources to explain the measured scalp potentials at any given time. This is an advantage when the exact number of underlying cortical sources is unknown and no complementary information is available from imaging methods (e.g., fMRI). Using the LORETA algorithm (Pascual-Marqui & Biscay-Lirio, 1993), this approach supports spatially smoothed solutions based on the assumption that the underlying patch of active cortex is spread over a certain cortical area rather than being a point source. This assumption is supported by highly correlated activity in neighboring neuronal populations (Haalman & Vaadia, 1997). In addition to the spatial filtering, we used the L2-Norm with temporal coupling (Darvas et al., 2001). Based on the physiologically plausible assumption that neural

[2]In more detail, Müller et al. (2003) found a dimension-specific cueing effect even when a specific target feature, such as 'red,' was directly pre-cued by a central red element (rather than a centrally verbal cue)—that is, in this case, even invalid color targets, say 'blue' ones, were detected more efficiently than equally unlikely targets defined in a different dimension.

activity develops over time, the temporal coupling acts as a filter preferring relatively smooth, rather than abrupt, changes in the time course of activity. Simulation studies demonstrated that the introduction of temporal constraints to existing CDRs leads to significant improvements in spatial and temporal accuracy due to the additional information provided by the time-dependent model constraint (smoothness in time) (Darvas et al., 2001). This advantage over non-coupled current density reconstructions was most pronounced in the case of noisy data because of the low-pass filter properties of the temporal coupling, but also in the ability to separate sources. However, as any other source reconstruction, the inverse solution is ill-posed and the results should be considered as an approximation of underlying cortical source locations, rather than an exact anatomical description of the contributing structures.

Method

Participants

Twelve observers took part in the Experiment (2 female; age range 21–25 years). All were right-handed, had normal or corrected-to-normal vision, and reported no history of neurological disorder. Observers were either paid or received course credit for participating. All observers provided written informed consent, and the experimental procedure was approved by the ethics committee of the Department of Psychology, University of Munich, in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). One participant had to be excluded from the analyses, due to excessive artifacts in the electroencephalogram (EEG) recordings.

Stimuli and Procedure

Observers were seated in a dimly lit experimental chamber. Stimuli were projected by a beamer (Sanyo PLC-XU47, Osaka, Japan), situated 60 cm above the observer's head, on a 150 cm $\times$ 150 cm white screen. The observer viewed the screen from a distance of 130 cm, with the centre of the display adjusted to the individual straight-ahead line of view.

Successively presented cue and target displays each consisted of a circular array of eight colored stimuli on a black background. The stimuli were equidistant (3.9° of visual angle) from a white fixation cross in the screen center (see Figure 1). Each stimulus array contained one singleton, which was equally likely defined in either the color or the shape dimension (*red* or *green* circle, of diameter 2.4°; blue *diamond* or *triangle*, 2.1° $\times$ 2.1° and, respectively, 2.8° $\times$ 3.2° in size), among seven identical distracters (blue circles, 2.4° in diameter). All stimuli were matched in luminance. The singleton could appear randomly at one of the six lateral array positions; however, its location was always the same in the cue and the subsequent target display. Observers were instructed to maintain central fixation throughout a trial and to indicate the dimension of the singleton *target*, using their left- or right-hand index finger to respond 'color' or 'shape,' respectively. The response buttons were positioned vertically aligned to avoid spatial stimulus-response compatibility effects. Half the observers started with the left index finger on the upper button and the right index finger on the lower button, and vice versa for the other half. For all observers, the response button assignment was reversed in the second half of the experiment.

One experimental session consisted of eighteen blocks of 72 trials each. A trial started with a white fixation cross for 500 ms, followed by the cue display for 200 ms. After a constant cue-target interval of 900 ms (during which only the fixation cross was visible), the target display was presented for 200 ms. The trial was terminated by the observer's response or after a maximum of 1000 ms. During the inter-trial interval, a black screen was shown for 1000 ms. The feature defining the singleton in the cue display (color: red or green; shape: diamond or triangle) was selected in pseudo-random order. With respect to the singleton feature in the cue display, the target display could contain (at the same position) a singleton defined by the same feature (same Dimension same Feature, sDsF), by a different feature in the same dimension (same Dimension different Feature, sDdF), or by a feature in a different dimension (different Dimension, dD), each with a probability of 1/3. On trials with targets defined in a different dimension, each of the two alternative features was equally likely.

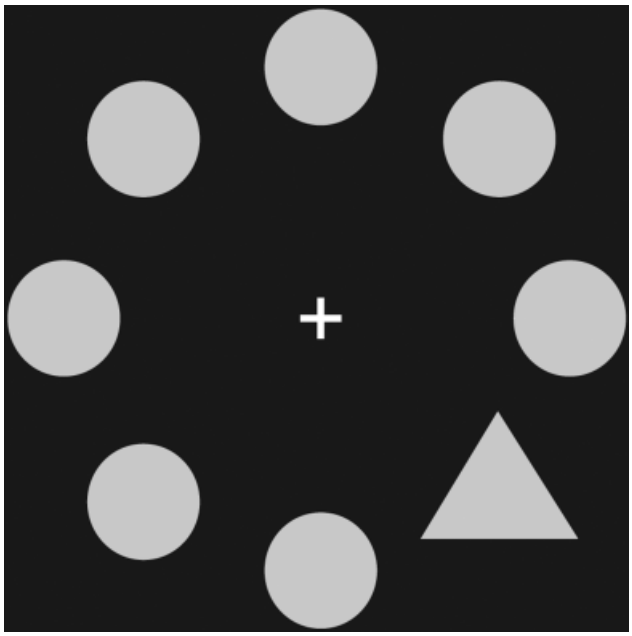

Figure 1. Example of the stimulus array used for the (preceding) cue and the (subsequent) target displays on a trial, with the singleton being defined in the shape dimension (the only triangle amongst circles). The arrays consisted of a circular arrangement of eight stimuli presented against a black background, with a white fixation cross in the center. Distractors were blue circles, and targets were defined in either the color (*red* or *green* circle) or the shape dimension (blue *triangle* or *diamond*). Participants were asked to discriminate the dimension of the singleton target as fast and accurately as possible.

EEG recording and data analysis. The EEG was recorded continuously, at a sampling rate of 500 Hz, using 64 Ag/AgCl electrodes, including those corresponding to the 10–10 system (American Electroencephalographic Society, 1994). The electrodes were mounted on an elastic cap (Easy Cap, Falk Minow Services, Munich, Germany). Horizontal and vertical eye movements were monitored by electrodes placed at the outer canthi of the eyes and the superior and inferior orbits, respectively. EEG signals were amplified using a 0.1–100-Hz bandpass filter via BrainAmps (BrainProducts, Munich, Germany) and filtered off-line using a 1–40-Hz bandpass (24 dB/Oct). All electrodes were referenced to Cz and re-referenced off-line to linked mastoids.

Event-related potentials (ERPs) were averaged off-line over an 800-ms epoch relative to a 200-ms pre-stimulus baseline. Eye movement artifacts were corrected for by means of independent component analyses (ICA) implemented in the Brain Vision Analyzer software (Brain Products).

Following the elimination of artifacts and trials with an incorrect response, the latencies of the P1, N1, and N2 components were determined individually as the maximum deflection within the respective time windows (P1: 80–140 ms; N1: 130–190 ms; N2: 230–300 ms) derived by visual inspection of the grand average potentials. Amplitudes were calculated using five sample points before and after the maximum peak deflection. Amplitudes and latencies of the P1 and N1 components were analyzed by repeated-measures analyses of variance (ANOVAs) with the factors cue-to-target 'Transition' (sDsF, sDdF, dD), target 'Dimension' (color, shape), target 'Side' (left, right), and 'Electrode Position' (left, right recording position) at electrode sites revealing the strongest effect of the experimental factor cue-to-target Transition (PO7 and PO8). Amplitudes and latencies of the anterior N2 component were analyzed using a repeated-measures ANOVA with the factors 'Transition' (sF, dF, dD), 'Electrode Site' (frontal, fronto-central, central), and 'Electrode Position' (left, midline, right). Since the present study was primarily designed to provide insight into the neural mechanisms underlying dimensional cueing effects, only the main effects and interactions involving the factor 'Transition' will be reported for the electrophysiological data. Whenever required, significant main effects and interactions were further examined using Tukey HSD post-hoc contrasts.

Spatio-temporal current density reconstruction (stCDR). A spatio-temporal coupled reconstruction algorithm (as implemented in the EaSI software package; Electro-anatomical Source Imaging, Brain Products), based on the LORETA algorithm (Pascual-Marqui & Biscay-Lirio, 1993), using a L2-Norm with temporal coupling (Darvas et al., 2001), was used for source reconstruction. Details of the models can be found in Darvas and colleagues (2001). To identify neural sources underlying dimension-specific P1 and tN2 effects, CDRs were based on separate averages for the three experimental conditions (sDsF, sDdF, dD) over the time window 0–400 ms relative to a -100 to 0-ms baseline. By computing source activity for the different experimental conditions in one combined computational step, activation strength of all data sets was standardized by the maximum source activation in one of the three conditions. In the second step, clusters of sources were identified using the clustering algorithm implemented in EaSI. Here, the strength of each source was computed and local maxima for each point in the respective time range were determined. This was followed by the computation of a matrix representing the distances between all maxima separately for each observer and data set. All sources located within a distance of 30 mm were combined into one cluster, yielding a mean location for the various clusters and mean source magnitude within a cluster taking into account the hemisphere of cluster location. Cluster locations were specified using the Talairach daemon (http://www.talairach.org), and the activations of all reconstructed clusters for the respective P1 and tN2 time ranges were subjected to repeated-measures ANOVAs with the factor cue-to-target Transition. Only clusters that exhibited a significant effect of this factor are reported in the Results.

Results

Behavioral Data

On 2.7% of all trials, observers reacted faster than 100 ms or slower than 1000 ms (sDsF 2.7%, sDdF 2.4%, and dD 2.9%). In addition, observers reacted incorrectly on 4.0% of all trials. The distribution of errors was shifted toward dD (different Dimension) trials, with 6.6% incorrect reactions as compared to 2.7% for sDsF (same Dimension same Feature) and 2.7% for sDdF (same Dimension different Feature) trials. A repeated-measures ANOVA with the factors 'Dimension' (color, shape) and 'Transition' (sDsF, sDdF, dD) revealed this difference to be significant [main effect of Transition, $F(2,20) = 7.09$, $p < .019$; $\eta^2 = 0.415$]. The two-way interaction was also significant [$F(2,20) = 4.41$, $p < .026$; $\eta^2 = 0.306$]: for validly cued dimensions, the percentages of errors were comparable between trials with and without a change in the target-defining feature (color: 2.7% and 2.6% for sDdF and sDsF; form: 2.7% and 2.8% for sDdF and sDsF). However, invalid-dimension cues were associated with significantly more errors when the target was defined by shape rather than color (5.4% vs. 7.8%).

RTs on correct trials were analyzed using the same ANOVA, which revealed only the main effect of Transition [$F(2,20) = 13.79$, $p < .001$; $\eta^2 = 0.580$] to be significant [main effect of Dimension: $F(2,20) = 2.91$, $p < .119$; $\eta^2 = 0.225$; interaction: $F(2,20) = 1.25$, $p < .31$; $\eta^2 = 0.111$]. Figure 2 presents the RTs dependent on the cue-target transition aggregated over color- and shape-defined targets. The pattern of cue-target transition effects replicates the pattern of inter-trial effects described by Found and Müller (1996): there was a significant RT cost for invalidly cued, relative to validly cued, dimensions (43.3-ms cost for dD vs. sDsF, $p < .001$, and 37.1-ms cost for dD vs. sDdF, $p < .003$), while there was no significant cost for invalidly cued, relative to validly cued, features within a dimension (6.3-ms cost for sDdF vs. sDsF, $p < .76$).

Electrophysiology

P1. The ANOVA of P1 amplitudes revealed a significant main effect of Transition [$F(2,20) = 8.94$, $p < 0.002$; $\eta^2 = 0.472$], with stronger P1 deflections when the target dimension was val-

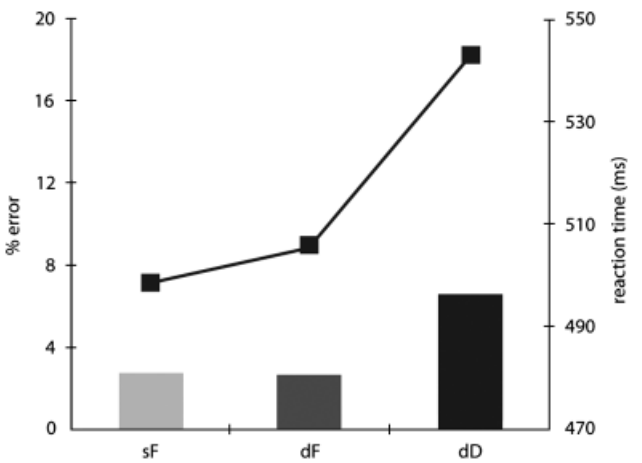

Figure 2. Mean reaction times (in milliseconds), and associated error rates (in percent), for target singletons, dependent on the identity of the singleton in the cue display: same dimension same feature (sF), same dimension different feature (dF), and different dimension (dD). Bars represent errors and the line reaction times.

idly cued (4.30 μV for sDsF and 4.23 μV for sDdF), rather than invalidly cued (3.97 μV for dD); this effect was strongest at electrode locations PO7 and PO8. The identical pattern of effects was observed for electrode pairs P3/P4 ($\eta^2 = .455$), P7/P8 ($\eta^2 = .293$), PO3/PO4 ($\eta^2 = .315$), and O1/O2 ($\eta^2 = .349$). With valid dimension cues, the P1 amplitudes were unaffected by whether or not there was a feature change between the cue and the target (post-hoc contrast sDdF vs. sDsF: $p < 0.70$). And invalid dimension cues led to less positive deflections compared to both valid-cue conditions (dD vs. sDsF: $p < 0.002$; dD vs. sDdF: $p < 0.012$). The interaction Target Side × Electrode Position was also significant [$F(1,10) = 11.69$, $p < 0.007$; $\eta^2 = 0.539$], with larger P1 amplitudes contralateral to the target hemifield (see Figure 3). After normalizing the data as suggested by McCarthy and Wood (1985), the interaction of Target Side × Electrode Position failed to reach significance [$F(1,10) = 1.03$, $p < 0.754$; $\eta^2 = 0.010$]. However, the absence of any interaction of the two factors Target Side and Electrode Location with the factor Transition [$F(2,20) = 0.004$, $p < 0.996$; $\eta^2 = 0.000$] underscores that P1 amplitudes were enhanced for dimensionally validly cued targets, irrespective of the hemifield in which the target was presented. No effects were revealed for P1 latencies.

N1. The identical analysis of N1 amplitudes revealed the main effects of Transition [$F(2,20) = 8.79$, $p < 0.002$; $\eta^2 = 0.468$] and Dimension [$F(1,10) = 6.007$, $p < 0.034$; $\eta^2 = 0.375$], as well as the interaction Target Side × Transition [$F(2,20) = 3.82$, $p < 0.039$; $\eta^2 = 0.276$] to be significant. Post-hoc contrasts revealed more pronounced N1 amplitudes for dimensionally invalidly cued targets as compared to validly cued targets (dD vs. sDsF: $p < 0.001$; dD vs. sDdF: $p < 0.04$), without an overall difference dependent on the featural validity of the cue (sDdF vs. sDsF: $p < 0.29$). The Target Side × Transition interaction was due to the fact that this dimension-specific pattern was observed only for targets in the left hemifield: N1 amplitudes were significantly more negative-going for invalid dimension cues ($ps < 0.03$ for dD vs. sDsF and dD vs. sDdF), with similar amplitudes for valid dimension cues irrespective of the featural validity of the cue (sDsF vs. sDdF: $p < 0.99$). In contrast, there was a more feature-specific pattern for targets in the right hemifield, with

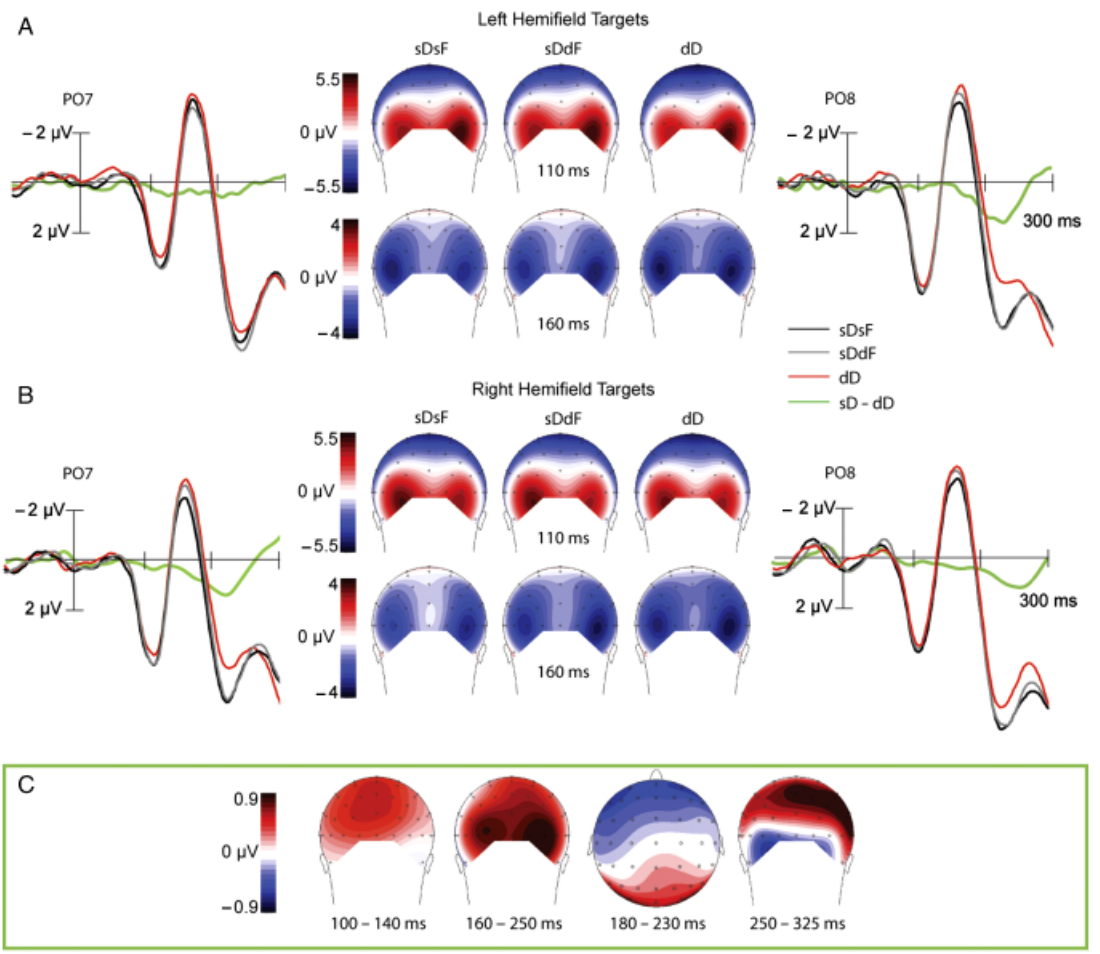

Figure 3. Grand-averaged ERP waveforms elicited over early visual areas at electrode positions PO7/PO8 contra- and ipsilateral to (A) left-hemifield targets and (B) right-hemifield targets in a 300-ms interval following stimulus onset. Black lines represent feature repetitions between the cue and target singletons (sDsF), dark gray lines intra-dimensional feature changes (sDdF), and red lines dimension changes (dD). The middle column displays scalp maps for the visual evoked P1 component (upper row) and the N1 component (lower row) for feature repetitions (sDsF), intra-dimensional feature changes (sDdF), and dimension changes (dD). (C) presents scalp maps for the difference waveform, computed by subtracting different-dimension (dD) from same-dimension trials (sD). Scalp maps are displayed for 4 distinct time windows, as described in Hillyard & Anllo-Vento, 1998, for comparison with the typical topography of the selection negativity (SN).

valid-dimension invalid-feature cues producing comparable N1 amplitudes to those for invalid-dimension cues (sDdF vs. dD: $p < 0.57$), but significantly more negative-going amplitudes than those for valid-dimension valid-feature cues (sDdF vs. sDsF: $p < 0.02$). Neither the Target Side × Electrode Position [$F(1,10) = 0.68$, $p < 0.800$; $\eta^2 = 0.007$] nor the Target Side × Electrode Position × Transition interaction [$F(2,20) = 2.65$, $p < 0.95$; $\eta^2 = 0.210$] reached significance. Analysis of N1 latencies revealed the four-way interaction to be significant [$F(2,20) = 4.09$, $p < 0.032$; $\eta^2 = 0.290$]. However, post-hoc contrasts did not substantiate any of the differences in onset latencies to be reliable.

N2. An ANOVA of the N2 amplitudes (see Figure 4) revealed the factor Transition to interact with both Electrode Site [$F(4,40) = 5.09$, $p < 0.002$; $\eta^2 = 0.337$] and Electrode Position [$F(4,40) = 3.87$, $p < 0.009$; $\eta^2 = 0.279$]. Both effects were replicated after normalizing the data before statistical analysis (p's < 0.003) (McCarthy & Wood, 1985). No other interactions involving the factor Transition reached significance; this was the case also after normalization (McCarthy & Wood, 1985). Post-hoc contrasts revealed reliable Transition effects at right frontal, midline, right fronto-central, and central electrodes. Importantly, these effects were purely dimension-specific ($p < .001$), with no difference between sDsF and sDdF conditions ($p < .531$). In summary, a change of the singleton-defining dimension was associated with enlarged tN2 amplitudes, with a slight right-lateralization largest over fronto-central electrode positions. An identical ANOVA for N2 latencies revealed a significant Transition × Electrode Site interaction [$F(4,40) = 4.47$, $p < 0.004$; $\eta^2 = 0.309$], due to prolonged latencies for dD conditions at frontal compared to fronto-central and central electrodes ($p < 0.038$).

Current density reconstruction. As N1 amplitudes were subject to higher-order interactions involving the factor Transition, source reconstruction was restricted to the P1 and N2 components. For the time window of the P1, differential activations for dimensionally validly and invalidly cued targets were revealed for clusters with centroids located in or near left lateral occipital cortex [BA18: $F(2,16) = 3.59$, $p < .050$; $\eta^2 = 0.310$], right lateral occipital cortex [BA18: $F(2,16) = 5.29$, $p < .017$; $\eta^2 = 0.398$], and the right cuneus [BA17: $F(2,10) = 6.16$, $p < .018$; $\eta^2 = 0.552$]. The bilateral middle occipital gyrus (BA 19) showed a strong tendency toward significance in both hemispheres, but failed to reach significance (BA 19 left, $p < .114$; $\eta^2 = 0.214$, and BA 19 right $p < .092$; $\eta^2 = 0.233$) (see Table 1).

For the time window of the tN2, clusters with centroids located in or near the left anterior cingulate cortex [BA 24: $F(2,20) = 12.26$, $p < .001$; $\eta^2 = 0.551$], left middle frontal gyrus [BA 10: $F(2,10) = 4.80$, $p < .035$; $\eta^2 = 0.490$], and the left frontopolar cortex [BA 9: $F(2,12) = 3.723$, $p < .055$; $\eta^2 = 0.383$] displayed dimension-based modulations. In the right hemisphere, the anterior cingulate cortex [BA 24: $F(2,16) = 7.53$, $p < .005$; $\eta^2 = 0.458$] and the right middle frontal gyrus [BA10: $F(2,10) = 4.50$, $p < .040$; $\eta^2 = 0.474$] revealed significantly increased activity for dimension change trials (see Figure 5).

In summary, for posterior (reconstructed) clusters, a similar pattern of activation was revealed: dimensionally validly cued targets were associated with increased activity as compared to invalidly cued targets, irrespective of the featural validity of the cue. In contrast, clusters located in or near prefrontal cortical

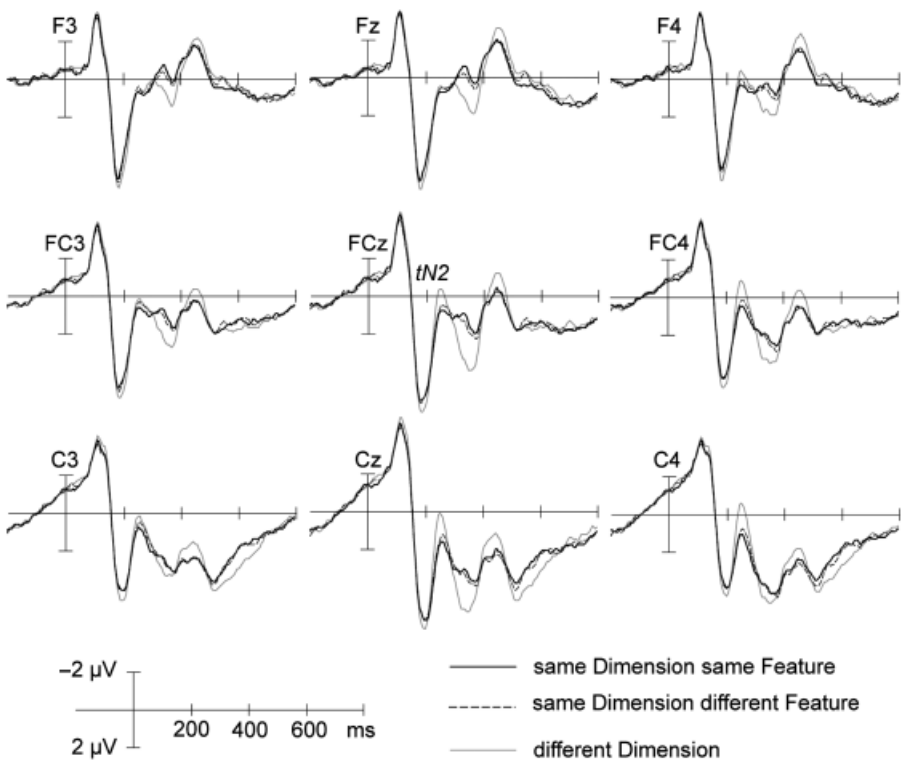

Figure 4. Grand-averaged ERP waveforms elicited over fronto-central electrode positions in the 500-ms interval following stimulus onset, relative to a 200-ms pre-stimulus baseline. Dark gray lines represent feature repetitions between the cue and target singleton (sF), dotted lines intra-dimensional feature changes (dF), and light gray lines dimension changes (dD).

Table 1. *Brain Areas Exhibiting Significant Effects of Visual Dimension Changes Based on stCDR*

Region	x	y	z	Brodmann area	partial eta^2	*N* subjects
P1 (80–140 ms)						
Left occipital lobe, cuneus	− 13	− 80	15	BA 18	0.310*	
Right occipital lobe, cuneus	10	− 90	6	BA 17	0.552*	
Right occipital lobe, cuneus	17	− 85	12	BA 18	0.398*	
N2 (240–300 ms)						
Left anterior cingulate	− 6	28	16	BA 24	0.551**	11/11
Left superior frontal gyrus	− 29	43	1	BA 10	0.490*	6/11
Left middle frontal gyrus	− 29	22	28	BA 9	0.383*	7/11
Right anterior cingulate	5	27	20	BA 24	0.458**	9/11

Note: Displayed coordinates (x, y, z) represent mean values averaged across observers. Effect sizes (partial eta^2 as estimated from repeated measures ANOVA for main effect of transition (sF, dF, dD). Significant effects are marked for values of $p<0.05$ and $p<0.01$ with * and **, respectively.

areas exhibited increased activity with dimensionally invalidly cued targets.

Discussion

The aim of the present study was to identify electro-cortical parameters associated with dimensional cueing effects. Behaviorally, such effects are manifest in faster RTs to targets defined in the same, as compared to a different, visual dimension as the cue. Here we show that, when the upcoming target location is indicated in advance, dimensional information has a significant influence on early visual evoked potentials.

As expected, the RT data confirmed previous findings (Müller et al., 2003) of faster reactions when the target single-

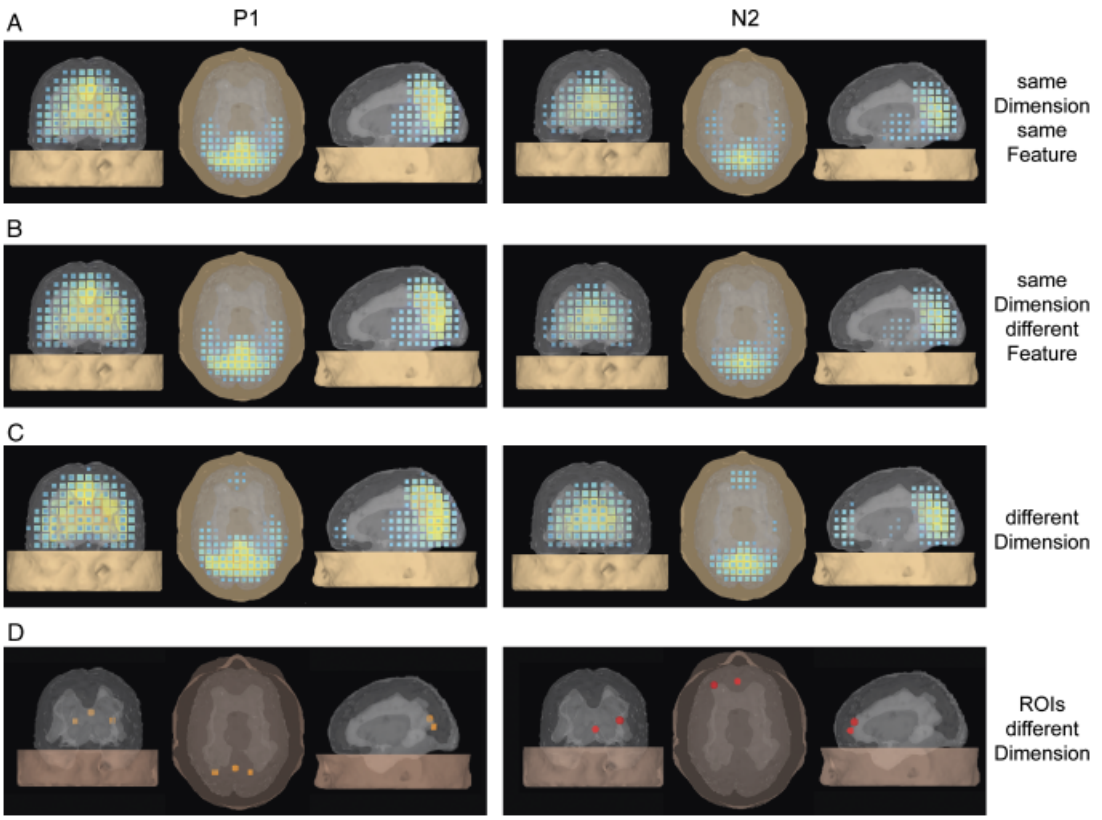

Figure 5. Spatio-temporal coupled current density reconstruction for same and different dimension trials. Left and right columns display current source activation for the visual P1 component and the tN2 component, for (A) same dimension same feature (sDsF), (B) same dimension different feature (sDdF), and (C) different dimension (dD) trials, respectively. Source activity was clipped to 30% of maximum source strength, displaying the strongest 70% of sources active during the reconstructed time period. Note that the source activity shown is based on grand average ERPs and does not represent single-subject reconstructions. Last row (D) displays regions revealing significant dimension-based modulations. Clusters are selected based on current density reconstruction for the time windows 80 to 140 ms for the P1 component and 240 to 300 ms for the tN2, respectively. Cluster centroids for the P1 were located in or near the left occipital (− 13, − 80, 15; BA 18) and the right occipital lobe (10, − 90, 6; BA 17 and 17, − 85, 12; BA 18). Cluster centroids based on source reconstruction for the tN2 were located in or near the left lateralized frontopolar cortex (− 29, 22, 28; BA 9) and the left anterior cingulate cortex (− 6, 28, 16; BA 24).

ton was defined in the same dimension as the preceding cue (e.g., color → color), compared to when the dimension changed (e.g., shape → color). Importantly, this same-dimension advantage was independent of whether or not the precise target feature within the repeated dimension matched that of the cue (e.g., red → red vs. red → green)—in other words, despite the cue consisting of a particular feature, its effect was dimension-specific in nature. This pattern points to a special role of visual dimensions in search guidance. Recall that, in the present experiment, the observer's task was not just to detect the presence of a target, but to respond to its defining dimension—so that one might ask whether the task requirements were responsible for the dimension-specificity of the effects. However, Found and Müller (1996) and Müller et al. (2004) had shown that such tasks produce essentially the same pattern of dimension-based inter-trial effects as a simple detection (target-absent/present) task or a task in which observers respond to the specific target-defining feature (see also Müller et al., 2003, who found a dimension-specific cueing effect even when a specific target feature, such as 'red,' was pre-cued). The latter finding is important, in that it shows that even when specific features are task-relevant, the effects are largely dependent on the broader target dimension. On this basis, it is unlikely that the present dimension-based RT effects were obtained simply because of the use of a dimension discrimination task.

Early Sensory Activations of Dimensional Cueing

With matching cue and target positions, P1 amplitudes were enhanced for targets defined in the *same* dimension as the cue, and this enhancement was independent of whether the target was defined by the same or a different feature relative to the cue. In accordance with dimension-based modulations of the P1 component, spatio-temporal coupled source reconstruction revealed effects of cue-target transition on source activity in or near primary and secondary visual areas. While targets defined in the cued dimension were associated with comparable source activity whether or not the target feature matched that of the cue, targets defined in a different dimension as the cue were associated with decreased activity in these same areas. This is in agreement with the assumption that visual information processing is enhanced in neural populations that process dimensionally attended information, and attenuated in areas that process unattended information—in line with the 'gain control' interpretation of the P1 (Luck et al., 2000). However, the absence of a baseline condition does not allow for a direct test of this hypothesis.

This pattern of effects is closely in line with the DWA, according to which dimensionally organized modules of visual analyzer units are (implicitly) weighted on a given ('cue') sensory event, thus expediting the emergence of the target's saliency signal at the level of the attention-guiding overall-saliency map on the next ('target') event. Enhanced P1 amplitudes might thus reflect the *correct weighting* of early visual input modules, facilitating the sensory coding of attributes singling out the target amongst nontargets. That is, when the cue appears in one dimension, say color, attentional weight resources are allocated to this dimension, thus enhancing the saliency of all kinds of singleton defined in the same dimension (whether or not they match the cue featurally). This weighting of cortical areas might be associated with a pre-activation of cortical columns, giving rise to enhanced activation when dimensional information fitting the weight set enters the visual system. Note that there was no explicit strategic reason to weight the color over the shape dimension or vice versa, since the cue predicted the upcoming target dimension only at chance level. This points to the largely implicit nature of the processes determining the allocation of attentional weight resources (see, e.g., Müller et al., 2004). Since the cue was 100% valid with respect to the target position, attention (originally summoned by the exogenous cue) would be endogenously maintained for the cued location (e.g., Müller & Rabbitt, 1989), which, by way of linked position and dimension expectancies (see, e.g., Kingstone, 1992; Töllner, Gramann, Müller, Kiss, & Eimer, 2008), would lead to enhanced P1 amplitudes for targets defined in validly cued dimensions. This suggests that the early visual system uses dimensional information in order to optimize target detection, which further underscores the implicit nature of dimensional weighting processes.

Note that, theoretically, this pattern of P1 amplitudes might have been the result of an underlying selection negativity (SN; e.g., Hillyard & Anllo-Vento, 1998). However, neither the time course nor the scalp topography of the difference wave ('attended targets' [sD] minus 'unattended targets' [dD]) show the typical negative process underlying the P1 and N1 components. In contrast to the typical SN waveform, the dimension-based modulation in the present investigation was characterized by an ongoing positivity in the difference wave lasting until approximately 270 ms post stimulus. A possible explanation for this may be that the experimental design fostered an SN-like process with onset of the cue stimulus; that is, dimension repetitions from cue to target display might have been accompanied by a priming of target discrimination in the cued dimension. This bias of selection toward a specific dimension might have lead to a relative positivity compatible with enhanced P1 amplitudes after target display onset. However, two points weaken this assumption. First, if some kind of selection negativity initiated with onset of the cue was the underlying factor for the observed P1 modulation, it should have been sensitive to not only dimensional, but also featural changes from cue to target display. This was clearly not the case in the present study. Second, any SN associated with onset of cue displays should be manifested in a negative shift for attended features, that is, valid dimension cues should have revealed a negative shift as compared to invalid cues in some time interval between cue and target display. Again, this was not the case.

Further support for a dimension-specific modulation of the P1 stems from a recent study by Schoenfeld and colleagues (2007), which reported dimensional selection to begin around 90 ms post-stimulus, based on combined electrophysiological, magneto-encephalographic, and hemodynamic measures of brain activity. In this study, observers were symbolically cued to attend to either the motion or color of an initially stationary array of gray dots and respond with a simple button press to one particular change in the cued dimension, but not in the non-cued dimension. Using a design broadly comparable to the present experiment, the authors noted the absence of any selection negativity. Even though several factors differed between the designs (symbolic dimension cues vs. direct feature cues, block-wise vs. trial-wise cueing, global-change targets vs. local singleton targets), essentially both studies required observers to tell apart the dimension of the target (Schoenfeld et al., 2007, p. 2475, refer to this as 'between-feature selection [motion vs. color]')—which stands in marked contrast to earlier studies that investigated the SN using intra-dimensional feature discrimination (Anllo-Vento, Luck, & Hillyard, 1998; Lange, Wijers, Mulder, & Mulder, 1998). This lends further support to the conclusion that the P1

modulation observed in the present study reflects dimension-, rather than feature-, based attentional processing.[3]

A somewhat different pattern of amplitude modulations was observed for the N1 component. The amplitudes of the N1 were comparable for left hemifield targets pre-cued by valid-dimension cues (irrespective of whether or not the cued feature was valid), which were less pronounced than those for targets preceded by invalid-dimension cues (dimension-specific effect pattern); in contrast, for right hemifield targets, enhanced negative amplitudes were evident not only for invalid-dimension cues, but also for valid-dimension invalid-feature cues, with less marked amplitudes only for valid-dimension valid-feature cues (feature-specific pattern). This hemispheric difference may be indicative of distinct roles of left and right visual areas in the attentional processing of target attributes. Previous studies of spatial attention have demonstrated an N1 modulation reflecting facilitated processing of targets that appear at the attended location (Luck, 1995; Mangun, 1995). While the design of the Experiment does not allow for any direct comparison of stimuli at attended versus unattended locations, these findings support the idea that the visual evoked N1 reflects the operation of a discriminative mechanism at attended locations (Hopf, Vogel, Woodman, Heinze, & Luck, 2002; Vogel & Luck, 2000). Importantly, hemispheric differences seem to play a significant role in the type of discrimination (dimension- vs. feature-based) involved.

Other studies investigating hemispheric differences underlying the processing of hierarchically organized patterns (Lamb, Robertson, & Knight, 1990; Robertson, Lamb, & Knight, 1988) demonstrated that the processing of global aspects of a pattern is more pronounced within the right posterior superior temporal (PST) area while the left PST is dominantly associated with processing of local aspects. With respect to the observed asymmetry in N1 amplitudes, this account might explain the observed hemispheric differences in N1-deflections: increased negative deflections over the left posterior cortex for invalidly cued dimensions would reflect the necessary discrimination process, i.e., the local processing of target identity, while increased negative deflections over the right posterior cortex would reflect the global aspect of attentional processing, i.e., the processing of an overall change from cue to target display (within or across dimensions). The advantage of such a hemispheric specialization would "provide a means for local and global levels of structure to be processed in parallel . . ." (Lamb, Robertson, & Knight, 1990).

Prefrontal Activations of Dimensional Cueing

Besides the dimension-based modulations of P1-amplitudes, dimensional cueing was found to further influence the amplitude of the transition N2, with the strongest modulation observed over fronto-central electrode positions. This tN2 effect occurred irrespective of intra-dimensional feature changes/repetitions of the target relative to the cue—demonstrating that the enlarged amplitudes of the tN2 originate from processes purely related to the (change in the) dimensional identity of the target relative to the cue, similar to the visual P1 component. The tN2 pattern observed in the present study replicates that described by Gramann et al. (2007), suggesting that similar processes are associated with visual dimension weighting in cross-dimensional cueing as well as in cross-dimensional search tasks. That is, a change of the singleton-defining dimension from the cue to the target display (but not a change in the defining feature within a repeated dimension) was reflected in enhanced amplitudes, with a slight right-lateralization largest over fronto-central electrode positions.

The topography of the tN2 points to generators in or near the anterior cingulate and/or the anterior frontal cortex (see Figure 5), and its latency corresponds to negative components accompanying perceptual mismatch, cognitive conflict, and response inhibition (Kiefer, Marzinzik, Weisbrod, Scherg, & Spitzer, 1998; Pritchard, Shappell, & Brandt, 1991; Wang, Cui, Wang, Tian, & Zhang, 2004). This systematic pattern of N2 effects provides further evidence for a role of frontal processes in the shifting of limited attentional ('weight') resources from the old, cue-defining to the new, target-defining dimension.

The results of our current density reconstruction are in line with previous fMRI studies of dimension weighting (Pollmann et al., 2000, 2006). Stronger source activations were evident for conditions in which the critical visual dimension was changed, a pattern that mirrors the amplitude variation observed for the tN2 component. Pollmann and colleagues demonstrated that activation in left lateral frontopolar cortex is associated with stimulus-driven dimension changes (Pollmann et al., 2000) and that patients with lesion in this brain area show increased reaction times for dimension change trials as compared to healthy controls (Pollmann et al., 2007). In contrast, top-down controlled dimension changes in singleton conjunction search was shown to be accompanied by increased activity in pregenual paracingulate cortex (Weidner et al., 2002). The present investigation revealed dimension-based modulation of activity in brain areas that closely match the results reported by Pollmann and colleagues. Both sources in or near the left lateralized frontopolar and anterior cingulate cortex demonstrated increased activity for targets defined in invalidly cued dimensions, but no differences in activation for targets in validly cued dimensions (irrespective of the featural validity). The fact that both anterior sources demonstrated the same dimension-based modulation can be explained by the cueing paradigm used in the present study: stimulus-driven changes from the cue to target display would parallel increased frontopolar activity in singleton feature search, while increased activity in anterior cingulate cortex might reflect top-down processes accompanying cue-related attention. However, due to the low spatial resolution of any EEG-based source reconstruction, the present results have to be considered tentative until complementary evidence from imaging studies is available.

Conclusion

In summary, the present—ERP and source reconstruction—findings provide further evidence for the existence of dimension-specific weighting mechanisms as proposed by the DWA. The close resemblance of the source locations revealed in the present study with the results of fMRI studies (Pollmann et al., 2000, 2006; Weidner et al., 2002) supports the proposal that left frontopolar and anterior cingulate regions play a critical role in dimensional weight setting that modulates sensory coding of (non-spatial) stimulus attributes in dorsal occipital regions. Our results suggest that the tN2 is likely to reflect the detection of a change in the target-defining dimension and the initiation of

[3]This is in line with Schoenfeld et al. (2007), who concluded: "When a color feature is to be selected from another feature such as motion, the enhanced processing in V4v begins very early (90–110 ms), whereas if one color is to be selected from another color the enhancement begins somewhat later (130–180 ms). . . . A similar finding was obtained for selection of motion information in area hMT" (p. 2476).

a corresponding weight shifting (Gramann et al., 2007). Most importantly, coding of targets defined in a correctly weighted dimension (and appearing at an attended location) is associated with increased P1 amplitudes, demonstrating dimension-based gain modulations to accompany spatial-attentional modulations within the first 110 ms of visual processing.

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