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The timing of feature-based attentional effects during object perception

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ABSTRACT

Allocating attention to basic features such as colour enhances perception of the respective features throughout the visual field. We have previously shown that feature-based attention also plays a role for more complex features required for object perception. To investigate at which level object perception is modulated by feature-based attention we recorded high-density event-related potentials (ERPs). Participants detected contour-defined objects or motion, and were informed to expect each feature dimension. Participants perceived contour-defined objects and motion better when they expected the congruent feature. This is consistent with modulation of the P1 when attending to lower-level features. For contours, modulation occurred at 290 ms, first at frontal electrodes and then at posterior sites, associated with sources in ventral visual areas accompanied by greater signal strength. This pattern of results is consistent with what has been observed in response to illusory contours. Our data provide novel insights into the contribution of feature-based attention to object perception that are associated with higher tier brain areas.

1. Introduction

Every waking moment we are confronted with a complex visual world, cluttered with an overwhelming amount of objects. To examine this world for relevant objects we can use various forms of information to guide attention to some part of the world. For example, we can use spatial information to allocate our attention to where an object of interest will likely appear. This will result in faster and more accurate processing of stimuli within that area (Bundesen, 1990; Posner, Snyder, & Davidson, 1980; Treisman & Gelade, 1980). Or we can use non-spatial information to cue attention to a certain feature dimension (e.g., colour as opposed to motion) or to a particular feature value (e.g., red as opposed to blue).

Central to feature-based attention is that it enhances processing of similar features regardless of their location and independent of the spatial focus of attention (Andersen, Müller, & Hillyard, 2009; Andersen, Fuchs, & Müller, 2011; Martinez Trujillo & Treue, 2004; Maunsell & Cook, 2002; Maunsell & Treue, 2006; Zhang & Luck, 2009). This can be seen behaviourally; participants are more successful in dividing their attention across spatially separate stimuli that share a common feature (e.g., same direction of motion) compared to opposing features (different motion direction; Saenz, Buracas, & Boynton, 2003) or entirely different feature dimensions (orientation vs. colour; Found & Müller, 1996; Schubö & Müller, 2009). It can also be seen in functional imaging where feature-based attention to motion appears to be associated with increased activity in motion sensitive areas for ignored stimuli given that the same motion direction is attended elsewhere (Saenz, Buracas, & Boynton, 2002). Also, neurophysiological data from monkeys suggest that neurons selective for a certain feature will increase their activity when attention is allocated to the same feature outside the neuron's receptive field (Martinez Trujillo & Treue, 2004; Motter, 1994; Reynolds & Desimone, 2003; Treue & Martinez-Trujillo, 1999). Finally, electrophysiological data show anticipatory as well as stimulus-related modulations due to feature-based attention. For example, Snyder and Foxe (2010) cued participants to motion or colour and observed modulations in alpha-band oscillations while the participants anticipated coloured or moving stimuli. Several labs have investigated electrophysiological responses to stimuli carrying attended and unattended visual features (Anllo-Vento & Hillyard, 1996; Eimer, 1995; Gramann, Töllner, Krummenacher, Eimer, & Müller, 2007; Hillyard & Münte, 1984; Töllner, Gramann, Muller, Kiss, & Eimer, 2008; Zhang & Luck, 2009). Importantly, Zhang and Luck (2009) asked participants to direct their attention to a stimulus with a particular colour and then presented another stimulus elsewhere that either had the same colour or a different colour. When it had the same colour it yielded a stronger P1 than when it did not. The authors took this

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as evidence for an early feedforward influence of feature-based attention on stimulus processing within the visual stream.

Most of the research on feature-based attention has focused on lower level feature dimensions that are processed by early visual areas, such as colour, orientation, direction of motion. However, we have recently shown that feature-based attention to complex features also modulates performance in tasks requiring object processing (Stojanoski & Niemeier, 2007). Specifically, we looked at perception of objects defined by line segments that require completion of their contour.

Before describing our previous study it should be pointed out that the visual system is equipped with special circuits to process object contours (Hess & Field, 1999). Though these contour integration mechanisms implicate a number of low and high visual areas (Kourtzi, Tolias, Altmann, Augath, & Logothetis, 2003), it appears the lateral occipital complex (LOC), an area involved in object perception (Malach et al., 1995), makes a key contribution to contour integration. For example, a series of fMRI/ERP studies using Kanisza figures showed that for stimuli presented foveally earliest contour related activity was reflected in a more pronounced N1 roughly 90 ms after stimulus onset associated with the LOC, and for stimuli presented laterally contour related activity resulted in a more pronounced positivity after the P2, 200–220 ms after stimulus onset (Murray et al., 2002; Murray, Foxe, Javitt, & Foxe, 2004). These data support the idea that contour-sensitive neural responses in lower-tier visual areas arise through recurrent processes controlled by higher visual areas (Lamme & Roelfsema, 2000). In this context, the role of higher visual areas such as the LOC has been interpreted in different ways. Stanley and Rubin (2003) suggested that the LOC performs filling in of the object's surface which then leads to the integration of the surrounding contour as a next step. Shpaner, Murray and Foxe (2009), however, have challenged this view providing evidence that contour processes associated with the LOC precede surface processing in the LOC. Finally, the LOC or similar high level visual areas might support contour integration by conveying object knowledge (Zemel, Behrmann, Mozer, & Bavelier, 2002). Despite these three studies being very different in their methods and claims, they agree in demonstrating the significance of object processing mechanisms for the perception of contours.

In an attempt to target these mechanisms of contour integration through feature-based attention, in our previous study we used a dual-task paradigm (Stojanoski & Niemeier, 2007) in which we engaged our participants' spatial and feature-based attention in a primary task that required them to detect contour-defined objects or motion stimuli. Concurrently we used a secondary task that tested how the participants perceived contours or motion outside their focus of attention in the opposite visual hemifield. We found that people were better at perceiving unattended (or less attended) contours when their attention was focused on detecting other contour-defined objects as opposed to when focusing on motion stimuli. We argued that these attentional effects involve higher level mechanisms of object perception in the LOC or similar areas. This is consistent with evidence that higher visual areas are significantly modulated by attention in monkeys (Chelazzi, Miller, Duncan, & Desimone, 1993; Maunsell & Cook, 2002) as well as humans (Lueschow et al., 2004; Niemeier, Goltz, Kuchinad, Tweed, & Vilis, 2005; O'Craven, Downing, & Kanwisher, 1999; Tallon-Baudry, Bertrand, Henaff, Isnard, & Fischer, 2005).

To confirm that indeed later, putatively higher level, visual mechanisms mediate the perceptual effects of feature-based attention on contours, in the present study we investigated the timing of these attentional effects using high density ERP recordings while probing perception of contour-defined objects when participants expected them as opposed to when they expected motion (Fig. 1). We predicted that when contours are expected they might modulate the same object processing mechanisms as those sensitive to the illusory contours of Kanisza figures (Murray et al., 2002). In particular, expected contours might yield a more pronounced positivity at posterior electrodes arising after the P2.

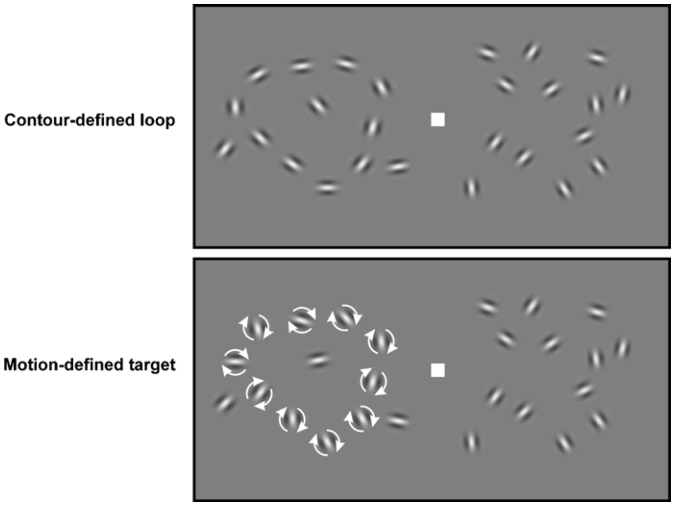

Fig. 1. Experimental stimuli. Participants were asked to view two arrays of gabors left and right of a fixation square and to guess which of them contained the target stimulus, i.e., a contour-defined or a motion defined loop. Contour-defined targets were formed by 10 roughly collinear gabors. Motion targets were formed by 10 gabors that were randomly oriented and revolved around their individual centres. To generate the motion every stimulus was displayed as a short movie with four video frames ($\sim$18.75 ms each). Two conditions were presented in a block design. At the onset of the contour block, participants were informed that a contour-defined loop was likely to appear with 80% validity, with motion target appearing the other 20%. The opposite was true for the motion block. The target object was equally likely to appear on the left or right visual field. In a two-alternative forced choice task, participants indicated whether the target appeared on the left or right side.

Alternatively, attention to contours might already involve earlier mechanisms associated with striate or extrastriate areas. For example, contour extraction linking contour segments constrained by position and orientation might work through lateral connectivity (Field, Hayes, & Hess, 1993). If this were the mechanism subserving effects of feature-based attention we would expect attentional effects to arise before the N1 (Hillyard, Vogel, & Luck, 1998).

2. Methods

2.1. Participants

Twenty-five (11 female) neurologically normal undergraduate introductory psychology students, (17–24 years, mean: 20.1 ± 2) participated in our study. All participants gave their informed and written consent prior to their inclusion in the study and were either paid or obtained course credit. All procedures were approved by the Human Participants Review Sub-Committee of the University of Toronto and have therefore been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All participants were healthy, had normal or corrected to normal vision, and most were right handed (4 left-handers) as confirmed with the Edinburgh handedness inventory (Oldfield, 1971).

2.2. Apparatus

Participants were tested in a dimly lit sound-proof room, seated 100 cm away from the monitor. Stimuli were presented on a 19-in. monitor (Viewsonic) at a refresh rate of 100 Hz and an average luminance of 26.8 cd/m^2. We implemented our experiment using Matlab (Math-Works) with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

2.3. Stimuli and procedure

For the present study we adopted a paradigm that we had previously developed to probe feature-based attention outside the spatial focus of attention (Stojanoski & Niemeier, 2007). Different from the original paradigm, here we abandoned the dual task and the rapid serial visual presentation. The limitation of that paradigm was that it required extensive training across several weeks and therefore was not feasible for an EEG experiment that required a large number of participants.

In this experiment each trial began with a fixation point (0.7° by 0.7°) presented in the centre of the screen that participants were instructed to fixate throughout the trial. Five hundred to 1000 ms later two windows subtending 6.8° by 6.8° appeared 5.1° left and right of fixation for 100 ms. Each of them contained scattered arrays of 13 luminance-defined gabors (spatial frequency: 2.1 cycles per degree, standard deviation: 0.2°) and in one of the arrays (with an equal probability of appearing on the left or the right), 10 of the gabors formed the target stimulus that participants were asked to find. The target stimulus was always an irregularly shaped loop randomly selected from a set of 100 loops (Stojanoski & Niemeier, 2007), and it was presented in one of two ways. One type was contour-defined loops that were formed by a closed chain of gabors (Fig. 1). These gabor were set to have, on average, 77.5% collinearity to make them somewhat difficult to see. That is, their orientation jittered by a random amount away from a tangential orientation relative to the imaginary outline of the loop. One hundred percent collinearity would mean no jitter, 77.5% would mean ±20.25 deg jitter, and 0% collinearity ±90 deg. We used this maximum amount of jitter for the second type of target stimulus to make the contours of these loops essentially impossible to see (Stojanoski & Niemeier, 2007, Experiment 2).

This stimulus was a motion stimulus. That is, the 10 gabors briefly rotated around their own centre (on average 63 deg/s for 100 ms; Fig. 1). Thus contour stimuli and motion stimuli occupied the same spatial area but differed in terms of the feature by which they were defined. Note that because stimuli were somewhat difficult to see they did not ‘pop-out’ unlike what has been shown, e.g., for Kanizsa figures with perfectly collinear inducers (Senkowski, Röttger, Grimm, Foxe, & Herrmann, 2005).

To examine how these stimuli were perceived when attention was cued to the congruent feature or the incongruent feature we informed participants before each block of 66 trials which feature would appear more frequently. In contour blocks, contour-defined loops would appear 80% of the time and motion would appear 20% of the time, whereas in motion blocks the percentages were reversed. This way, the entire block of trials served as a cue, because we were not sure whether cueing feature-based attention to contours might be somewhat inflexible, making it difficult to switch between motion and contours from one trial to the next. The advantage of cueing in a blocked design has been established by the dimension-weighting account (Found & Müller, 1996). Despite this departure from more common paradigms where each trial begins with an attentional cue, the present paradigm is conceptually similar in that participants are provided with the same kind of information at the beginning of each trial. For this reason we will refer to trials that carry the “80% feature” as “valid trials” and trials that carry the “20% feature” as “invalid trials”.

Five hundred to 1000 ms after stimulus presentation a grey response screen with the letters “R” (right side) and “L” (left side) above and below fixation, and participants clicked on one letter depending on the side on which they believed to have seen the loop. After each response there was a 500 ms intertrial interval.

Participants first completed a pretest version of the experiment in order to familiarize themselves with the task. Participants returned one to seven days later to complete the experimental session while we recorded ERPs. Both test sessions were identical, with the pretest session testing 4 blocks and the experimental session testing 12 or 16 blocks; contour and motion blocks were counterbalanced across participants.

2.4. *EEG data acquisition*

Continuous high-density electroencephalogram (EEG) was recorded using ASA (ANT B.V. Enschede, the Netherlands) from 64 sintered Ag/AgCl scalp electrodes mounted in an elastic cap utilizing the international 10-5 electrode system (Waveguard, ANT and ElectrodeArrays). On-line we used the left mastoid as a reference and re-referenced off-line to the average of both mastoids. Electrode AFz served as ground. Electrode impedances were kept below 5 kΩ. Eye movements were monitored with horizontal and vertical electro-oculograms. The EEG was amplified with an ANT high-density amplifier (22 bit, 71.5 nV/bit) at a sampling rate of 512 Hz. The data were bandpass filtered offline between 0.1 and 100 Hz. Trials with eye blinks and eye movements (>30 μV) were rejected offline based on the HEOG and VEOG (on average 15.04% of the trials were rejected). Trials were also removed based on an artifact rejection criterion of ±30 μV applied to all other electrodes.

2.5. *ERP analysis*

Epochs ranged from −100 to 600 ms relative to stimulus onset, with the prestimulus period serving as baseline. EEG data were then averaged across all trials for validly and invalidly cued contours and motion, separately.

To examine the resulting ERPs we first calculated successive pointwise paired *t*-*tests* (from −100 to 600 ms across all electrode sites) to compare validly and invalidly cued contours (and then for valid and invalid motion). However, only clusters of 11 or more consecutive time frames where $p < 0.05$ were deemed significant (Guthrie & Buchwald, 1991). We used these results as one guide to define time windows for subsequent analysis.

As a second analysis we performed a brain electric field analysis using Cartool to obtain unbiased criteria to segment the data into components based on a cluster analysis of electric field distributions across time (Brunet, Functional Brain Mapping Laboratory, http://brainmapping.unige.ch/cartool.php). The analysis is designed to segment ERP data into periods of relatively stable activity, called microstates. The analysis is appropriate for ERP data because brain electric field configurations often change abruptly and remain stable for relatively long stretches of time reflecting stable functional brain states. After concatenating all conditions across all time points (from −100 pre- to 600 ms post-stimulus), a *k*-means cluster analysis used linear correlations between electric field distributions at individual time points to sort the data into a subset of temporal clusters, also called maps of electrical activity. The number of maps was based on two competing criteria (Murray, Brunet, & Michel, 2008) that would (a) find the smallest amount of clusters that would (b) explain a maximum of the variance in the data. Therefore, we used a cross-validation criterion (the ratio between the global explained variance and the degrees of freedom, given the set of maps; Pascual-Marqui, Michel, & Lehmann, 1995) and a modified Krzanowski-Lai criterion (a dispersion measure of the quality of the clusters that is based on the pair-wise distance of all topographies included in a given cluster; Krzanowski & Lai, 1985). Following the results of the initial phase of the cluster analysis (grouping disparate maps), the second phase of the sequentialization process re-merged similar maps that were temporally dissociated. That is, highly correlated maps (segments) were merged together across conditions, with the requirement that each map be at least 10 ms long. The resulting sequences of maps in each group-averaged condition were statistically tested by back projecting the topography of each map onto the individual participants' ERP data. This way each time point was labeled by one of the maps based on spatial correlations (Brandeis, Lehmann, Michel, & Mingrone, 1995), and provides a measure of which maps best represent each condition (Murray, Imber, Javitt, & Foxe, 2006). Finally, we ran a topographic analysis of variance (TANOVA), a non-parametric statistical test using the global dissimilarity measure as the dependent measure between two maps at every time point (Lehmann & Skrandies, 1980).

The advantage of the topographic cluster analysis and subsequent TANOVA is that it avoids issues related to experimenter biases in that it preselects time windows for analysis (Foxe, Murray, & Javitt, 2005; Murray et al., 2004, 2006). Further, its independence of referencing avoids differential findings based on the selection of reference electrodes, and is insensitive to absolute changes in amplitude (Murray et al., 2008).

Our third analysis computed the global field power (GFP) for each subject, condition and time point as another way of isolating changes in the electric field. Specifically, GFP analysis computes standard deviation as a measure of the scalp electric field strength at a given time (Murray et al., 2008). Therefore, it can be used to estimate the differences in the electric field strength of the signal between conditions (Lehmann & Skrandies, 1980). GFP analysis complements the topographic analysis in that modulations in GFP can occur regardless of whether the electric scalp topography is the same or different. That is, two experimental conditions having the same electric topography might still differ in their GFP which would then suggest that the conditions activated the same neural generators to different degrees (for further details see Murray et al., 2008). To look at such differences we subjected the GFP data to a successive *t*-tests analysis.

In our final set of analyses, we performed repeated measures ANOVAs with factors Condition (valid vs. invalid cue), Hemisphere (Left vs. right), and Scalp region (averaged over each hemisphere—Occipital: PO8/PO7, PO6/PO5, PO4/PO3, O2/O1, Central: TP8/TP7, CP6/CP5, CP4/CP3, CP2/Cp1, P8/P7, P6/P5, P4/P3, P2/P1, Posterior frontal: FT8/FT7, FC6/FC5, FC4/FC3, FC2/FC1, T8/T7, C6/C5, C4/C3, C2/C1, Anterior frontal: FP2/FP1, AF8/AF7, AF4/AF3, F8/F7, F6/F5, F4/F3, F2/F1; following guidelines from Dien & Santuzzi, 2005). For each ANOVA, the dependent variable was the ERP amplitude averaged across each scalp region and specific time windows. These were selected based on the results of the successive *t*-tests, cluster analysis, and GFP analysis as well as previous findings on contour integration (see Section 3 for details). Finally, source localization analysis of the validly cued contour and motion conditions were computed using standardized Low Resolution Electromagnetic Tomography (sLORETA), with a weighting factor calculated using lead field normalization (source weighted LORETA; Palmero-Soler, Dolan, Hadamschek, & Tass, 2007; Pascual-Marqui, Esslen, Kochi, & Lehmann, 2002), using ASA (ANT B.V. Enschede, the Netherlands). This procedure infers the neural generators by relying on standardized current density estimates, despite its low resolution (Pascual-Marqui et al., 2002). To account for the noise in the signal and to avoid underestimating deep cortical sources, we applied swLORETA normalization which produces a smaller localization error for deep noisy sources. The solution space was calculated on a head model based on magnetic resonance images of 305 participants from the Montreal Neurological Institute. The results of the topographic pattern analysis, GFP and the cluster plots of successive *t*-tests defined time windows of interest.

3. Results

3.1. *Behavioural results*

A repeated measures ANOVA with factors Stimulus (contours vs. motion) and Cueing (valid vs. invalid cues) found a significant main effect of Cueing ($F_{(1,25)} = 8.03$; $p = 0.009$, $\eta p^2 = 0.243$), suggesting that participants more accurately perceived contours

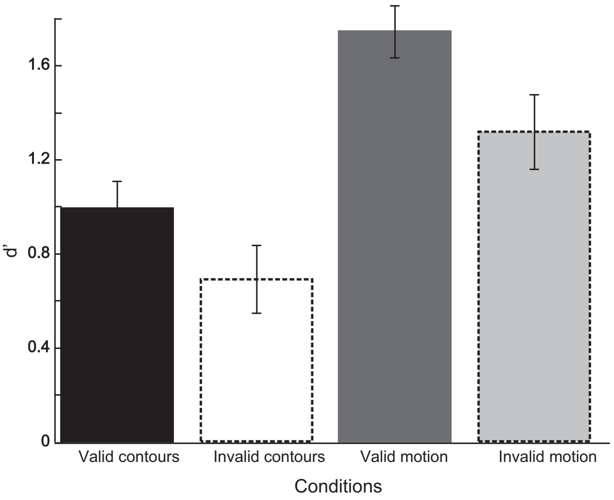

Fig. 2. Behavioural and event related potential results. The bar graph indicates mean performance accuracy (with SEM) for validly and invalidly cued contour- and motion-defined targets.

or motion when they expected the respective feature compared to when they expected the other feature (Fig. 2). The significant main effect of Stimulus ($F_{(1,25)} = 19.05$; $p = 0.0001$, $\eta p^2 = 0.432$) reflects that motion stimuli were easier to perceive than contours, indicating that contour and motion stimuli were not perfectly matched in difficulty or saliency, perhaps because our participants benefited more from training motion stimuli than from training contour stimuli and more so than expected based on our pilot data. A potential problem with motion stimuli becoming too easy to perceive could have been a ceiling effect in perceptual performance with no room for attentional modulations. However, because the Stimulus by Cueing interaction was clearly insignificant ($F_{(1,25)} = 1.43$; $p = 0.24$, $\eta p^2 = .053$), attentional manipulations seem to have remained approximately the same for contours and motion.

Therefore, direct comparisons between contour- and motion-based effects will have to be treated with care. But, comparisons between cueing effects are feasible.

3.2. Electrophysiological results: general overview

Group averaged ERPs for both validly and invalidly cued contour and motion conditions produced components such as a C1 at posterior medial electrodes and a P1, an N1, and a P2 at posterior lateral and posterior medial electrodes. We observed a relative negative deflection in a 250–410 ms latency range after stimulus onset that was more pronounced at occipital and frontal electrodes, in addition to a late (460–600 ms) positive going deflection at occipital, central and frontal electrodes in both contour and motion conditions (Fig. 3a and b).

3.3. Cluster plots of successive *t*-tests

To gain a general insight into the experimental effects of these data and an estimate of their temporo-spatial structure, we first ran successive *t*-tests that compared ERPs for validly and invalidly cued contours, and separately for motion at each time point for each electrode (Fig. 4a and b).

The earliest modulation between validly and invalidly cued contours occurred 290 ms after stimulus onset with greater negativity for valid contours at anterior frontal electrodes and, somewhat later, greater positivity at posterior and central electrodes. This period extended until 525 ms or perhaps beyond.

Earlier effects occurred for validly vs. invalidly cued motion stimuli. The earliest effect occurred from 108 to 133 ms, overlapping with the P1 latency, and was due to a greater positivity at central parietal electrodes for validly cued motion compared to invalidly cued motion. Shortly after that, from 185 to 353 ms, we observed greater positivity at occipital and parietal electrodes. Finally, a third period of greater positivity for valid compared to invalidly cued motion stimuli re-emerged from 363 to 480 ms at occipital and parietal electrodes.

3.4. Topographic pattern analysis

To investigate these results further, next we conducted a topographic pattern analysis of the brain's electric field configuration (Fig. 5; also see Section 2). We found that 30 different scalp topographies best explained the ERP data (−100 to 600 ms) for all four validly and invalidly cued contour and motion conditions (global explained variance: 95.6%). Here we focused on maps 21–30 beginning from 64 ms after stimulus onset. Earlier maps had low levels of global field potential and poor signal-to-noise ratios (Fig. 5).

Map 21 comprised a C1 at medio-occipital electrodes and the beginning of a P1 at latero-occipital electrodes. Maps 22 and 23 encompassed the rise of an N1 starting at occipital and then extending to ventral occipital and parietal electrodes. This was followed by a right-biased transition period (during map 24) to a P2 (during map 25) and a negative going deflection thereafter (during map 26, note that the deflection was only relative to the previous positive going P2).

Later topographies (maps 27–30) featured varying forms of frontal and occipital negativity, as well as central positivity with map 27 occurring for validly cued contours and validly cued motion only. However, for validly vs. invalidly cued contours differences in topography were not statistically reliable: A topographic analysis of variance (TANOVA) – spatial correlation as a measure of distance between two maps at each time – indicated that none of the maps yielded significant differences between valid and invalid contours (see Fig. 5a). In addition, we back-fitted the maps that emerged from the cluster analysis onto individual participants' ERPs to statistically assess which maps best represented valid and invalid contour conditions (Murray et al., 2008). By using number of time frames (duration) as the dependent measure from the "fitting" procedure, again we found no evidence for topographic differences between validly and invalidly cued contours.

In contrast, the TANOVA comparing validly and invalidly cued motion revealed four periods of significance that satisfied our criterion of significance (11 consecutive time points with a *p*-values < 0.05). The first period encompassed map 25 and the early portion of map 26, the second occurred during maps 27 and 28, the third began at the end of map 29 and continued during map 30, and the fourth period occurred during map 30 (see Fig. 5b). The results of the back-fitting indicate that maps 22 ($t_{(1,25)} = -2.136$; $p = 0.043$), 25 ($t_{(1,25)} = -2.96$; $p = 0.007$) and 28 ($t_{(1,25)} = -2.107$; $p = 0.046$) occurred more frequently in the valid motion condition than the invalid motion condition.

3.5. Global field potentials

While these differences in topography suggest that cueing resulted in differences in brain mechanisms, cueing might also cause differences in the response strength of neural mechanisms despite no detected differences in maps. Here we used global field potential (GFP, Lehmann & Skrandies, 1980; also see Section 2). As one note of caution, GFPs (especially smaller ones) depend on the numbers of trials underlying the ERPs. That is, because the invalid condition had fewer trials, this resulted in more noise-based within-subject variability than in the valid condition. This becomes

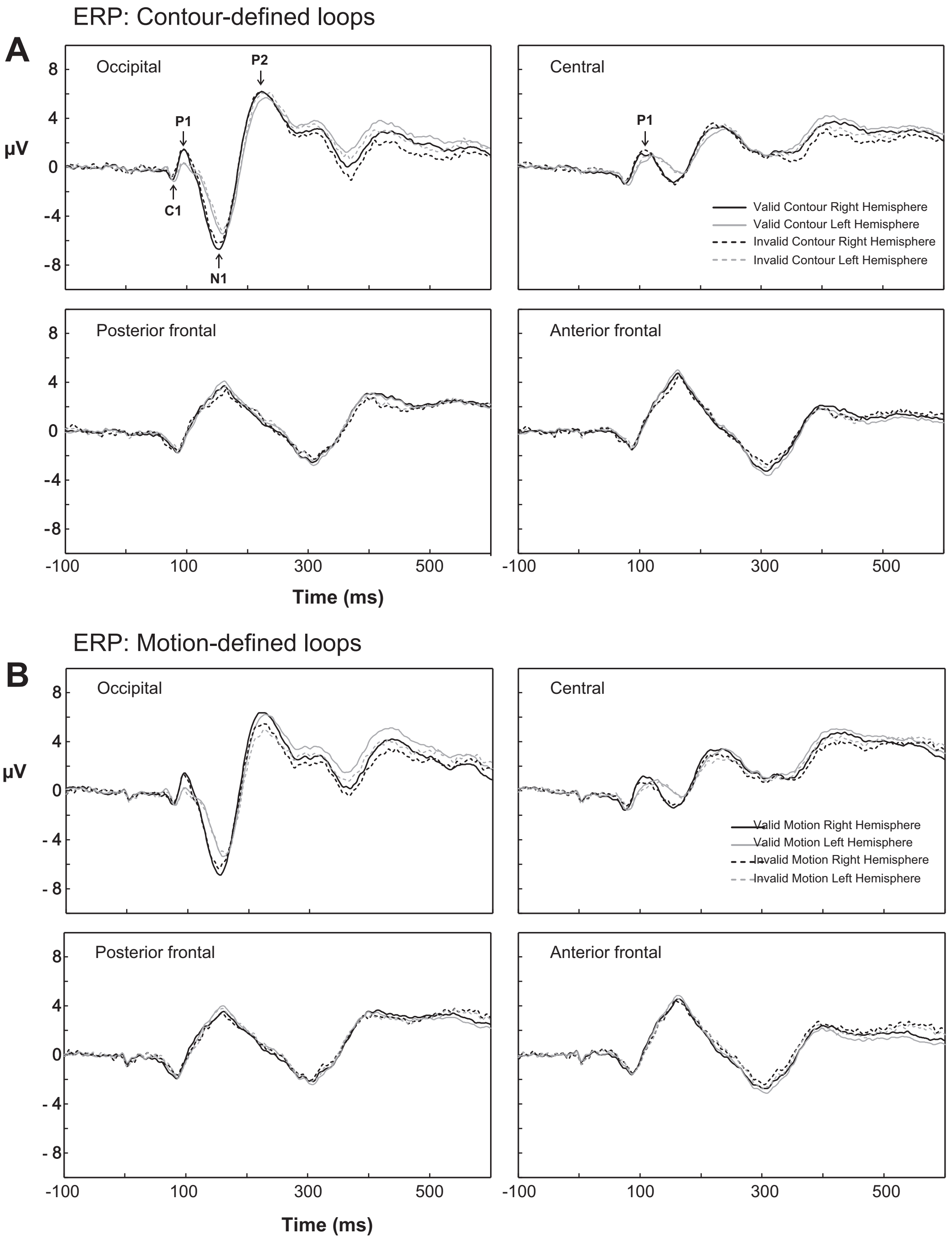

Fig. 3. Event-related potential results. (A) Contour defined loops: group-averaged ($N = 25$) ERPs from each stimulus condition divided into the mean of four scalp topographic locations, occipital, central, posterior frontal, and anterior frontal. (B) Motion targets: group-averaged ($N = 25$) ERPs from each stimulus condition divided into the mean of four scalp topographic locations, occipital, central, posterior frontal, and anterior frontal.

particularly obvious for early GFP values between −100 and 66 ms, that is (supplementary figure 1), at times when differences in GFP based on experimentally induced neural responses are unlikely. The early (pre-) stimulus difference disappeared when we randomly unselected trials in the valid condition and recalculated GFP values based on equal numbers of trials in the two conditions and differences for later times increased. At the same time, statistical differences disappeared probably because unselecting valid trials reduced the reliability of the GFP measures.

For this reason, we submitted the original valid and invalid GFP values for both contour and motion conditions after 66 ms to successive *t*-tests (Fig. 5a and b), much like those conducted for the ERP data. First, for the contour conditions, differences in signal strength fulfilling our criterion of significance (11 consecutive significant time frames) occurred between 287 and 350 ms which corresponded with the latter portion of map 26 of the topographic pattern analysis. The results of the successive *t*-tests comparing the valid and invalid motion conditions, revealed an earlier time window between 216 and 330 ms as the only period of signal strength modulation.

It is worth mentioning that in both the contour and motion conditions small difference appeared from 145 to 164 ms, and 122 to 142 ms, respectively. However, these time windows did not reach our criterion for significance (11 consecutive time frames).

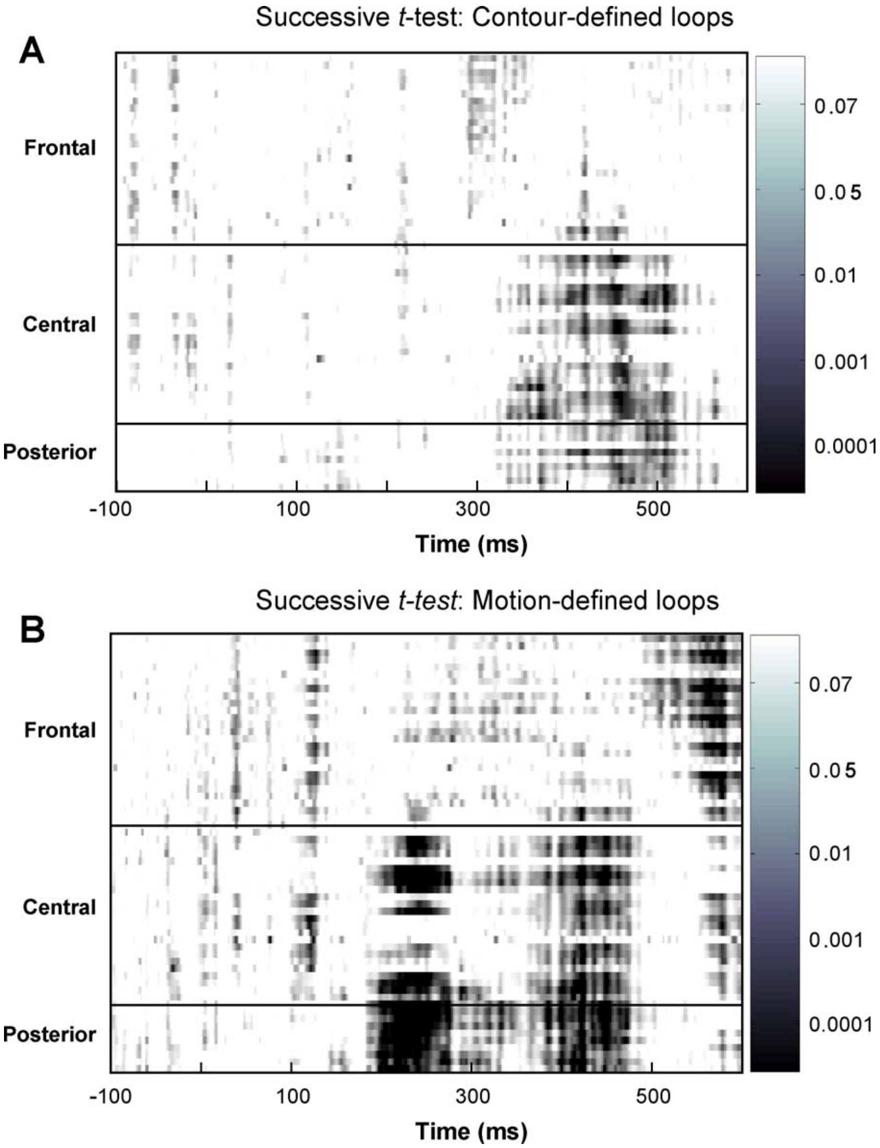

Fig. 4. Successive *t*-tests. (A) ERP waveform modulations were examined by calculating successive paired *t*-tests for each time point and electrode sites. The *x*-, *y*-, and *z*-axes represent time, electrode location (from posterior electrodes and moving up to frontal electrodes) and *p*-value (colour values), respectively. The results for contour-defined loops (A) indicate the earliest modulation of a cueing effect appeared roughly 290 ms after stimulus onset, initially at frontal electrodes, and followed by posterior areas. In contrast, earliest signs of the cueing effect for motion (B) appeared at a time window consistent with the P1 (108–133 ms).

3.6. ANOVAs

The timings of the maps obtained from the topographic pattern analysis guided our next analysis that inspected average ERP amplitudes in a complementary manner to the successive *t*-test analysis, the topographic segmentation analysis and the GFP analysis. We focused on five time windows of interest: (a) we looked at 109–133 ms (map 22) because the first *t*-test analysis of the ERP data had suggested significant differences between valid and invalid motion responses; (b) we tested 202–243 ms (map 25) because of the cueing effects observed for the motion conditions in the successive *t*-tests, GFP and TANOVA; (c) we inspected 242–357 ms (map 26) because our GFP analysis suggested differences in signal strength for the motion as well as for the contour conditions; (d) we tested 351–366 ms to examine the differences in topography as suggested by the topographic analysis (map 27 present only in the valid condition, though significant only for motion); (e) we looked at 353–405 ms (map 28) because results of the successive *t*-test for both contours and motion revealed extensive periods of modulation during that time.

For the first time window (map 22, 109–133 ms) we observed an effect of Scalp region ($F_{(1.05,\,25.36)} = 8.78$; $p = 0.006$), which reflects the polarity inversion of the N1 and P1 across the scalp (Murray et al., 2004), consistent with differences in topographies as suggested by the back-fitting procedure of maps for motion stimuli. No other main effects reached significance (Table 1). A significant Stimulus by Cueing interaction ($F_{(1,24)} = 4.45$; $p = 0.046$) indicated that the cueing effect elicited differential patterns of activation for motion and contours. No other interactions reached significance ($F < 3.38$; $p > 0.07$). To better understand the Stimulus by Cueing interaction, we conducted ANOVAs for each stimulus type separately. Only for motion did we find an effect of Cueing ($F_{(1,24)} = 11.82$; $p = 0.02$), not for contours ($F_{(1,24)} = 0.45$; $p = 0.51$). This is consistent with our *t*-tests, topographic pattern analysis and GFP analysis.

For the second time window (map 25, 202–243 ms), we found a significant main effect of Scalp region ($F_{(1.11,26.66)} = 10.65$; $p = 0.002$), reflecting greater negativity over frontal areas and positivity over posterior areas across the stimulus conditions. We observed no significant main effects of Stimulus, Cueing, or Hemisphere ($F < 2.41$; $p > 0.13$). However, we found a number of

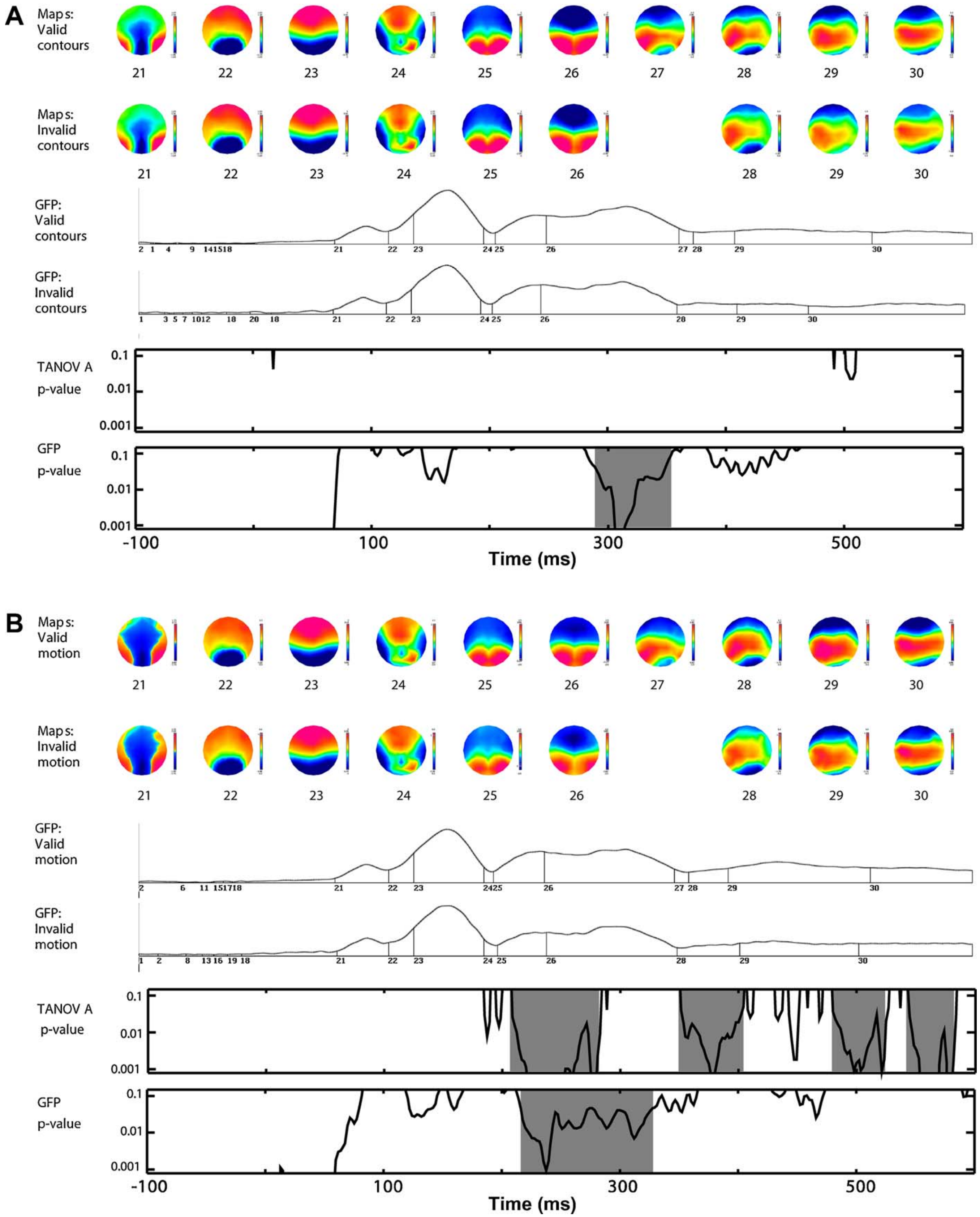

Fig. 5. Topographic pattern analysis, TANOVA and GFP. (A) Results of the spatiotemporal topographic pattern analysis reveal segments of stable neural configuration for validly and invalidly cued contours. Each map (with an independent voltage scale in microvolts) is identified with a number corresponding to a segment. The segment numbers are displayed below the maps. Two statistical tests are provided: TANOVA indicated the maps were not significantly different, and results of successive pointwise paired *t*-tests of the GFP revealed modulations in signal strength starting at roughly 290 ms (shaded grey region). (B) Results of the topographic pattern analysis, the TANOVA, and the GFP analysis for the valid and invalid cued motion condition.

Table 1

Presented are statistical results from 2(Stimulus) × 2(Cue) × 4(Scalp region) × 2(Hemisphere) ANOVAs for each of the five time windows of interest. At each time window with a significant interaction between Stimulus and Cue, separate 2(Cue) × 4(Scalp region) × 2(Hemisphere) ANOVAs were preformed for contours and motion (first three time windows). All results (*F* and *p* values) are shown.

Valid contours
Invalid contours
Time window 1
109–133 ms

Source	*F*	*p*
Stimulus (S)	4.25	0.05
Cueing (C)	0.939	0.343
Scalp region (Sr)	8.78	0.006
Hemisphere (H)	0.883	0.357
(S) × (C)	4.45	0.046
(S) × (Sr)	1.803	0.189
(C) × (Sr)	2.053	0.161
(S) × (H)	0.022	0.883
(C) × (H)	0.124	0.728
(Sr) × (H)	3.384	0.068
(S) × (C) × (H)	0.028	0.868
(S) × (Sr) × (H)	0.954	0.379
(C) × (Sr) × (H)	2.657	0.088
(S) × (C) × (Sr)	1.323	0.268
(S) × (C) × (Sr) × (H)	0.493	0.57

Valid contours
Invalid contours
Time window 2
202–243 ms

Source	*F*	*p*
Stimulus (S)	2.412	0.133
Cueing (C)	0.201	0.658
Scalp region (Sr)	10.653	0.002
Hemisphere (H)	0.075	0.787
(S) × (C)	10.199	0.004
(S) × (Sr)	2.412	0.125
(C) × (Sr)	9.44	0.004
(S) × (H)	0.547	0.467
(C) × (H)	0.348	0.561
(Sr) × (H)	2.688	0.097
(S) × (C) × (H)	4.287	0.049
(S) × (Sr) × (H)	0.554	0.647
(C) × (Sr) × (H)	1.008	0.364
(S) × (C) × (Sr)	17.336	0.0001
(S) × (C) × (Sr) × (H)	3.979	0.04

Valid motion
Invalid motion
Time window 3
242–357 ms

Source	*F*	*p*
Stimulus (S)	0.93	0.344
Cueing (C)	0.039	0.846
Scalp region (Sr)	15.145	0.0004
Hemisphere (H)	0.151	0.701
(S) × (C)	0.003	0.954
(S) × (Sr)	4.975	0.015
(C) × (Sr)	10.612	0.001
(S) × (H)	1.118	0.301
(C) × (H)	2.816	0.106
(Sr) × (H)	2.925	0.053
(S) × (C) × (H)	0.09	0.924
(S) × (Sr) × (H)	1.14	0.313
(C) × (Sr) × (H)	10.412	0.0002
(S) × (C) × (Sr)	4.245	0.021
(S) × (C) × (Sr) × (H)	8.78	0.0004

Valid motion
Invalid motion
Time window 4
351–366 ms

Source	*F*	*p*
Stimulus (S)	6.13	0.021
Cueing (C)	6.53	0.427
Scalp region (Sr)	1.624	0.215
Hemisphere (H)	4.735	0.04
(S) × (C)	0.71	0.791
(S) × (Sr)	6.273	0.16
(C) × (Sr)	15.118	0.0003
(S) × (H)	0.004	0.951
(C) × (H)	1.136	0.297
(Sr) × (H)	5.773	0.12
(S) × (C) × (H)	2.368	0.137
(S) × (Sr) × (H)	0.491	0.608
(C) × (Sr) × (H)	0.724	0.483
(S) × (C) × (Sr)	0.232	0.721
(S) × (C) × (Sr) × (H)	0.12	0.855

Valid contours
Invalid contours
Time window 5
353–405 ms

Source	*F*	*p*
Stimulus (S)	8.773	0.007
Cueing (C)	5.036	0.034
Scalp region (Sr)	2.406	0.13
Hemisphere (H)	5.667	0.026
(S) × (C)	0.64	0.803
(S) × (Sr)	0.429	0.539
(C) × (Sr)	12.607	0.001
(S) × (H)	0.006	0.939
(C) × (H)	0.358	0.555
(Sr) × (H)	7.917	0.004
(S) × (C) × (H)	2.852	0.104
(S) × (Sr) × (H)	0.543	0.583
(C) × (Sr) × (H)	1.036	0.366
(S) × (C) × (Sr)	0.78	0.422
(S) × (C) × (Sr) × (H)	0.345	0.659

Valid contours
Invalid contours
Time window 1
109–133 ms

Source	*F*	*p*
Cueing (C)	0.456	0.506
Scalp region (Sr)	8.610	0.006
Hemisphere (H)	0.907	0.350
(C) × (Sr)	3.785	0.054
(C) × (H)	0.108	0.745
(Sr) × (H)	3.236	0.074
(C) × (Sr) × (H)	1.901	0.166

Valid contours
Invalid contours
Time window 2
202–243 ms

Source	*F*	*p*
Cueing (C)	1.870	0.184
Scalp region (Sr)	11.906	0.001
Hemisphere (H)	0.038	0.847
(C) × (Sr)	0.385	0.584
(C) × (H)	1.929	0.178
(Sr) × (H)	2.215	0.137
(C) × (Sr) × (H)	5.542	0.130

Valid contours
Invalid contours
Time window 3
242–357 ms

Source	*F*	*p*
Cueing (C)	0.015	0.902
Scalp region (Sr)	20.86	0.000
Hemisphere (H)	0.636	0.433
(C) × (Sr)	6.139	0.016
(C) × (H)	0.899	0.352
(Sr) × (H)	1.596	0.219
(C) × (Sr) × (H)	0.181	0.757

Valid motion
Invalid motion

Source	*F*	*p*
Cueing (C)	11.816	0.02
Scalp region (Sr)	8.835	0.006
Hemisphere (H)	0.844	0.367
(C) × (Sr)	0.395	0.558
(C) × (H)	0.019	0.892
(Sr) × (H)	2.475	0.064
(C) × (Sr) × (H)	0.961	0.372

Valid motion
Invalid motion

Source	*F*	*p*
Cueing (C)	5.064	0.034
Scalp region (Sr)	9.392	0.004
Hemisphere (H)	0.123	0.729
(C) × (Sr)	17.602	0.0001
(C) × (H)	4.061	0.055
(Sr) × (H)	3.147	0.068
(C) × (Sr) × (H)	0.782	0.434

Valid motion
Invalid motion

Source	*F*	*p*
Cueing (C)	0.025	0.876
Scalp region (Sr)	9.816	0.002
Hemisphere (H)	0.0001	0.992
(C) × (Sr)	9.682	0.001
(C) × (H)	3.216	0.086
(Sr) × (H)	2.349	0.11
(C) × (Sr) × (H)	11.059	0.0002

significant interactions involving Cueing: a Stimulus by Cueing interaction ($F_{(1,24)} = 10.2$; $p = 0.004$), a Cueing by Scalp region interaction ($F_{(1.08,26.16)} = 9.44$; $p = 0.004$), a Stimulus by Cueing by Scalp region interaction ($F_{(1.23,29.56)} = 17.34$; $p = 0.0001$), a Stimulus by Cueing by Hemisphere interaction ($F_{(1,24)} = 4.29$; $p = 0.049$), and a four-way interaction between Stimulus, Cueing, Scalp region and Hemisphere ($F_{(1.43,34.32)} = 3.98$; $p = 0.04$). No other interactions reached significance ($F < 2.69$; $p > 0.097$). These results indicate that cueing differentially modulated ERP signals in the two stimulus conditions. A follow-up ANOVA for contours revealed that during this latency, processing validly cued contours produced less positivity over occipital and parietal regions that were more pronounced over the left hemisphere, indicated by a significant three-way interaction between Cueing, Scalp region and Hemisphere ($F_{(1.53,36.69)} = 5.54$; $p = 0.013$). This result was surprising because it disagreed with our other analyses. For that reason we conducted 8 additional *t*-tests to compare valid and invalid contours at each of the four scalp regions in both hemispheres. None of the tests were significant ($t(25) < 1.85$; $p > 0.076$; these differences diverged further from significance after Bonferroni correction). A different and more prominent pattern of effects was seen for motion stimuli where greater positive going deflections occurred for validly compared to invalidly cued motion targets in particular at occipital and central electrodes. This was reflected in a main effect of cueing ($F_{(1,24)} = 5.06$; $p = 0.034$) and a Cueing by Scalp region interaction ($F_{(1.12,26.96)} = 17.6$; $p = 0.0002$).

The third time window (map 26, 242–357 ms) was marked by a main effect of Scalp region ($F_{(1.14,27.39)} = 15.14$; $p = 0.0004$) and a Stimulus by Scalp region interaction ($F_{(1.73,41.4)} = 4.97$; $p = 0.015$). We also found a sequence of significant interactions involving cueing: a Cueing by Scalp region interaction ($F_{(1.33,31.86)} = 10.61$; $p = 0.0012$), three-way interactions of Cueing with Stimulus and Scalp region ($F_{(1.94,46.53)} = 4.24$; $p = 0.021$) and with Scalp region and Hemisphere ($F_{(1.99,47.89)} = 10.61$; $p = 0.0012$), and a four-way interaction between Stimulus, Cueing, Scalp region and Hemisphere ($F_{(2.13,51.16)} = 8.78$; $p = 0.0004$). Other main effects and interactions did not reach significance ($F < 2.92$; $p > 0.053$). The subsequent ANOVA for the contour conditions revealed a significant Scalp region by Cueing interaction ($F_{(1.18,28.27)} = 6.14$; $p = 0.015$) that was reflected in greater positivity over central parietal regions and greater negativity over anterior frontal regions. In contrast, in the motion conditions we observed a significant Scalp region by Cueing interaction ($F_{(1.18,28.27)} = 6.14$; $p = 0.015$) and a Cueing by Scalp region by Hemisphere interaction ($F_{(1.84,42.42)} = 11.1$; $p = 0.0002$). This indicated the cueing effect was more pronounced over occipital and parietal areas of the left hemisphere.

For the fourth time window, Map 27 (351–366 ms), the results of the ANOVA suggested the cueing effect produced a different pattern of activation across the scalp. This is reflected in a Cueing by Scalp region interaction ($F_{(1.13,27.27)} = 15.11$; $p = 0.0003$), highlighting that cueing produced greater modulation at posterior (occipital and central parietal) sites. We also found main effects of Stimulus ($F_{(1,24)} = 6.13$; $p = 0.02$), and Hemisphere ($F_{(1,24)} = 4.73$; $p = 0.039$), a significant interaction between Stimulus and Scalp region ($F_{(1.11,26.8)} = 6.27$; $p = 0.016$) and a Scalp region by Hemisphere interaction ($F_{(1.5,36.18)} = 5.77$; $p = 0.011$). Taken together this emphasizes that contours produced greater positivity than motion in particular over the left hemisphere. No other effects were significant ($F < 5.77$; $p > 0.14$).

The fifth time window, map 28 (353–405 ms), elicited greater positivity for motion stimuli compared to contours (main effect of Stimulus; $F_{(1,24)} = 8.77$; $p = 0.007$), greater positivity for validly cued targets than invalidly cued ones (main effect of Cueing; $F_{(1,24)} = 5.03$; $p = 0.034$), and greater positivity over the left hemisphere than the right (main effect of Hemisphere; $F_{(1,24)} = 5.66$; $p = 0.026$). In addition, a significant Cueing by Scalp region interaction ($F_{(1.71,28.26)} = 4.38$; $p = 0.039$) indicated more pronounced cueing effects at posterior electrodes, and Scalp region by Hemisphere interaction ($F_{(1.43,34.41)} = 7.91$; $p = 0.004$) suggested differences in topography depending on hemisphere with greater central positivity on the left side and more extended negativity at occipital and frontal electrodes on the right side. No other effects were found to be significant ($F < 2.85$; $p > 0.1$).

3.7. Source localization

To obtain a tentative insight into the signal sources for both group averaged validly cued contour and motion conditions we computed standardized Low Resolution Electromagnetic Tomography (sLORETA) source estimates with leadfield normalization using the standardized weighted Low Resolution Electromagnetic Tomography (swLORETA), at two time latencies: for motion we looked at map 22 (108–133 ms) as the first period of modulation of cueing for motion, and for contours we examined map 26 (242–357 ms), the first time window of differences in GFP. In both cases we focused on the valid conditions because the TANOVAs had suggested no significant differences in topography between validly and invalidly cued conditions. Sources for motion during the first time window (108–133 ms) were observed in extrastriate cortex, mostly in the right hemisphere (MNI coordinates [mm]: $x = 30$, $y = -75$, $z = -15$; Fig. 6B). Sources for contours during the second time window (242–357 ms) were found for both hemispheres in ventral regions of visual cortex anterior to extrastriate cortex and in posterior parts of superior parietal cortex (MNI coordinates [mm] $x = 45$, $y = -60$, $z = 0$; Fig. 6A). Although source localization provides converging evidence that our effects are mediated by anterior visual areas, such as LOC, one should be careful in overinterpreting the locations of the neural generators. Only with more sensitive measures such as fMRI can direct claims be made about the locus of our effects.

4. Discussion

We used high density EEG recordings to investigate the neural correlates reflecting the influences of feature-based attention on object perception. We employed a cueing paradigm, in which we informed participants that objects defined by contours would appear with a probability of 0.8, whereas motion stimuli would appear with a probability of 0.2, or vice versa.

We found that participants were more accurate in detecting stimuli defined by the validly cued feature as opposed to the invalidly cued feature. This confirms our previous observation (Stojanoski & Niemeier, 2007) that contours are better perceived when feature-based attention is directed to contours compared to attention directed to motion. As we will argue it suggests that feature-based attention pertains not only to relatively simple visual features, such as colour but also to complex visual features (contours) potentially associated with higher level visual areas.

Indeed, it has been proposed that perception of contours is intimately linked to higher tier visual mechanisms in the LOC (e.g., Murray et al., 2002). For this reason and because activity in higher tier visual areas is strongly modulated by attention (Chelazzi et al., 1993; Lueschow et al., 2004; Maunsell & Cook, 2002; Niemeier et al., 2005; O'Craven et al., 1999; Tallon-Baudry et al., 2005) we predicted that feature-based attention when cued to contours should involve neural mechanisms subserving object perception. Therefore, they should be reflected in modulations of ERP signals that occur later than attentional modulations of ERP signals elicited by motion stimuli.

We found our predictions confirmed. We observed early attention-based modulation of ERPs around the time of the P1, but

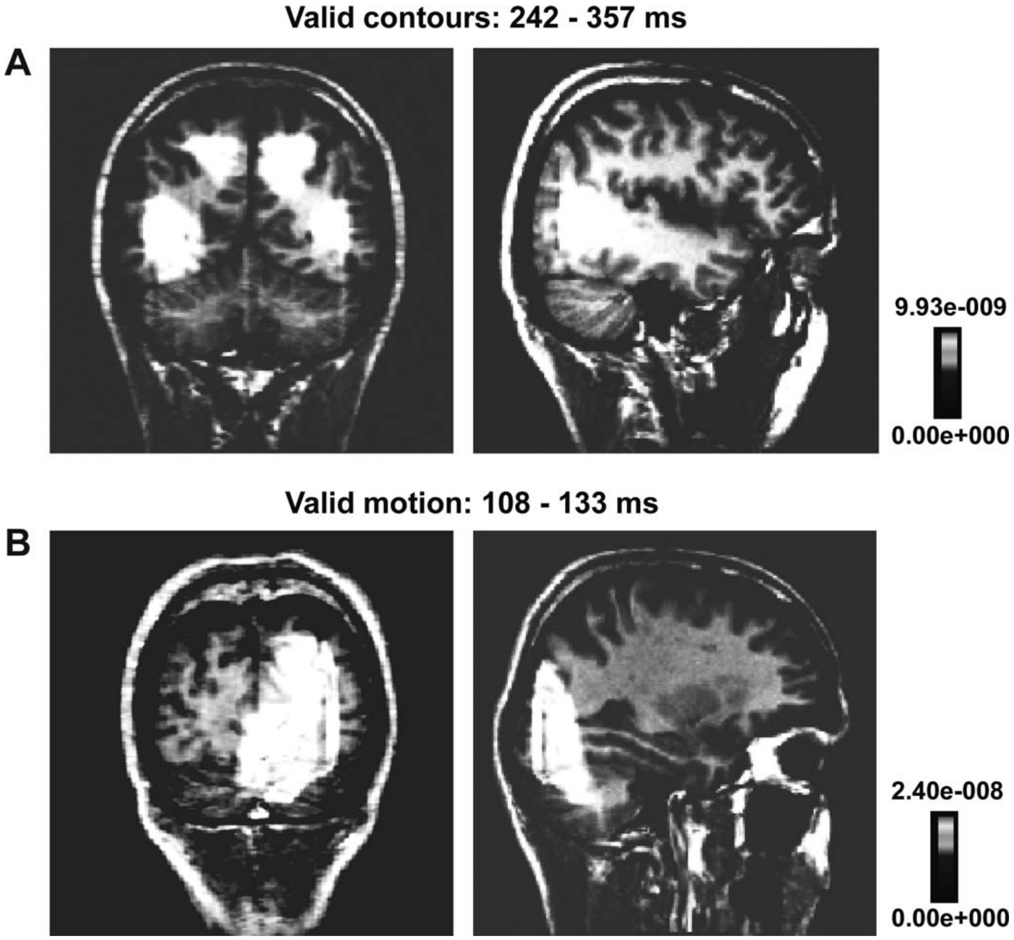

Fig. 6. Source localization using standardized weighted low resolution electromagnetic topography (swLORETA). (A) Sources for the valid contour condition (242–357 ms). (B) Sources for the valid motion condition (108–133 ms).

only for motion stimuli and not for contours. The motion effect is in good agreement with Valdes-Sosa, Bobes, Rodriguez, and Pinilla (1998), who showed modulation of the P1 when attending to motion. Moreover, Zhang and Luck (2009), recently showed that feature-based attention (within feature dimension) to colour modulates the amplitude of the P1, and they concluded that the latency of their effect reflected feature-based attention to be governed by feedforward sensory activity. Our results add to this observation, suggesting that similar processes are modulated for motion perception as well and that they occur not only when attention is cued to different feature values within the same feature dimension (i.e., different colours, Zhang & Luck, 2009) but also when attention is cued to different feature dimensions (motion vs. contours; Valdes-Sosa et al., 1998). In addition, we observed later phases of attentional modulations beginning with an amplification of the P2 for validly cued motion stimuli that were also essentially consistent with Zhang and Luck (2009). In contrast to ERPs during motion conditions, those during contour conditions appear to yield much later modulations. We found that validly vs. invalidly cued attention modulated electrical brain activity in response to contours after the P2: about 290 ms after stimulus onset according to *t*-tests at individual electrodes and about 287 ms according to global signal strength, and source localization for that time period implicated areas in the ventral stream, anterior to extrastriate regions.

The timing of these effects is markedly later than the effects Valdes-Sosa et al. (1998) observed while participants attended to motion, and later than what Zhang and Luck (2009) reported for feature-based attention to colour. Here, we could have, in principle, expected similar modulations of early feedforward processes. The first reason is that certain contour completion processes seem to exist in striate and extrastriate areas. For example, it has been speculated that visual areas as early as V1 extract contours by means of mutually enhancing connections between neurons with similar orientation sensitivity within neighbouring receptive fields (Field, Hayes, & Hess, 1993). The second reason that makes early attentional effects feasible is, our paradigm was sufficiently sensitive to find them if the effects existed: we presented target stimuli together with distractor gabors, thus warranting visual competition – specifically then feature-based attention amplifies the P1 (Zhang & Luck, 2009) – and latencies observed for our motion data confirm that our paradigm was suitable to detect early effects.

Instead, the timing of the attentional effects for contours resembles that of influences that illusory contours have on ERPs at posterior electrodes, which have been shown to be associated with the visual object area LOC (Murray et al., 2002). Murray and colleagues presented arrays of visual inducers that either did or did not form Kanisza figures and found that contour-sensitive effects arose comparatively late. They observed increased negativity around the time of the N1 for foveally presented Kanisza figures and greater positivity only after the P2 for peripherally presented stimuli.

Though we too used peripheral stimuli and observed effects within the same time range, it is not surprising that our data are not entirely consistent with those of Murray et al. (2002). That is, only in the present study did significant differences first arise at frontal electrodes and only our source localization for the respective time window suggested superior parietal areas to be involved in the contour perception task in addition to ventral visual areas. This might be due to the fact that our stimuli differed in several ways from Murray and colleagues'. More importantly, only our paradigm systematically modulated participants' attention to contours (as opposed to presenting stimuli with and without contours) and required to locate the target stimuli. Finally, we found some evidence for effects earlier than those that Murray et al. (2002) had observed for peripheral stimuli. One effect was a transient increase in signal strength between 145 and 164 ms that was marginally briefer than our criterion of significance. If significant, it would have suggested an effect around the time of the N1, somewhat unexpected because Murray and colleagues observed effects at the N1 only for foveal Kanisza figures, not for peripheral ones. The second possible, earlier effect was a small cue-sensitive interaction around the time of the P2. This effect showed up only based on an ANOVA conducted on average ERPs for a time window motivated by the motion data. Indeed, we were not able to confirm the effect with any other analysis method. What is more, it occurred for left posterior and left central electrodes only and indicated a trend for a larger P2 amplitude for the invalid condition (except, modulations at no electrode site reached significance when tested separately). A similar effect was reported by Anllo-Vento and Hillyard (1996). They observed a more prominent P2 at posterior electrodes for ignored motion directions (and colours). However, it is difficult to integrate Anllo-Vento and Hillyard's (1996) motion data with our contour data because the most obvious comparison with our motion data fails: for our motion conditions we obtained an effect at the P2 opposite to Anllo-Vento and Hillyard's. Furthermore these authors found no modulations at the P1. Therefore, further research is required to clarify whether the two effects are indeed statistically reliable and, if so, whether they can be explained by increased sensitivity due to our distractor gabors and/or due to the attentional manipulations conducted here.

To sum up for now, we argue our data suggest that feature-based cueing effects observed for the motion and the contour perception task modulated very different mechanisms. For motion it involved early processes presumably associate with extrastriate cortex. For contours, on the other hand, we found evidence of contour perception known to reside in high-level visual areas, probably the LOC (Murray et al., 2002). However, are our results actually explained by feature-based forms of attention or are alternative interpretations possible? In the following we will address these alternatives and show that they cannot explain our data.

Are our data influenced by differences in arousal because contour blocks on average are more difficult than motion blocks? This is unlikely because contour blocks mixed valid contour trials and invalid motion trials, and motion blocks mixed valid motion trials and invalid contour trials. So, blocks differing in arousal should have resulted in a stimulus-by-cueing interaction of behavioural performance, and extended stretches of ERP differences between valid and invalid trials. Both we did not find. Further support against the arousal account comes from our previous study (Stojanoski & Niemeier, 2007) where we used a related paradigm and systematically manipulated task difficulty of a primary task. This had no bearings on contour perception probed with a secondary task. Finally, Valdes-Sosa et al. (1998) reported ERP responses to attended features of objects that were consistent across easy and difficult tasks. Therefore, in the current study, it is unlikely that arousal would produce differential effects for validly and invalidly cued trials.

Do our effects reflect an unspecific effect of perceptual priming due to valid stimuli in a given block appearing more often than invalid stimuli? We argue that such differences cannot explain our electrophysiological effects. Priming has been shown to reduce electrophysiological responses, contrary to our observation that the valid condition increases signal strength. Furthermore, priming typically suppresses the amplitude of the P1 over occitpitotemporal sites (Henson, Rylands, Vuilleumeir, & Rugg, 2004; Schendan & Kutas, 2003). This is earlier than our effects for contours (and opposite to our effects for motion at that time). Later priming effects do exist (e.g., Grill-Spector, Henson, & Martin, 2006; Gruber & Müller, 2005; Henson et al., 2004), but those are opposite to our contour effects. Finally, priming effects decelerate with numbers of stimulus repetitions. For example, Grill-Spector et al. (2006) observed that priming effects plateaued after six to eight repetitions. If we use this as a benchmark for our experimental design where a block of trials presents validly cued contours about 53 times, and invalidly cued contours 13 times, both validly cued- and invalidly cued contours would reach the plateau within the first block of trials and remain there for the rest of the experiment. Therefore, in our experiment priming differences should have played no significant role.

The same is true for the third alternative explanation for our results, an oddball effect for infrequent events, manifested in some form of a P3 component (e.g., Polich, 2007). But P3 components at posterior electrodes at posterior electrodes should increase for unexpected events. In contrast, we found that invalidly cued contours produced greater negativity at roughly 300 ms over central and occipital electrodes.

Did our paradigm cue not feature-based attention but object-based attention? There are at least two interpretations of object-based attention. One refers to attention being confined to the surface of the attended object (Egly, Driver, & Rafal, 1994). Conceptually, this form of attention is different from feature-based attention because it is essentially based on spatial information. Indeed, Martinez and colleagues (Martinez, Ramanathan, Foxe, Javitt, & Hillyard, 2007) demonstrated that attention spreading across the surface of an object has similar effects on ERPs as spatial attention to a certain location. The second, non-spatial aspect of object-based attention refers to attention inducing binding processes between visual features of a given object (e.g., O'Craven et al., 1999; Schoenfeld et al., 2003). Both interpretations of object-based attention refer to enhanced processing of the object that is attended (e.g., Duncan, Humphreys, & Ward, 1997), not enhanced processing of an object that is presented elsewhere in an unattended part of the visual field. However, the latter is what we have previously demonstrated to be the case for attention to contours (Stojanoski & Niemeier, 2007).

Could feature-binding aspects of object-based attention have co-occurred with feature-based attention such as binding between motion and shape or contours and shape? We believe this is unlikely to have played an important role. It is possible that participants directed their attention to other aspects of our stimuli, not only their contours or motion. But features such as contrast, spatial frequency, as well as the location of the gabors were the same for contour stimuli and motion stimuli and so could not have explained differences in ERPs depending on whether participants expected contours or motion. Contour-defined loops did have a clearly defined shape whereas the shape of motion-defined loops was less obvious and based on our previous data difficult to use (Stojanoski & Niemeier, 2007). But the shapes of the loops were unpredictable. So participants had no useful information about the shapes of the stimuli that would have optimized their task performance.

Another interpretation of our results is not necessarily at odds with the idea of a feature-based attentional effect. It pertains to certain object perception mechanisms called "object closure", that is, the point at which people begin to recognize an object in a (usually difficult) recognition task. This cognitive event has been found to be associated with a relative negative deflection called 'Ncl' (i.e., a negativity associated with closure) at electrodes over parieto-occipital scalp regions ~220 ms after stimulus onset (Doniger et al., 2001), and it might be governed by feedback from areas in frontal and medio-temporal cortex (Sehatpour et al., 2008).

However, despite the similarity in timing we believe that the effects observed here are unlikely to reflect an Ncl. To begin with, previous studies on the Ncl used object recognition paradigms with items from familiar object categories rather than loops with random, unfamiliar shapes. This limits the extent to which studies can be compared. More significantly however, in the present study we observed that valid cueing of contour-defined loops was associated with greater posterior positivity together with more accurate perception than invalid cueing. This appears to be contrary to what should be expected from an Ncl: valid cueing should have increased the probability of object closure and thus resulted in greater negativity.

One could speculate that invalid cues might have caused perception to recruit processes underlying the Ncl to a greater extent. However, this would likely involve increased neural activity which is inconsistent with our observation that valid cues were associated with greater signal strength as measured with the GFP – similar to what has been reported for the perception of Kanisza figures (Murray et al., 2006). Therefore, our findings are opposite to the current understanding of the Ncl – greater negativity and stronger neuronal signal when recognizing incomplete objects (Doniger et al., 2001; Murray et al., 2004, 2006).

Nevertheless, the latency of our effects makes it possible that they include feedback processes from non-visual or multisensory areas. For example, Sehatpour, Molholm, Javitt, and Foxe (2006) asked participants to perform an object recognition task of fragmented images and found synchronous engagement of the prefrontal cortex, the LOC, and the hippocampus, with strongest beta-band coherence starting at 228 ms. Moreover, in an integrated ERP and functional imaging study using similar fragmented stimuli, Sehatpour et al. (2006) found activation in fronto-temporal cortex at about 270 ms. Similar patterns of activation have been reported for non-human primates showing activation in frontal and inferotemporal areas in response to object representations (Miyashita & Hayashi, 2000), likely mediated by the direct connections from prefrontal to inferotemporal cortex (Chelazzi et al., 1993; Rempel-Clower & Barbas, 2000). In addition, here we found evidence for an involvement of parietal areas.

Whether the cueing effects that we observed reflect ‘top-down’ input into visual processes such as those in LOC, will have to be investigated further. However, it is clear that some form of top-down control must have occurred. Otherwise our participants (just like participants in about any experimental paradigm) would have been unable to follow instructions and use the attentional cues. For example, Folk, Remington and Johnston (1992) have shown that when participants are looking for a colour-singleton target in a cueing task, colour-singleton cues will reflexively capture attention but onset cues will not, suggesting that this top-down influence extends to basic levels of sensory enhancement.

Such effects on basic levels of feature-dimension specific processing have been described by the dimension-weighting model (Found & Müller, 1996; Müller, Heller, & Ziegler, 1995). The model stipulates that prior knowledge about a feature dimension produces an amplification of the weighted saliency signal for that dimension relative to other dimensions, which might also have been the basis for the feature-dimension specific changes in contour or motion perception that we observed in the present study as well as before (Stojanoski & Niemeier, 2007). As for contour perception, however, more research is required to identify the exact processes that are altered. That is, later visual areas such as the LOC might (in part) function as specialized contour extractors (e.g., Murray et al., 2002). Alternatively, the LOC might provide statistical priors about shapes that aid contour extraction in earlier areas (Rao & Ballard, 1999).

In conclusion, in the current study we observed an early cue-dependent modulation of the P1 in extrastriate areas in response to motion stimuli but no such effect for contour stimuli. What is more, we found evidence that feature-based cueing of attention to contours (but not to motion) is specifically associated with higher tier visual processes, potentially in the LOC. Because modulations in signal strength were not accompanied by significant differences in topography for that task it can be tentatively speculated that feature-based attention primarily altered gating mechanisms in LOC rather than recruiting different neural networks, though a spatially more accurate imaging method will have to confirm this claim. Our data are consistent with the idea that feature-based attention aids the visual system in the perception of contours and thus in perceiving the world in a coherent manner.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuropsychologia.2011.08.017.

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