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Late electrophysiological modulations of feature-based attention to object shapes

BOBBY BOGE STOJANOSKI[a,b] AND MATTHIAS NIEMEIER[b,c]
[a]Brain and Mind Institute, Department of Psychology, Western University, London, Ontario, Canada
[b]Department of Psychology, University of Toronto Scarborough, Toronto, Ontario, Canada
[c]Centre for Vision Research, York University, Toronto, Ontario, Canada

Abstract

Feature-based attention has been shown to aid object perception. Our previous ERP effects revealed temporally late feature-based modulation in response to objects relative to motion. The aim of the current study was to confirm the timing of feature-based influences on object perception while cueing within the feature dimension of shape. Participants were told to expect either "pillow" or "flower" objects embedded among random white and black lines. Participants more accurately reported the object's main color for valid compared to invalid shapes. ERPs revealed modulation from 252–502 ms, from occipital to frontal electrodes. Our results are consistent with previous findings examining the time course for processing similar stimuli (illusory contours). Our results provide novel insights into how attending to features of higher complexity aids object perception presumably via feed-forward and feedback mechanisms along the visual hierarchy.

Descriptors: EEG/ERP, Feature-based attention, Object perception, Cluster analysis

Objects in natural scenes are difficult to perceive; they often occlude one another, thereby limiting the amount of available visual information for perception. To overcome these limitations, we can use prior information about objects and scenes to enhance perception. One strategy is to direct attention to a particular location in space if we expect an object there (Posner, 1980), or we attend to nonspatial properties of objects (e.g., Rossi and Paradiso, 1995).

This so-called feature-based attention has been demonstrated to influence the processing of several visual features such as motion and color. For example, Saenz, Buracas, and Boynton (2003) found that participants were better at concurrently monitoring speed changes in two composite motion patterns if they paid attention to the same motion direction in the two patterns compared to opposite motion direction. Likewise, participants showed an advantage for detecting concurrent luminance changes in two dot patterns when they paid attention to dots of the same color compared to two different colors.

The perceptual benefits of feature-based attention correspond with changes in brain activity. Functional imaging studies have demonstrated that activity increases specifically in areas most responsive to the attended feature, such as V3A and V4 for color and MT+ for motion (e.g., Andersen, Hillyard, & Müller,2008; Beauchamp, Cox, & DeYoe, 1997; Liu, Hospadaruk, Zhu, & Gardner, 2011; Saenz, Buracas, & Boynton, 2002; Schoenfeld et al., 2003), and multiple areas from V1 to the lateral occipital complex (LOC) for orientation (Liu, Larsson & Carrasco, 2007). Furthermore, on the level of single cells, neural firing rates increase or decrease depending on how similar an attended feature is to the feature preferred by a neuron (e.g., Chen, Hoffmann, Albright, & Thiele, 2012; Hayden & Gallant, 2005; McAdams & Maunsell, 2000; Motter, 1994; Treue & Martinez-Trujillo, 1999).

These attention-dependent changes in neural activity appear to arise at a comparatively early stage of processing. For example, Zhang and Luck (2009) found that feature-based attention to color influenced electrophysiological brain activity at the time of the P1 component as early as 80 ms after stimulus onset (also see Bondarenko et al., 2012), and even Valdes-Sosa, Bobes, Rodriguez, and Pinilla (1998) reported a similar time course for attention to motion stimuli, though these effects might have been due to object-based attention. Either way, it is clear that feature-based attention is capable of modulating early, presumably rather feed-forward processes, consistent with the fact that motion and color are visual feature dimensions that the visual system begins to extract a few synapses past the photoreceptors.

However, it is unclear whether feature-based attention operates in a similar temporal manner if it is directed to more complex visual features, given that these types of features are extracted later. For example, perceiving contours of objects requires orientation-sensitive filters together with mechanisms that process the collinearity of adjacent contour segments (e.g., Hess & Field, 1999). What is more, contour perception, at least of incomplete

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Address correspondence to: Matthias Niemeier, Department of Psychology, University of Toronto Scarborough, 1265 Military Trail, Toronto, ON M1C 1A4, Canada. E-mail: niemeier@utsc.utoronto.ca

contours, crucially depends on later visual processes and is probably associated with higher-level object areas such as the LOC (Murray et al., 2002).

We have previously demonstrated that contour perception is influenced by feature-based attention in similar ways as simpler features (Saenz et al., 2002). That is, we found that participants perceived object contours outside the spatial focus of attention more easily when at the same time they performed a difficult contour detection task compared to a difficult motion detection task (Stojanoski & Niemeier, 2007). Our results could not be explained by attentional mechanisms altering orientation sensitivity of neurons in striate or extrastriate areas (Liu et al., 2007). Instead, the data suggested that attention to motion inhibited contour perception, arguably at relatively late processing stages.

To confirm that feature-based attention to contours modulated brain activity at times later than the P1 (Valdes-Sosa et al., 1998; Zhang & Luck, 2009), we recently recorded electrophysiological signals while participants performed a contour perception task, either when they expected contours or motion, and we measured activity when they performed a motion perception task, either when expecting motion or contours (Stojanoski & Niemeier, 2011). We found that, during the motion task, attention modulated the P1, consistent with previous reports (Valdes-Sosa et al., 1998; Zhang & Luck, 2009). However, during the contour perception task, attention to contours modulated event-related potentials (ERPs) only at the time of the N2, 290 ms after stimulus onset, and we found that these signals approximately originated from regions anterior to extrastriate areas, perhaps consistent with the LOC. This suggests that feature-based attention modulates earlier or later neural processes depending on the attended feature, and that later modulations reflect altered activity in higher-tier visual areas such as the LOC, and/or changed activity in striate and extrastriate areas due to feedback from higher-tier areas or local bootstrapping.

However, our research on contours remains limited (Stojanoski & Niemeier, 2007, 2011), because contrasting attention to contours versus motion manipulates feature-based attention across different feature dimensions, whereas other studies compared attention to different feature values within the same feature dimension (such as to a certain color or a certain motion direction; McAdams & Maunsell, 2000; Motter, 1994; Saenz et al., 2002, 2003; Treue & Martinez-Trujillo, 1999; Zhang & Luck, 2009). Though both forms of attention, across and within feature dimensions, are regarded as feature-based forms of attention, they might not be based on the same mechanisms (Found & Müller, 1996). Therefore, it is possible that the late effects that we observed for feature-based attention to contours have less to do with cueing for complex features and more to do with the fact that we cued across feature dimensions. The latter form of cueing might be slower because it involves competition between distinct neural networks associated with motion and contours, respectively, that might evolve more slowly due to longer and fewer axonal connections. In contrast, competition among subpopulations of neurons representing different feature values within the same area or network might be resolved more quickly.

Unfortunately, within-feature dimension cueing (rather than between-feature dimension cueing) is not possible for contours because feature values of contours are undefined. Therefore, in the current study, we decided to investigate the feature dimension of shape. Our aim was to test whether cueing feature-based attention within the dimension of shape also produces late modulations of the ERP signal.

Comparatively late ERP modulations due to feature-based attention have been reported before (e.g., Eimer, 1995, used feature-based attention to drive the redistribution of spatial attention). However, our research differs from those studies in that we superimposed distractors onto our stimuli to establish competition between targets and nontargets. This has been shown to be critical in driving early attentional effects modulating ERPs (Zhang & Luck, 2009). What is more, previous studies using shape stimuli in the context of visual search were not directly interested in the processes underlying object perception, but other processes such as how object processing modulated visual search (Schubö & Müller, 2009; Võ & Wolfe, 2012). Moreover, the stimuli used previously were clearly discernible from the background with little or no distractors (e.g., Howard, Pharaon, Körner, Smith, & Gilchrist, 2011; Liu, Meng, Wu, & Huang, 2012).

In the present study, we explored the neural mechanisms underlying attentional influences on object perception, in the context of challenging perceptual conditions. We measured electrophysiological correlates of object perception while participants expected the correct or incorrect shape of pillows and flowers. Thus, we examined the influences of feature-based attention to shapes on the perception of objects. The objects were imperfectly defined by their contours so as to avoid pop-out, which could be processed preattentively (but see Volberg, Wutz, & Greenlee, 2012). Given that the LOC is important to shape processing (James, Culham, Humphrey, Milner, & Goodale, 2003; Kanwisher, Woods, Iacoboni, & Mazziotta, 1997; Malach et al., 1995), is strongly modulated by attention (Murray & Wojciulik, 2004; Niemeier, Goltz, Kuchinad, Tweed, & Vilis, 2005; other studies), and ventral temporal areas activation during object perception have been timed (using magnetoencephalography) to around 235–335 ms (Halgren, Mendola, Chong, & Dale, 2003), we hypothesized that attending to shapes should modulate the ERP signal at latencies similar to the effects described by Stojanoski and Niemeier (2011).

Method

Participants

Twenty-three neurologically normal undergraduate students (mean age: 20.3 years, 8 female) participated in our study (two participants were removed from the electroencephalography [EEG] analysis due to noisy signals). 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 (21) as confirmed with the Edinburgh handedness inventory (Oldfield, 1971).

Apparatus

Participants were tested in a dimly lit room seated 100 cm away from a 19-inch CRT monitor (Viewsonic, resolution: 1,024 × 768 pixels, refresh rate: 100 Hz, average luminance: 27.2 cd/m^2). We implemented our experiment using MATLAB (MathWorks, Natick, MA) with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

Stimuli and Procedure

We used a perceptually difficult object recognition task in which participants were instructed to perceive pillow- or flower-shaped objects composed of black and white lines embedded in an array of distracter lines. Participants then reported the main object color while their attention or expectation was cued to one of the two shapes.

Specifically, participants were instructed to fixate on a black fixation square (0.7° across) that appeared in the middle of a gray screen. One thousand to 1,500 ms later, an array (6.8° × 6.8°) of 76 black and 76 white scattered lines (4.95 pixels long) appeared. Thirty-eight of the lines, either mainly white or mainly black (ratio: 28 to 10), formed the outline of a flower or a pillow, about 3.4° across.

To construct pillows and flowers, trial by trial we first defined their virtual contours. Both types of contours were centered around the fixation point with 6–20 pixels positional jitter left- or rightward and were composed of four partial circles. Half circles were used for the flowers and arranged so that they intersected one another before meeting at their ends to form the convex shapes of the flowers' petals. Alternatively, for the concave sides of the pillows we used nonintersecting quarter circles that only met in one tangential point. As another (deliberately introduced) difference, flowers had symmetry axes with roughly vertical and horizontal orientation whereas pillows had roughly oblique symmetry axes. Also, the radius of the quarter circles was larger to equate the total length of the outlines of pillows. This was necessary to ensure that object contours had equally sized gaps when formed by the lines (see below).

Next, we selected 11 equidistant nodes on each circle segment, 44 for the entire shape. Six of the nodes, different from trial to trial, were dropped to create random gaps. To make the outlines visible, we then superimposed a randomly distributed array of distracter lines. The lines closest to the nodes were selected to become part of the object's contour. That is, they were slightly shifted to be centered on the respective node, and their orientation was chosen to be tangential to the contour at the node, except we added orientational noise within a range of ±11.8°, so that the resulting lack in collinearity together with the gaps in the contours and the ratio of white and black lines made it difficult to perform the task (~75% correct responses in naive observers). Also, we drew the lines in random order onto the gray background to avoid depth cues between object and background whenever white and black lines overlapped. Finally, we asked participants to report the color of the majority of the objects' lines so as to keep responses orthogonal to the shape cues and avoid nonperceptual response biases.

After 100 ms, the lines were replaced by a midgray screen, and after a delay of 700–1,200 ms (to reduce confounding motor activity), the words BLACK and WHITE appeared above and below fixation; participants were required to click on the word that corresponded to the main color of the object. A 500-ms intertrial interval followed (see Figure 1).

To examine how attention to higher-level features influences object perception, we cued within the feature dimension of shape. That is, we told participants which shape to expect in each block of 66 trials. In the valid pillows condition, pillows appeared 80% of the time and flowers appeared 20% of the time; the opposite was true for the valid flower condition. This way, we used the entire block of trials as the cue (advantages described by Found & Mu?ller, 1996), equivalent to the cueing strategy established by Stojanoski and Niemeier (2011).

Cueing attention to shapes constitutes a methodological challenge because different shapes will usually differ on multiple levels, and each object level could potentially be sufficient to tell the two shapes apart (e.g., Wolfe & Horowitz, 2004, for what features could possibly trigger earlier brain processes). However, here we were interested in participants using shape information at the global level of the entire shape. To this end, we pursued three strategies that we will illustrate by revisiting our stimulus and task design:

1. We eliminated shape cues at low levels to render bottom-up strategies useless: Because both shapes used the same black and white lines, it was essentially impossible to tell apart shapes on that level or by piecing lines together with bottom-up processes.
2. We reduced the usefulness of intermediate levels of shape cues: Although objects differed in their local features (apparent curvature, flower petals vs. pillow tips, etc.), searching for local features of the expected shape was made more difficult by contour gaps, limited collinearity, and distracter lines—using only this information would lead to frequent false alarms. What is more, because participants were asked to report the main color of the objects, a larger number of their lines had to be identified correctly. As a second possibility, participants could have searched for combinations of local features (curvature plus flower petals, etc.) instead of searching for the shapes as a whole. But, such combinations would be equivalent to a feature-conjunction search and less efficient than searching for just one feature. We argue that a feature search for shapes as a whole was quite feasible because the shapes' structure was simple, they were saliently different from one another, and as per repetition they were highly familiar to our participants.
3. We further encouraged participants to direct attention to the objects' shapes as a whole by providing obvious global shape cues: We chose the symmetry axes for pillows and flowers (and thereby their tips and petals) to differ by 45° so as to entice participants to look for these global cues.

Pillow and flower blocks were presented in pseudorandom sequence, counterbalanced across participants, for each testing session. A first session for training consisted of 4 blocks during which participants could familiarize themselves with the task. One to 7 days later, participants completed 12–18 blocks while we recorded EEG.

EEG Data Acquisition

We recorded continuous high-density EEG 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). The left mastoid served as online reference; offline, we recalculated the reference based on the average of the left and right mastoids as well as to the average of all electrodes. Electrode AFz served as ground. Electrode impedances were kept below 5 kΩ. The EEG signal was amplified with an ANT high-density amplifier (22 bit, 71.5 nV/bit) at a sampling rate of 512 Hz. The data were band-pass filtered offline between 0.1 and 100 Hz. Eye movements were monitored with horizontal (HEOG) and vertical electrooculograms (VEOG). Trials were detected and removed automatically using a 30 μV standard deviation threshold criterion within a 200-ms sliding time window across HEOG and VEOG electrodes.

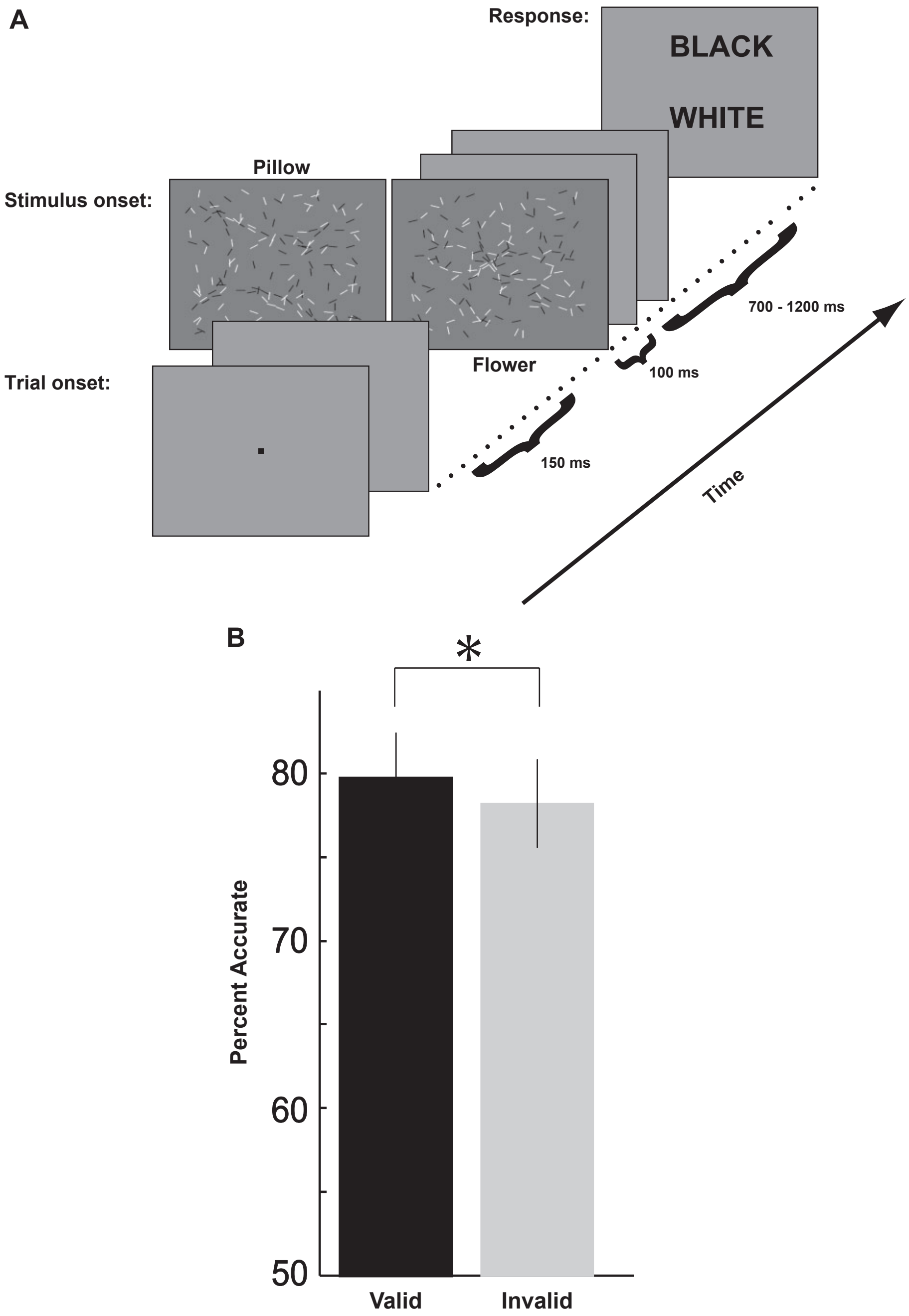

Figure 1. A: A representative example of the types objects used in the study (left: pillow, right: flower) in the context of a typical trial. Individual line segments were presented centrally and either formed the incomplete outline of a pillow or flower. Participants were informed at the start of each block what shape to expect (with 80% validity). Their task was to indicate the color of the object presented in each trial. The object could either be black or white, with proportionately the same number of distractor line segments of the color opposite the object. B: A bar graph representing mean performance accuracy (with *SEM*) for validly and invalidly cued objects, collapsed across type of shape.

ERP Analysis

Epochs ranged from −100 ms to 600 ms relative to stimulus onset, with the prestimulus period (−100 ms to 0 ms) serving as baseline. EEG data were then averaged across all valid and invalid trials, collapsing across pillows and flowers to avoid confounding influences specific to the chosen object shapes.

To examine timing differences in our ERP data, we ran a topographic pattern analysis using Cartool to obtain unbiased criteria for segmenting the data into distinct stable periods of neural activity (Brunet, Functional Brain Mapping Laboratory, https://sites.google.com/site/fbmlab/). The analysis takes advantage of the fact that ERPs are usually comprised of relatively prolonged periods of stable activation, called microstates, with quick transitions in between. Therefore, a k-means cluster analysis takes the concatenated grand-averaged data across all time points and uses linear correlations between electric field distributions (i.e., maps) at each time point to sort the data into temporally unique maps. The optimal number of segmented maps was based on (a) the fewest clusters that would (b) provide the largest global explained variance in the data (for a review, see Murray, Brunet, & Michel, 2008). Therefore, two criteria were used: a cross-validation criterion—the ratio between the global explained variance and the degrees of freedom, given the measure of the set of maps (Pascual-Marqui, Esslen, Kochi, & Lehmann, 2002) and a modified Krzanowski-Lai criterion—a dispersion quality of the clusters that is based on the pairwise distance of all topographies included in a given cluster (Krzanowski & Lai, 1985). The resulting set of maps (each with a minimum duration of 10 ms), which reflect differences in the underlying neural generators in the brain, are then compared between conditions. Comparing maps is tenable because maps are normalized to their global field power and independent of a reference electrode, and are therefore insensitive to differences in amplitude.

Next, we ran a topographic analysis of variance (TANOVA), a nonparametric statistical test using global dissimilarity, as the dependent measure between group-averaged maps at every time point (Lehman & Skandies, 1980). This analysis is complemented by a comparison of electric field strength: we calculated global field power (GFP) at each time point, for each subject and condition (Lehman & Skandies, 1980). GFP is a modified measure of the standard deviation of the scalp electric field at a given time and provides information about the strength of the electric field across conditions, even if the results of the topographic analysis yield no differences, suggesting overlapping neural generators activated to different degrees (e.g., Murray et al., 2008). To compare GFP differences, we computed successive pointwise paired *t* tests between the valid and invalid conditions, using a criterion of 11 consecutive time points (approximately 22 ms; Guthrie & Buchwald, 1991).

Finally, to explore the factorial structure of our data and for reference to classic ERP component analysis, we subjected ERP amplitude values, averaged across specific time windows (guided by the results cluster analysis and GFP), to a series of repeated measures ANOVAs with factors cue (valid vs. invalid), 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 Dien and Santuzzi, 2005). Additional targeted analyses inspected the P1 and N1 based on prior results (Zhang & Luck, 2009) and apparent trends, respectively.

Results

Behavioral Results

As expected, participants were more accurate when the presented stimulus had the cued shape ($M = 79.8\%$, $SD = 12.8$) compared to the invalidly cued shape ($M = 78.2\%$, $SD = 12.6$; factor validity of two-way ANOVA: $F(1,22) = 5.46$; $p = .029$). This effect was observed in 17 out of 23 participants. Also, pillows and flowers were perceived equally well (factor shape of two-way ANOVA: $F(1,22) = 1.57$, $p > .224$), and there was no interaction between validity and shape, $F(1,22) < 0.01$, $p = .937$.

Electrophysiological Results: General Overview

Figure 2 shows ERP waveforms for validly and invalidly cued conditions divided into occipital, central, posterior frontal, and anterior frontal scalp regions for the left and right hemisphere. Canonical ERP components, such as the P1 and N1, and P2, were found in both cueing conditions.

Topographic Pattern Analysis

To identify these components as part of the brain's activity as a whole, we chose an unbiased approach that segmented ERPs into independent microstates, or "maps" of stable activity using a k-means cluster analysis (Lehmann & Skandies, 1980). Based on the selection criteria (see Methods), we found 11 maps that best explained the ERP data for both the valid and invalid conditions (global explained variance = 96.1%). The first two maps (< 70 ms) were discarded due to low GFP and poor signal-to-noise ratio. Map 3 (70–107 ms) encompassed the P1 at lateroposterior electrodes. Map 4 (107–125 ms) reflected the decline of the P1 and the early phase of the N1, most prominently at occipital electrodes. The N1 continued through maps 5 (125–145 ms; with nearly identical time for valid and invalid) and 6 (145–190 ms), gradually extending to lateral occipital channels. The P2 was seen in map 7 (190–247 ms) over central and occipital electrodes, followed by an N2, a relative negativity over the same electrodes in map 8 (247–330 ms). In map 9 (320–440 ms), we found relative positivity over central and occipital electrodes, but relative negativity over frontal electrodes. Maps 10 and 11 (valid: 437–600, transition for valid: 513 ms, transition for invalid: 468 ms) encompassed central positivity with changes to greater negativity over posterior channels and reduced negativity over frontal channels.

To examine whether valid and invalid maps differed statistically in topography, we used a TANOVA to identify time points at which the two conditions were systematically dissimilar. This was the case during map 8 (252–283 ms) and map 10 (482–504 ms; Figure 3).

Global Field Potentials

Even with topographies showing no differences before 252 ms, there might have been differences in signal amplitude. Therefore, we calculated GFP measures in response to valid and invalid stimuli and then computed successive *t* tests on the GFP values (Figure 3; note that we included data after 70 ms because early GFP values are small and therefore would be importantly influenced by the differences in numbers of valid and invalid trials; we have previously shown that for larger GFPs the effect essentially disappears, Stojanoski & Niemeier, 2011). Given our significance criterion of 11 consecutive significant time frames (approximately 22 ms), greater signal strength during the invalid condition first emerged between 287 ms to 341 ms corresponding to the second half of map 8. Significantly greater signal strength in the invalid condition also appeared between 385 ms to 526 ms (comprising the latter half of map 9, map 10, and the first portion of map 11) and 548 ms to 600 ms (latter portion of map 11).

ERP Component Analysis

To ensure that our analyses so far had not overlooked attentional effects at earlier times and possibly to explore the factorial structure of effects, we conducted a series of additional tests of mean ERP differences in amplitude submitted to repeated measures ANOVAs with cue, hemisphere, and scalp region as factors. Time windows for this analysis were selected based on the results of the topographic pattern analysis or based on the relevant time window

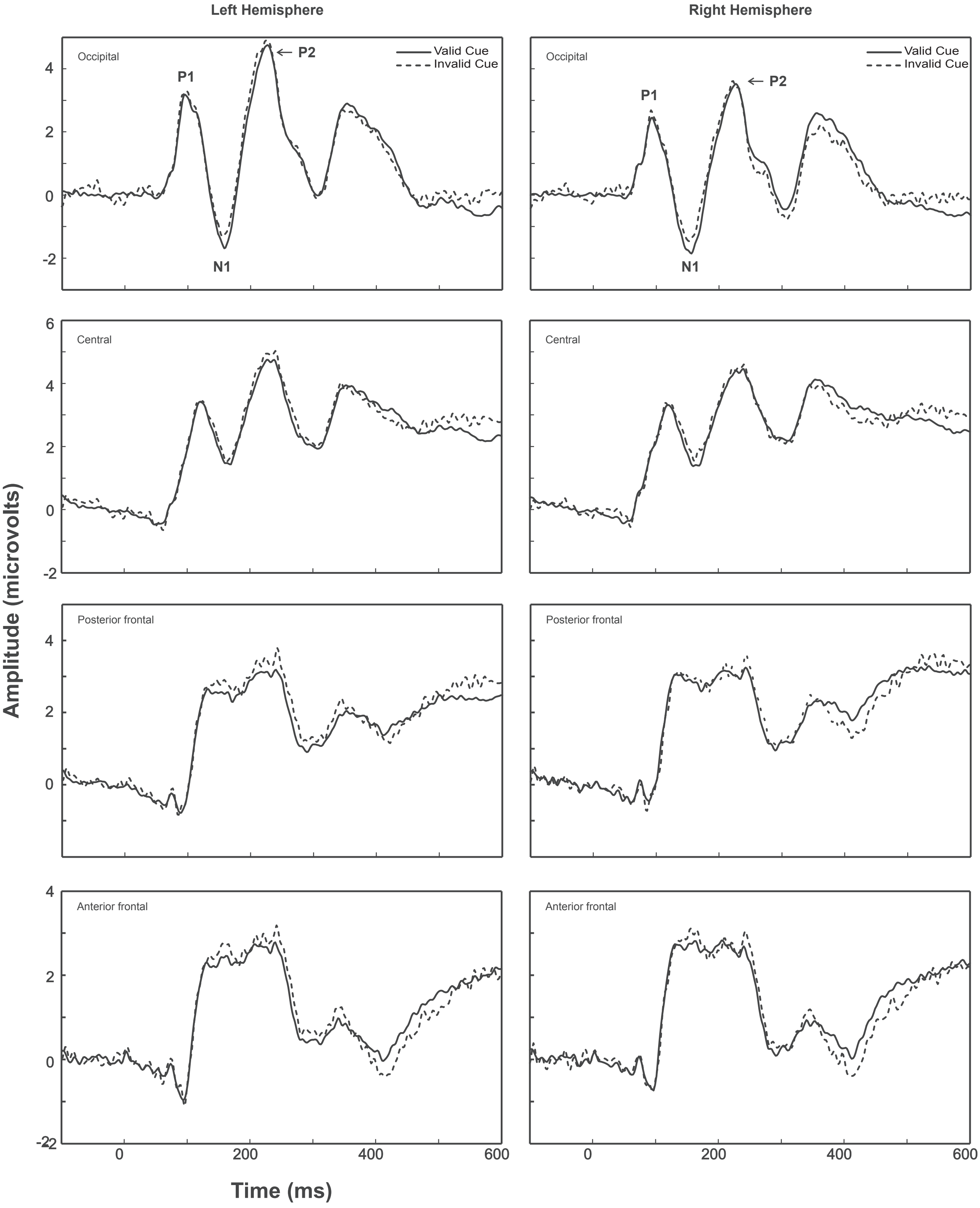

Figure 2. Grand-averaged ERP results ($N = 21$) from each condition (valid vs. invalid) divided into the mean of eight scalp topographic locations: occipital, central, posterior frontal, and anterior frontal for both the right and left hemisphere. The difference between the two conditions is most visible over occipital electrodes, with significant differences emerging after 322 ms, despite examining earlier components such as the N1.

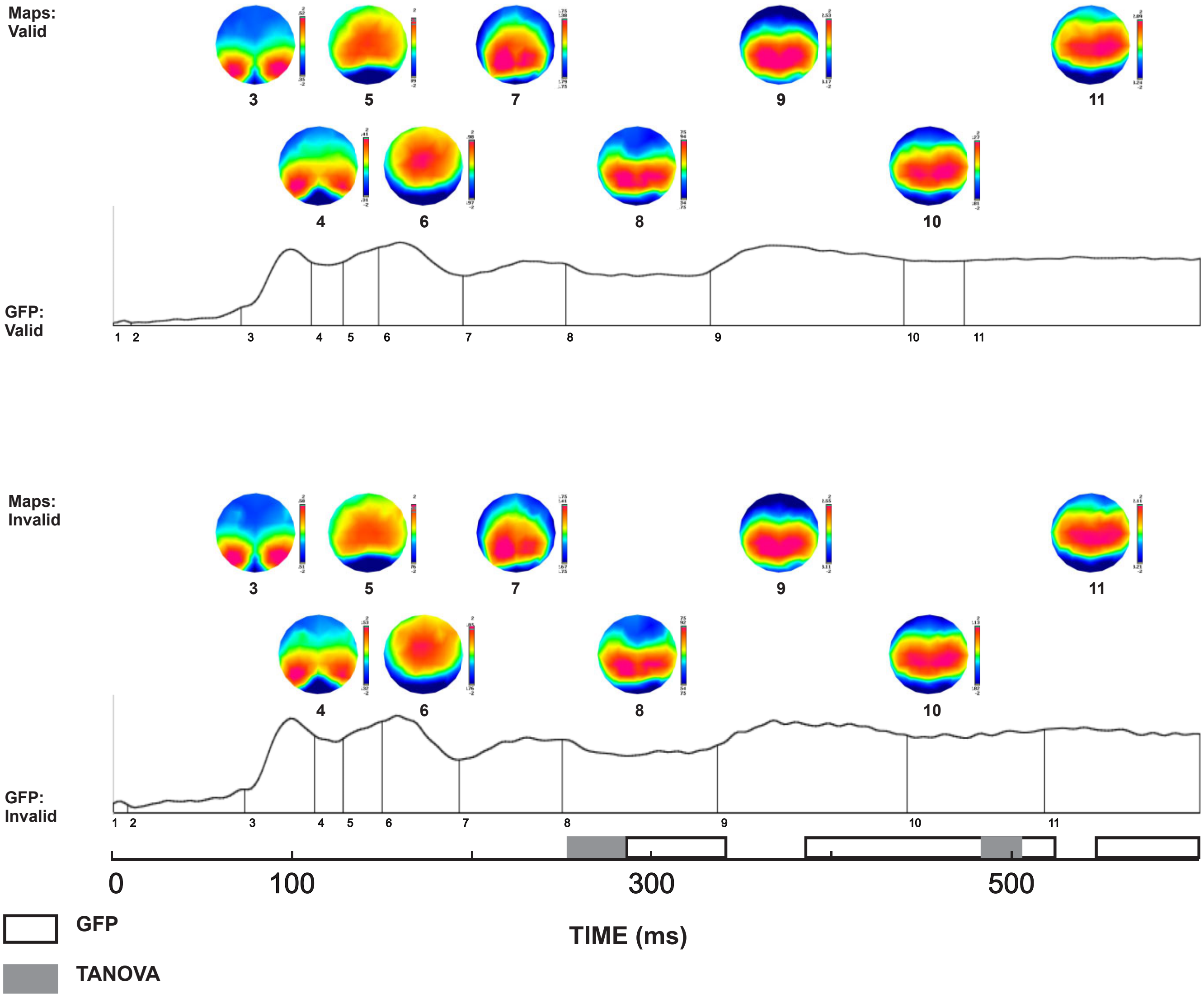

Figure 3. Results of the spatiotemporal topographic pattern analysis revealed segments of stable neural configuration for validly and invalidly cued shapes. Each map is identified with a number corresponding to a segment displayed below the maps. Two statistical tests are provided: TANOVA indicated significant differences ($p < .05$ for 11 consecutive time frames) from 252 ms to 283 ms (within map 8) and 482 ms to 504 ms (within map 10; open white box). Successive pointwise paired *t* tests ($p < .05$ for 11 consecutive time frames) of the GFP revealed modulations in signal strength starting at 287 ms to 341 ms and again at 385 ms to 526 ms (shaded gray region).

from previous findings. Four time periods, guided by the cluster analysis, were of interest. Two early periods were selected based on previous reports of early ERP modulations: (1) 80–130 ms (i.e., the time window of the P1) was selected because of previously reported modulations by feature-based attention to color (80 ms–130 ms, i.e., the P1, consistent with Zhang and Luck, 2009; in addition, Volberg et al., 2012, reported similarly timed modulations for contours vs. no contours); (2) 130–180 ms (i.e., the N1) was selected because of reported modulations by illusory contours (Murray et al., 2002). Time periods (3) and (4) were selected based on our previous findings of late ERP modulations by attention to complex features (Stojanoski & Niemeier, 2011). Specifically, we explored the part of map 8 (252 ms–283 ms) that coincided with the earliest differences in TANOVA, and we selected map 9 (330 ms–440 ms) because this latency overlapped with the second time period of GFP modulation.

The ANOVAs revealed four significant effects (for a complete account of all F tests, see Table 1): A significant main effect of scalp region at the second time window (130–180 ms; $F(1.095,19.717) = 12.88$; $p = .001$) simply reflected the polarity inversion of the N1 across the scalp. The analysis for the third time window, 252 ms–283 ms, revealed a Scalp Region × Cueing interaction, $F(1.378,24.78) = 4.09$; $p = .042$, reflecting slightly stronger effects over the right hemisphere. The fourth time window, 330 ms–440 ms (map 9), was marked by a significant main effect of scalp region, $F(1.22,22.01) = 8.82$; $p = .0007$, reflecting greater negativity over frontal areas and positivity over posterior areas in both conditions. Furthermore, the fourth time window yielded a significant main effect of cueing, $F(1,18) = 5.34$; $p = .033$, indicating that cueing feature-based attention produced greater positivity in the valid-cued condition relative to the invalid-cued condition. That is, overall the valid condition showed relatively greater

Table 1. *Results from 2(Cue) × 2(Hemisphere) × 4(Scalp Regions) ANOVAs for Four Time Windows of Interest*

Valid versus invalid Time window 1 80–130 ms Source	*F*	*p*	Valid versus invalid Time window 2 130–180 ms Source	*F*	*p*
Scalp region	3.819	.06	Scalp region	12.88	.001*
Hemisphere	0.321	.578	Hemisphere	0.19	.891
Cue	3.163	.092	Cue	0.264	.613
Scalp Region × Hemisphere	1.93	.176	Scalp Region × Hemisphere	2.84	.09
Scalp Region × Cue	3.01	.08	Scalp Region × Cue	1.352	.271
Hemisphere × Cue	3.523	.077	Hemisphere × Cue	0.18	.676
Scalp Region × Hemisphere × Cue	1.22	.306	Scalp Region × Hemisphere × Cue	0.264	.766
Valid versus invalid Time window 3 252–283 ms			Valid versus invalid Time window 4 385–526 ms		
Source	*F*	*p*	Source	*F*	*p*
Scalp region	2.676	.114	Scalp region	8.816	.0007*
Hemisphere	0.619	.442	Hemisphere	1.778	.199
Cue	0.693	.416	Cue	5.341	.033*
Scalp Region × Hemisphere	2.181	.143	Scalp Region × Hemisphere	1.751	.197
Scalp Region × Cue	4.092	.042*	Scalp Region × Cue	2.24	.125
Hemisphere × Cue	4.69	.044*	Hemisphere × Cue	0.443	.514
Scalp Region × Hemisphere × Cue	1.391	.261	Scalp Region × Hemisphere × Cue	1.333	.276

*Significant main effects and interactions.

positivity compared to the invalid condition, which was most noticeable across all the electrodes over the right hemisphere. Therefore, consistent with other analyses, the results of the ANOVA revealed significant modulation of the ERP signal primarily at later latencies.

Despite not finding significant differences in mean amplitude at the two early time windows, we conducted a series of *t* tests comparing ERPs at the spatial and temporal peaks of the P1 and N1. We found no significant effects at the P1 (e.g., PO3 to PO8: $t = 0.212$; $p = .835$). *T* tests inspecting the N1 for several combinations of posterior electrodes found trends of significance, though only before Bonferroni correction (all occipital electrodes: $t = 2.013$; $p = .059$; O1, O2, PO3 to PO6: $t = -2.02$; $p = .0589$; PO5 to PO8: $t = 1.99$; $p = .0623$).

Discussion

In the current study, we investigated the electrophysiological correlates of visual feature-based attention to the dimension of shape while participants performed a difficult object perception task. Participants tried to identify the incomplete outlines of pillows or flowers among distracter lines and then report the object's predominant color. We found that they reported more accurately when they correctly expected a shape during valid trials compared to unexpected shapes during invalid trials. Crucially, this behavioral difference was reflected in the ERPs—the observed late modulations of the electrophysiological signal were a result of expecting the correct shape.

Our ERP data revealed late effects across several statistical analyses. Comparisons of topography and global signal strength indicated that shape cues modulated ERPs after 252 ms, but none of our analyses revealed any earlier feature-based effects.

Were our behavioral feature-based effects, though significant, perhaps too small and cueing too inconsistent to produce earlier ERP modulations? We argue that this is unlikely. To begin with, due to training, participants performed better than planned. The targeted level of 75% correct responses should have produced larger cueing effects, which suggests that observed behavioral effects rather underestimated true influences of attention. Other reasons for the relatively small behavioral effects are less convincing. One reason would be inconsistent use of the attentional cue across participants. However, we found that 17 out of 23 participants did show the effect. Inconsistency within participants is also unlikely. It implies that more consistent usage of the cue would have been more advantageous. But then, why would participants not be motivated to use the cue consistently, especially given that performance was far from ceiling? What is more, shape cues remained the same across entire blocks of trials, thus cognitive inertia helped participants focus their attention on the respective valid shape. Finally, behavioral effects do not necessarily map in a linear way onto electrophysiological data. For the time frame of the N2, we did obtain clear modulations of ERPs depending on cue validity, whereas for the P1 and N1 time frames, we did not, even with more specialized (and more alpha-error prone) analyses. In sum, given that we tested a large number of participants and obtained robust effects at later times, we believe that our results provide grounds to assume that the absence of earlier ERP modulation has nothing to do with a weak attentional effect.

However, is it possible that our paradigm was altogether unsuitable to produce feature-based modulations of the P1, and might P1 effects be a rarity? We believe that was not the case. There is a growing literature that shows early P1 effects for feature-based attention. Though the effects reported by Valdes-Sosa and colleagues (1998) might have been governed by object-based rather than feature-based attention, Zhang and Luck's (2009) observation of P1 modulations has been confirmed by a recent study from our lab (Stojanoski & Niemeier, 2011) using a paradigm similar to the current one, as well as by Bondarenko and colleagues (2012). Based on these studies, it appears that P1 effects require some combination of perceptually challenging stimuli (e.g., due to distracters overlapping with the stimulus) and feature-based attention already being deployed to the respective feature. Both these aspects were part of the current paradigm.

Could our effects reflect influences of perceptual priming rather than attention? If priming was a factor, then we should have seen a reduction in the electrophysiological signal at early time windows (Henson, Rylands, Ross, Vuilleumeir, & Rugg, 2004; Schendan & Kutas, 2003). However, our effects occur much later. Sometimes, late priming effects are observed, too (e.g., Grill-Spector, Henson, & Martin, 2006; Gruber & Müller, 2005; Henson et al., 2004), which would suggest reduced amplitudes, but that was not the case—at least not for our earliest effects (252–283 ms). The most important reason why none of our effects could be explained by priming is that 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. Given the relatively short time frame in which timing is most powerful, and given that we only use two types of shapes, both validly and invalidly cued pillows and flowers should have reached the plateau within the first block of trials and remained there for the rest of the experiment. Thus, for both early and late ERP modulations, priming cannot have played a significant role in the present study; the effects are due to attentional cueing.

Therefore, our shape-based attentional effects are consistent with the late onset of effects around the time of the N2 that we have previously observed for attention to contours (Stojanoski & Niemeier, 2011). In contrast, our effects occurred substantially later than the modulations around the time of the P1 reported for attention to other features such as color and motion (Stojanoski & Niemeier, 2011; Valdes-Sosa et al., 1998; Zhang & Luck, 2009).

These timing differences cannot be explained by feature-based attention being cued to different feature dimensions as opposed to specific values within a feature dimension. We used between-dimension cueing (contours vs. motion; Stojanoski & Niemeier, 2011) as well as within-dimension cueing (pillows vs. flowers) and found nearly no difference in the timing of our effects. Other explanations are unlikely, as well: Though greater retinal eccentricity can delay contour sensitive effects (Murray et al., 2002), it cannot play a role here since we presented stimuli foveally, whereas our previous experiment used stimuli outside the fovea. Therefore, if eccentricity had any effect at all, presenting stimuli foveally should have caused ERP effects to occur earlier. Furthermore, the absence of earlier effects cannot be explained by using a more challenging task. We kept performance at a similar level to our previous study where only attention to motion produced early effects. Another similarity was that we used distracting line segments that were presented together with the stimuli, which Zhang and Luck (2009) have shown to be an important factor in amplifying modulations of the P1, at least for attention to color. Instead, we argue that our late attentional effects arise for reasons specific to cueing attention to the shape of object contours.

One might argue that attention could have been directed to aspects of the stimuli that are more basic than their shapes. In fact, though pillows and flowers were composed of the same lines with the same colors, the lines formed different incomplete circle segments with different radiuses. Furthermore, the two symmetry axes of the shapes were differently oriented. Therefore, one could assume that attention may have been directed to local object parts, such as the apparent curvature or orientation of object parts, and, according to Wolfe and Horowitz (2004), curvature and orientation may be a rather basic feature. However, this would have been a poor perceptual strategy for four reasons: (1) the objects' contours were incomplete, making local strategies prone to false alarms. Telling which lines belonged to the object contour and which ones were distracters was difficult without perceiving the entire object first; (2) the task was to report the color of the majority of the object lines, thus a local strategy would often produce incorrect answers; (3) the perceptual strategy would make no use of the global shape cue of object axis orientation; and (4) the strategy would operate against the default dominance of global over local perception (Navon, 1977). Therefore, an attentional strategy directed to features other than shape is unlikely, and the late ERP effects appear to be easier to explain with shape-based attention. But what are the reasons for the late effects?

Even if shape perception processes differ from motion and color perception in several ways, these differences do not necessarily account for the long delays. That is, perception extracts object shapes and contours based on orientation-sensitive filters in striate or extrastriate areas (e.g., Hess & Field, 1999), whereas it begins extracting color and motion only a few synapses beyond the photoreceptors. This, however, only amounts to a small delay given that neurophysiological studies suggest that visual information travels to early cortical areas within tens of milliseconds (e.g., Bullier, 2001). Although it is unlikely that ERPs will reflect the same timing, one might wonder whether modulations of the P1 or even C1 should be observed.

In principle, such early ERP effects are not inconceivable, even for shapes. A growing literature suggests that the C1 and P1 are sensitive to surprisingly complex tasks including perception of fearful faces (Pourtois, Grandjean, Sander, & Vuilleumier, 2004; West, Anderson, Ferber, & Pratt, 2011), task set effects on visual word perception (Proverbio & Adorni, 2009), and attention to natural or human-made objects (Zani & Proverbio, 2012). These effects are probably associated with combinations of simple feed-forward filters, as this has been successfully implemented in machine vision studies on scene categorization (e.g., Torralba & Oliva, 2003) and face processing (Viola & Jones, 2001).

Still, even more complex filter mechanisms in higher visual areas could produce ERP effects that are earlier than ours. The sight of clearly visible objects has been shown to modulate ERPs no later than the N1 (e.g., Doniger et al., 2000; Murray et al., 2002; Rousselet, Macé, & Fabre-Thorpe, 2004; Tanaka & Curran, 2001), and the same is true for certain forms of object-based attention, which let spatial attention spread across the surface of objects (Kasai, 2010; Kasai, Moriya, & Hirano, 2011; Kravitz, & Behrmann, 2008; Martínez, Teder-Sälejärvi, & Hillyard, 2007). Furthermore, focusing on just one kind of local feature (flower petals vs. pillow tips) would have implied ignoring available information. Focusing on conjunctions of such local features (petals plus degree of curvature) would have required inefficient feature-conjunction searches (Wolfe & Horowitz, 2004). Therefore, we argue that the most likely reason for our late effects is that the incompleteness of our stimuli requires the visual system to extract shape information likely based on multiple iterations. Probably only at these later processing stages are participants able to make the fine-grained discriminations between pillows and flowers. Previous studies examining the time course of object perception provide evidence for a late stage of object processing (Martinovic, Gruber, Ohla, & Muller, 2009) that reflects more detailed fine-grained object identification (Clarke, Taylor, Devereux, Randall, & Tyler, 2012; Halgren et al., 2003; Liu, Agam, Madsen, & Kreiman, 2009). It is likely that feature-based attention is acting upon these later object-processing mechanisms required to differentiate pillows from flowers. These late effects can be driven by iterations, either in higher-tier object areas (such as LOC; Halgren et al.,

2003) or implemented in feed-forward and feedback projections between low- and high-level areas (Lamme & Roelfsema, 2000). The significance of feedback connections has been included to provide a physiologically plausible interpretation of object perception (Dura-Bernal, Wennekers, & Denham, 2011) and has been pointed out in computational approaches to vision (e.g., Kersten, Mamassian, & Yuille, 2004; Rao & Ballard, 1999. Furthermore, there is ample physiological evidence that feedback projections are available throughout the visual cortex, and at least for a range of stimuli at early stages (Bullier, 2001). Though our study provides no direct evidence that equivalent processes are involved, alternative effects should have occurred earlier.

In conclusion, in the current study we used an approach that to our knowledge is unique in that we cued within the higher-level feature dimension of shape in the context of an object perception task. Previous studies on feature-based attention often used features of lower-level complexity (e.g., color, orientation, motion) in the context of simple perceptual tasks, (e.g., transient detections such as changes in luminance or motion). However, attention is often closely linked to the brain functions on which it operates (Awh, Armstrong, & Moore, 2006; Moore & Fallah, 2001). With our new approach, we provide evidence that cueing feature-based attention to shapes influences object perception, and that this influence modulates the ERP signal at later latencies (252 ms–502 ms) consistent with the time course of our previous findings on contour-based attention. Though more research is required to demonstrate that these effects pertain to locations outside the spatial focus of attention, our results provide insight into the flow of information along the visual hierarchy, possibly reflecting the interplay of feed-forward and feedback projections. Further research is required to identify more specifically the factors that determine the nature and the time course of these projections and the degree to which these effects pertain to other aspects of object perception.

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