

Colour expectations during object perception are associated with early and late modulations of electrophysiological activity

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Abstract It is well known that visual expectation and attention modulate object perception. Yet, the mechanisms underlying these top-down influences are not completely understood. Event-related potentials (ERPs) indicate late contributions of expectations to object processing around the P2 or N2. This is true independent of whether people expect objects (vs. no objects) or specific shapes, hence when expectations pertain to complex visual features. However, object perception can also benefit from expecting colour information, which can facilitate figure/ground segregation. Studies on attention to colour show attention-sensitive modulations of the P1, but are limited to simple transient detection paradigms. The aim of the current study was to examine whether expecting simple features (colour information) during challenging object perception tasks produce early or late ERP modulations. We told participants to expect an object defined by predominantly black or white lines that were embedded in random arrays of distractor lines and then asked them to report the object's shape. Performance was better when colour expectations were met. ERPs revealed early and late phases of modulation. An early modulation at the P1/N1 transition arguably reflected earlier stages of object processing. Later modulations, at the P3, could be consistent with decisional processes. These results provide novel insights into

feature-specific contributions of visual expectations to object perception.

Keywords EEG/ERP · Object perception · Visual expectation · Figure/ground · Attention

Introduction

Inevitably, a person studying perception will come across the same strange black-and-white image composed of random dots, and when asked “Do you see the dog?” they will realize that indeed, embedded in the image, there is a scene with a Dalmatian (Gregory 1970). This demonstrates the long-known phenomenon that visual expectation aids object perception. Consistent with it, more recent and formal approaches to object perception argue that the visual system attempts to predict its sensory inputs through feedback projections from higher- to lower-tier areas, that is, in principle it is clear that the brain is able to convey prior information to cope with the overabundance and incompleteness of information about the surrounding sensory world (e.g. Clark 2013; Desimone and Duncan 1995; Dolan et al. 1997; Harrison and Tong 2009; Hegdé and Kersten 2010; Rao and Ballard 1999; Yuille and Kersten 2006). Yet, how these top-down mechanisms work specifically remains largely unclear. Important cues to their understanding may come from examining how the neural correlates of perception develop over time.

To our knowledge, only a few studies have investigated the timing of visual expectation effects in difficult object perception tasks. For example (Melloni et al. 2011) manipulated object visibility and expectations with decreasing and then increasing signal-to-pixel-noise ratios. They found that expectations relative to no expectations reduced the

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second positive deflection of the visual event-related potential (ERP), called the P2 at around 180–270 ms (and apparently increased the subsequent second negative deflection or “N2”). Two studies by Stojanoski and Niemeier (2014) showed poorly visible objects and controlled expectations about object shapes or about the object-defining feature dimension (i.e. their contours; Stojanoski and Niemeier 2011). In both studies, the N2 showed greater positivity with valid compared to invalid expectations at around 250 ms and later. Thus, despite variations in tasks, stimuli and degrees of perceptual learning, studies so far agree that visual expectations cause modulations of visually evoked potentials that occur late compared to how quickly signals could travel through the entire visual system (e.g. ERPs in response to the sight even of complex visual objects modulate the first negative deflection or “N1” at about 120–170 ms; Bentin et al. 1996; Murray et al. 2006; Rossion et al. 2000; Rousselet et al. 2008). Therefore, visual expectations in object perception tasks seem to afford multiple rounds of recurrent processing before a percept emerges (Lamme and Roelfsema 2000).

Earlier ERP modulations of the P1 between ~80 and 160 ms have been reported in feature-based attention tasks (Zhang and Luck 2009; for similarly early effects in terms of time and areas see: Andersen et al. 2011; Anllo-Vento et al. 1998; Bondarenko et al. 2012; Eimer 1997; Müller et al. 2006; Schoenfeld et al. 2007). Although the terms “attention” and “expectations” often seem to pertain to the same or at least similar top-down processes (e.g. Egner et al. 2010; Spratling 2008; Summerfield and Egner 2009), the term “feature-based attention” is commonly referred to in the context of relatively simple, non-spatial visual features, such as colour, motion direction and spatial frequency (e.g. Maunsell and Treue 2006; although see Wolfe and Horowitz 2004, for a comprehensive discussion of what is a feature). Furthermore, feature-based attention is typically tested in simple tasks probing detection of transients such as colour flicker or sudden changes in motion direction. Finally, as one of the defining aspects of feature-based attention, it supports processing of congruent features outside the spatial focus of attention, throughout the visual field (Bartsch et al. 2014; Boehler et al. 2011; Rossi and Paradiso 1995; Saenz et al. 2003, 2002; Treue and Martinez Trujillo 1999).

However, such non-spatial properties are not restricted to simple detection tasks. Object perception too is modulated outside the focus of attention depending on whether participants expected motion or object-defining contours (Stojanoski and Niemeier 2007), thereby supporting the notion that visual expectation for object perception and attention to colour or motion for transient detection could in some ways recruit the same or similar neural resources, despite differences in relevant features and tasks. So then, it

would be feasible to assume that visual expectations could yield early ERP modulations if participants expected object features such as colour or features that aid early stages of object perception.

However, early ERP modulations are not necessarily to be expected. Even within the realm of feature-based attention research, there is evidence that feature-based processes involve at least two independent mechanisms, one that pertains to attention to readily available visual stimuli, perhaps involving basic forms of gestalt perception, and one that recruits working memory or memory buffers for attentional sets, even when visual input is not imminently present (Mendoza et al. 2011). In other words, different feature-based processes could be more or less involved depending on the particular task or respective goals and strategies (e.g. Navalpakkam and Itti 2007; Bridwell et al. 2013). Given this, it would be feasible that expectation-based modulations of object perception reflect different neural mechanisms (Melloni et al. 2011; Stojanoski and Niemeier 2011, 2014) whose timing is unrelated to the timing of feature-based attention (e.g. Zhang and Luck 2009).

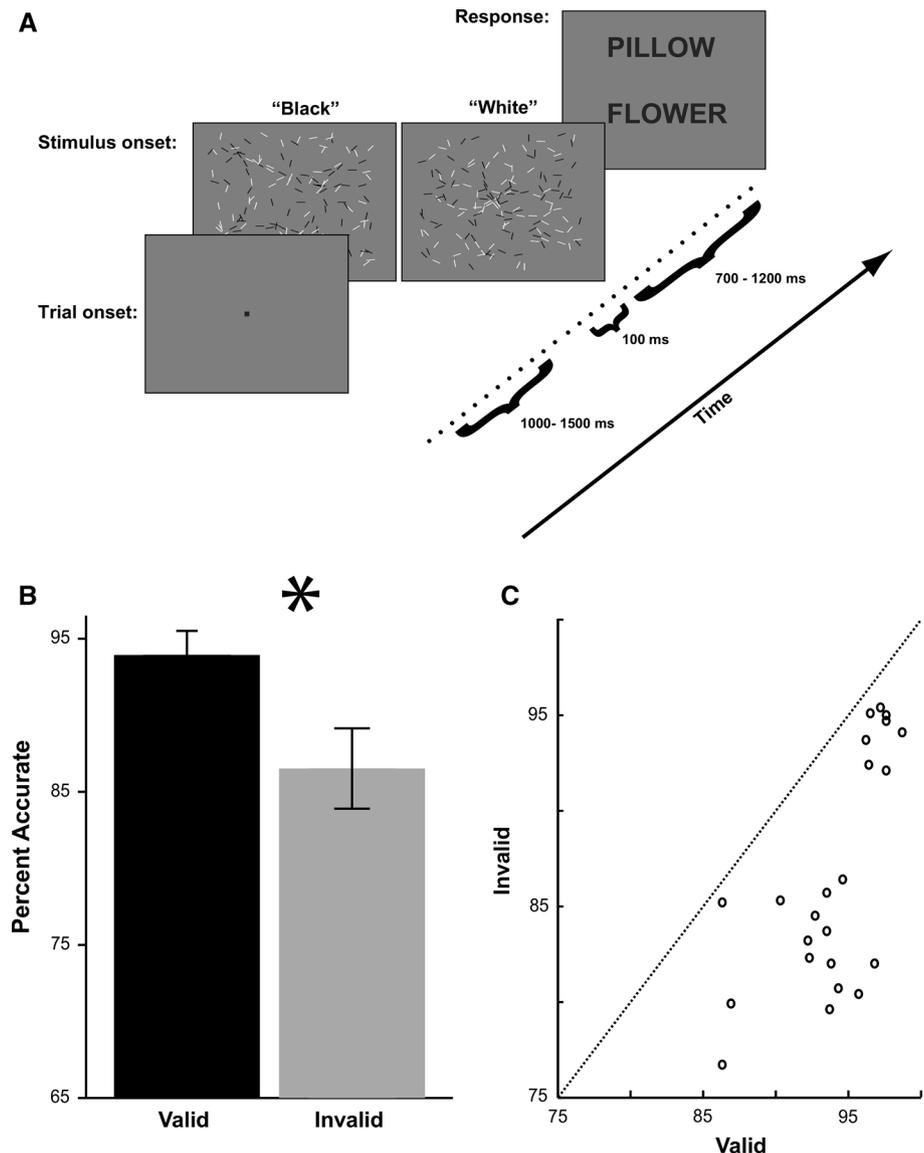
In the current study, we tested whether top-down influences of visual expectations can influence the electrophysiological signals associated with object perception tasks earlier than reported so far if these expectations pertain to the object’s colour rather than its shape or other more complex aspects of the stimuli. Alternatively, expectations might modulate perception within a later time window regardless of the type of top-down information. Therefore, we examined ERPs in response to a perception task with objects defined by degraded contours. Participants reported the shape of objects, while they correctly or incorrectly expected the objects to have a certain colour, thereby facilitating or impeding basic aspects of object perception, such as figure/ground perception and/or contour integration. If complexity of the cued feature mattered, we should observe early ERP modulations near the P1. However, if the task or its complexity mattered, ERP modulations should occur later. We found that ERPs were modulated early, at the P1/N1 transition. Interestingly, we also observed later modulations possibly reflecting later perceptual or decisional processes.

Methods

Participants

Twenty-three (13 female) undergraduate students from the University of Toronto Scarborough participated in the study for course credit. All participants confirmed an absence of any neurological challenges, reported normal or corrected-to-normal vision and ranged in age from 17 to

Fig. 1 a A representative trial, including examples of the types of objects used (*left* pillow, *right* flower) in the experiment. Individual line segments were presented centrally and either formed the incomplete outline of a pillow or flower. Stimuli were presented for 100 ms and then replaced by a grey screen (not shown). Participants were informed at the start of each block what object colour to expect (with 80 % validity). Their task was to indicate the object's shape in each trial. The object could either be a pillow or flower, with the same number of line segments forming the shape and serving as distractors. **b** A bar graph representing mean performance accuracy (error bars represent bootstrapped 95 % confidence intervals) for validly and invalidly cued objects collapsed across type of colour. **c** Scatterplot of individual participants



23 years ($M = 18.34$, $SD = \pm 1.23$). Two participants were left-handed as confirmed by the Edinburgh Handedness Inventory (Oldfield 1971). Prior to their inclusion in the study, participants gave their informed and written consent. All procedures were approved by the Human Participants Review Sub-Committee of the University of Toronto.

Apparatus and procedure

The participants were tested in a quiet, dimly lit room. They were seated 100 cm away from a 19-inch CRT monitor (ViewSonic, refresh rate: 100 Hz, 1024 by 768 pixels, average luminance of 26.8 cd/m^2). The experiment was programmed in MATLAB (MathWorks, Natick, MA) along with the Psychophysics Toolbox (Brainard 1997; Pelli 1997).

Our paradigm investigated how the electrophysiological correlates of object perception change depending on whether people expect the object to have a certain colour (luminance polarity) or whether their expectations are wrong. Each trial started with participants fixating a centrally presented square (0.7° across). One thousand to 1500 ms later, a display containing 152 lines (5 pixels long) appeared centrally on the screen with up to ± 20 pixels horizontal jitter. Thirty-eight of the lines (ratio 28–10) formed the incomplete and jagged outline of a shape, either a “pillow” or a “flower” (Fig. 1; description below). After 100 ms, a grey screen masked the display for 700–1200 ms (to discourage preparatory motor activity). Only then, the words “pillow” and “flower” appeared above and below the fixation square, and participants selected their response per

mouse click (10-s timeout). Subsequently, there was a 500-ms delay before the next trial.

We grouped trials into blocks of 66, each starting with instructions displayed and read to the participants to inform them which object colour, white or black, would be more likely (about 70 vs. 30 %). Thus, we used a non-spatial, feature-based approach to cueing expectations similar to a Posner paradigm (Posner 1980) with entire blocks of trials providing “valid” or “invalid” colour cues (note that object perception during valid as well as invalid trials could benefit from participants knowing that only one of two shapes were possible; however, shape information was the same across conditions; equivalent to a Posner task were it is clear that a target appears at one of the two locations but nowhere else). On average, 11.4 experimental blocks were tested with the order of the conditions counterbalanced within subjects and randomized between subjects.

Stimuli

To construct pillows and flowers, trial by trial we first defined their virtual contours. Both types of contours were centred on the fixation point 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. Instead, for the concave sides of the pillows, we used non-intersecting quarter circles that only met in one tangential point (see Fig. 1a). As another 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.

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. The remaining nodes were superimposed with a random array of distracter lines. The lines closest to the nodes were shifted to be centred on the respective node, and their orientation was chosen to be tangential to the contour’s local orientation, except we added orientational jitter within a range of $\pm 11.8^\circ$, so that the resulting lack in collinearity (together with the gaps in the contours) made it difficult to perform the task (~75 % correct responses in naive observers). Controlling object visibility with orientation jitter has the advantage that local aspects of the display remain unchanged. We drew the lines in random order onto the grey background to avoid depth cues between object and background whenever white and black lines overlapped. “Black” object contained 28 black lines and but also 10 white lines to encourage participants to perceive the objects as a whole; “white” objects had the opposite colour ratio. The colour ratio of the background lines was chosen so that each trial showed the same numbers of white and black lines. We decided to focus on

achromatic colours to keep luminance contrast at high levels across all participants so that we could safely ignore inter-individual differences in the influence of luminance on gestalt visibility (Gregory 1977) and instead manipulate visibility selectively along the dimension of contour collinearity. The same kind of stimuli was used by Stojanoski and Niemeier (2014). However, the previous study investigated shape expectations.

Data acquisition

Continuous high-density electroencephalographic (EEG) data were acquired with a 128-channel Electrical Geodesics Inc. (EGI) system (v. 200) consisting of Ag/AgCl Geodesic Sensor Net electrodes, using the Net Amps 300 amplifier, and Net Station software running on a Mac Pro computer. EEG data were referenced to Cz online, and the computed average of all electrodes was selected as the reference offline. Electrode impedances were kept below 70 k Ω . The EEG was acquired at a sampling rate of 250 Hz.

ERP analysis

Using Cartool (Functional Brain Mapping Laboratory, <http://brainmapping.unige.ch/cartool.php>; Brunet et al. 2011), the data were filtered offline between 0.1 and 80 Hz using a second-order Butterworth filter with -12 dB/octave roll-off sliding window filter as implemented in Cartool. Trials with amplitudes greater than 60 μ V indicative of eye movements or blinks were removed based on frontal electrodes near the eyes. To compute ERPs for valid and invalid conditions, “black” and “white” trials were first averaged together. Epochs were selected from -100 to 600 ms post-stimulus onset; the pre-stimulus time frame was used as the baseline.

We used several statistical approaches to analyse data to capture different aspects of potential changes in ERP signals. The first method used consecutive t tests to compare valid and invalid trials at all electrodes and time points to gain a spatiotemporal overview of the ERP effects. A criterion of 11 or more consecutive time frames where $p < 0.05$ (Guthrie and Buchwald 1991) was used to determine significance.

The second method analysed the scalp electric field. For this, we ran a k -means cluster analysis to identify temporally unique periods of activity, called maps. Cluster analysis was applied as a data-driven approach to select important time periods for subsequent analysis. Template maps were then back-projected onto individual ERP data where the duration of each map was used as a measure to determine which maps best represented each subjects’ data.

As a third method, we computed a topographic analysis of variance to compare scalp topographies at every time

point between the two conditions. By incorporating the underlying neural generators displayed in the landscape of each scalp topography, differences found with other methods could be confirmed; other differences emerged that otherwise could not have been found by only looking at individual electrodes (i.e. effects that are subtle at individual electrodes but emerge when voltages across the entire scalp are inspected).

Fourth, we examined changes in the electric field strength by computing the instantaneous global field potential (GFP), a measure of variance across electrodes, that is, a measure of variability in the topography of voltages, for each subject and condition (Lehman and Skandries 1980). It has been shown that modulation of the GFP reflects changes in the strength of the electric field (Murray et al. 2008). We excluded data before map 6 (76 ms) because maps 1–5 occur before the onset of the stimulus and/or have poor signal-to-noise ratio.

Also, to follow up with the effects obtained with the methods above, we submitted the identified time windows to repeated measures ANOVAs with the factors cue (valid vs. invalid), hemisphere (left vs. right) and scalp region (averaged across 4 regions—occipital (right: 96, 85, 91, 84, 90, 77, 76, 83; left: 65, 59, 58, 71, 70, 67, 66, 60); central (right: 62, 115, 109, 108, 101, 102, 103, 97, 98, 104, 93, 92, 86, 87, 80, 79, 78; left: 31, 54, 55, 61, 37, 53, 52, 42, 36, 47, 51, 41, 46, 50, 45, 40, 39); posterior frontal (right: 116, 110, 117, 124, 111, 105, 106, 112, 118, 5; left: 7, 30, 13, 12, 20, 29, 35, 28, 34, 24); and anterior frontal (right: 122, 123, 2, 3, 9, 10, 4; left: 18, 19, 23, 22, 27, 26, 33)] (for a detailed overview of the statistical procedures, please also refer to Stojanoski and Niemeier 2011).

Results

Behavioural results

Participants were more accurate in reporting the shape of the stimuli in the validly cued colour condition [$M = 93.8\%$, 95% CI (92.42, 95.3)] compared to the invalidly cued colour condition [$M = 86.4\%$, CI (84.17–88.97)]; Wilcoxon signed-rank test: $Z = -4.198$; $p < 0.00001$; Cohen's $d = 1.533$; Fig. 1b].

Electrophysiological results

Cluster plots of successive t tests

Group-averaged ERPs for the valid and invalid conditions produced similar amplitudes at the P1, N1 and P2 components (Fig. 2). Successive t tests revealed difference between the two conditions first at 124 ms and extended

to 173 ms primarily over occipital electrodes, corresponding to the transition from the P1 to the N1. Differences also emerged from 460 to 592 ms, with greater positivity for valid trials relative to invalid trials, most saliently at central electrodes, later spreading to occipital electrodes. To examine the relationship between behavioural and ERPs, we calculated their correlations and ran a nonparametric test by calculating the Monte Carlo estimates of significant probabilities based on the permutation distribution. We found no direct relationship between ERP differences and differences in behaviour, perhaps because participants mainly responded correctly during valid and invalid trials.

Topographic pattern analysis

To segment ERPs into unique topographies (maps) of stable periods of activity, we ran a k -means cluster analysis. The number of maps was based on the standard selection criteria (i.e. a cross-validation criterion and a Krzanowski–Lai criterion; Murray et al. 2008). Fifteen maps were found to explain 96.7% of the variance across the two conditions. As seen in Fig. 3, map 6 encompassed the bilateral P1, which transitions in maps 7 (invalid condition only) and 8 into the N1 during maps 9 and 10. The P2 first appeared in map 11 with greater positivity at central and occipital electrodes, transitioning into maps 12 (P2 and N2) and 13 (P3). For maps 14 and 15, core regions of positivity drifted from posterior to more central sites, such that posterior electrodes produced negative going deflection and frontal electrodes became more positive. Of interest is that map 7 corresponding to the late stage of the P1 was not observed in the valid condition. Instead, map 6 which is present in both conditions persists for a longer latency in the valid condition.

This qualitative observation was consistent with the corresponding statistical test. That is, we back-projected the maps produced by the clustering onto the original data; topographies at each time point that most correlated with one of the cluster maps, based on global dissimilarity, were assigned the same label (Brunet et al. 2011; Murray et al. 2008). We fitted maps 7 and 8 (116–152 ms) onto individual subject ERPs within the time range that these maps occupied because they were the only maps that differed between the two conditions. The result showed that map 7 was present more frequently in the invalid condition, while map 8 appeared more often in the valid condition during this time period ($t_{(22)} = \pm 2.077$; $p < 0.05$; $d = 0.072$). Although this difference was quite small, it appears to be reliable given that the previous successive t test analysis identified an effect for nearly the same time window.

Next, we ran a topographic pattern analysis (sometimes referred to as “TANOVA”, note, however, that a TANOVA is not an analysis of variance but a nonparametric

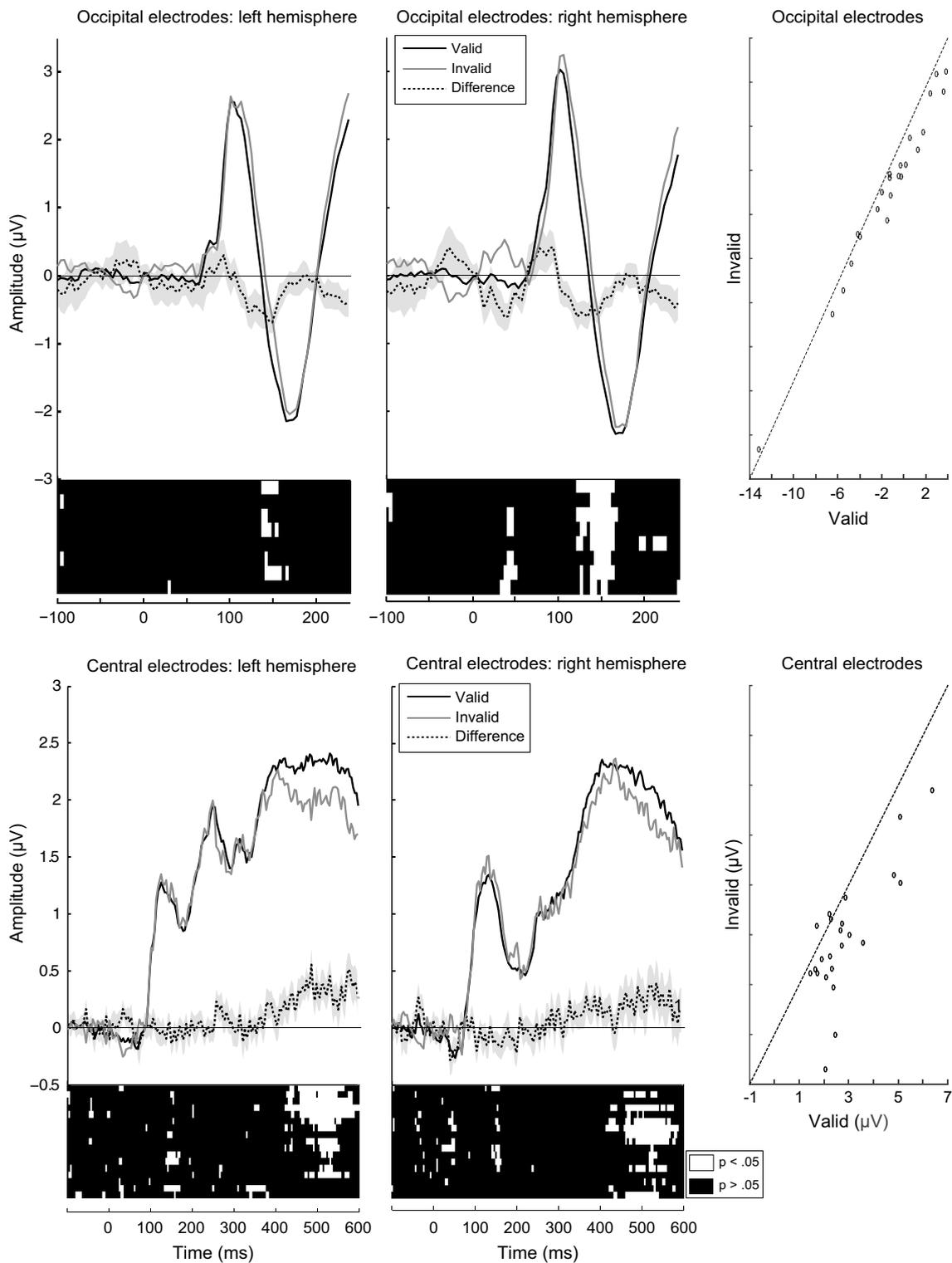


Fig. 2 Grand-averaged ERP results from each condition (valid vs. invalid) averaged across eight occipital electrodes (*top row*) and 16 central electrodes (*bottom row*) separately for *left* and *right* hemisphere (*left* and *right column*, respectively). Difference waves are plotted with a standard error envelope. Successive pointwise paired t tests ($p > .05$ for 11 consecutive time frames) comparing the valid and invalid conditions are provided for each scalp region (ERP plot).

Statistically significant time windows are encapsulated with a *dotted rectangle*. Early effects (*white specs* in the probability plots before 100 ms) were shorter than 11 consecutive tests and therefore not considered as significant. *Scatterplots* show voltages of individual participants for the early and the late effect, averaged across posterior and central electrodes, respectively

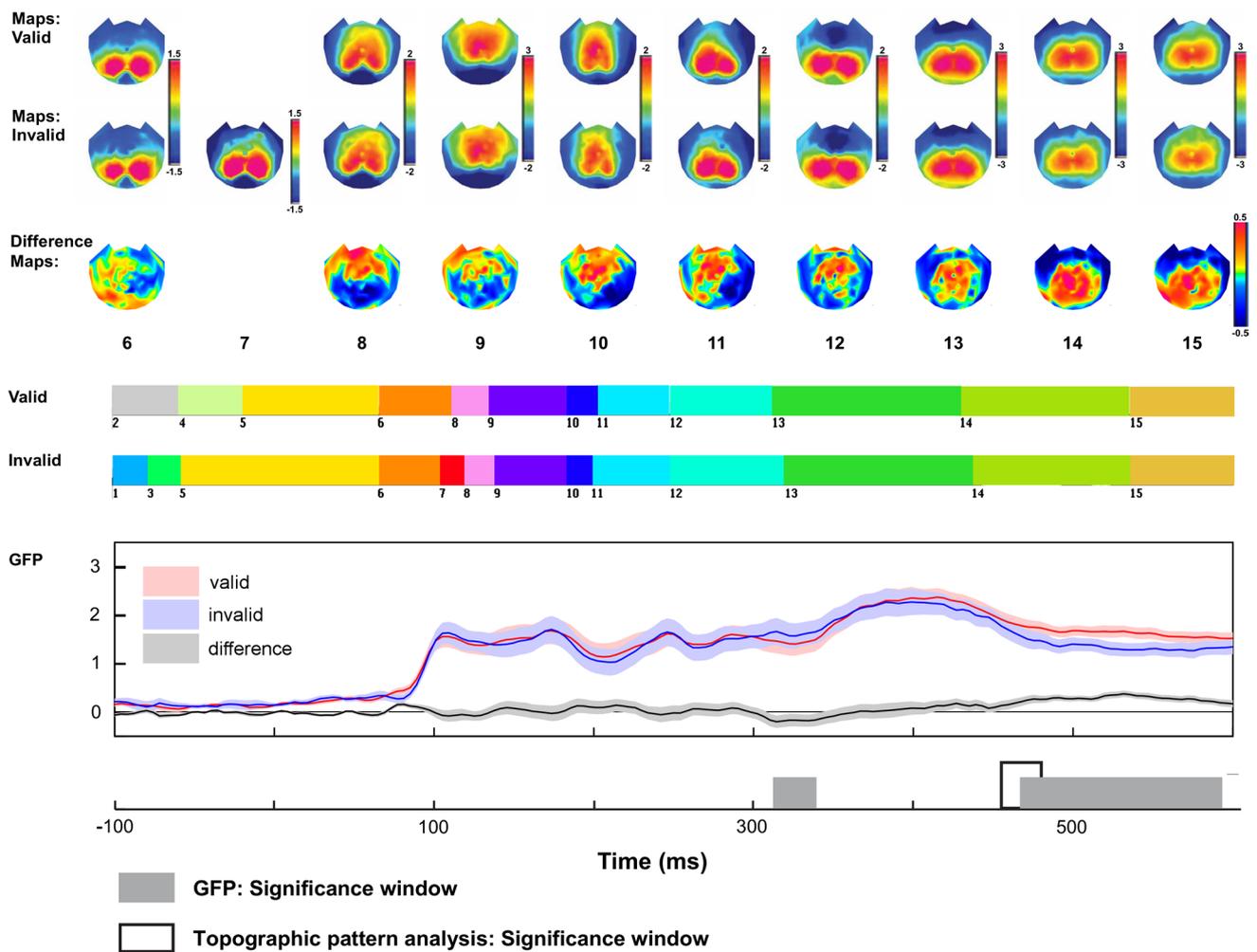


Fig. 3 The spatiotemporal topographic pattern analysis revealed segments of stable neural configuration for validly and invalidly cued colours. Segments are *numbered* and plotted as maps together with *colour bars* that illustrate the time lines of the maps. The only difference between the two conditions was that map 7 is only present in the invalid condition. GFP curves are plotted with standard error envelopes. Successive pointwise paired *t* tests ($p > 0.05$ for 11 consecutive

time frames) of the GFP revealed two time windows of modulation in neural strength: (1) from 312 to 340 ms and (2) from 467 to 592 ms (*grey boxes*). The difference at around 75 ms encompassed only 8 consecutive time points. Topographic pattern analysis indicated significant differences ($p < 0.05$ for 11 consecutive time frames) from 450 to 476 ms (within map 14; *open white box*)

randomization test of global dissimilarity that uses permutations to estimate differences between scalp topographies, e.g. Murray et al. 2008). The topographic pattern analysis revealed topographic differences arguably reflecting differences in underlying neural generators from 450 to 476 ms (map 14).

While topographic pattern analyses shed light on differences between the distributions of the electric signal across the scalp, they do not assess the strength of these signals. Therefore, we computed the instantaneous GFP. Cue-dependent modulation of the GFP first occurred between 312 and 340 ms with greater signal strength in the valid condition. This latency coincided with the end of map 12 and the start of map 13, which coincides with the N2. We

have previously shown (Stojanoski and Niemeier 2011, 2014) that this time frame is associated with feature-based attentional effects on object perception. A second period of large differences in the GFP appeared from 467 to 594 ms (map 14 and 15); the signal strength was higher for the invalid condition compared to the valid condition (Fig. 3).

ANOVAs

To explore the factorial structure of the observed effects, we ran repeated measures ANOVAs by dividing the electrodes into eight regions across the scalp (left and right hemisphere over occipital, central, posterior frontal and anterior frontal electrodes). The first ANOVA targeted a

time window that encompassed the transition from the P1 to the N1 (116–173 ms) over posterior electrodes. It was selected because at this latency the results of the *k*-means cluster analysis revealed differences between the two conditions at maps 7 and 8, and the cluster plot of successive *t* tests revealed modulations in the ERP signal from 124 to 173 ms. The ANOVA revealed a significant interaction between scalp region and cue ($F_{(1.45,31.12)} = 7.70$; $p = 0.005$). Pairwise *t* tests comparing mean amplitude for valid and invalid conditions at each scalp region revealed modulation of the ERP signal at this latency over occipital electrodes ($t_{(22)} = -3.69$; $p = 0.001$; significant after Bonferroni correction), with greater positivity for invalid trials. No other significant effects were found ($t < 0.88$; $p > 0.366$).

The second time window of interest, between 312 and 340 ms, was selected based on the GFP analysis. The ANOVA produced a scalp region effect ($F_{(1.157,25.451)} = 12.28$; $p = 0.001$) due to polarity inversion. Also, we found a significant main effect of cue ($F_{(1.157,22)} = 5.01$; $p = 0.036$) and a significant interaction between scalp region and cue ($F_{(1.25,27.686)} = 5.08$; $p = 0.025$). These effects were driven by greater positivity for valid trials over posterior frontal electrodes ($t_{(22)} = 3.15$; $p = 0.005$; significant after Bonferroni correction), whereas central and posterior sites produced no differences ($F < 2.404$; $p > 0.135$).

The third time window, 460–592 ms, was selected based on the differences we found in the successive *t* tests, also consistent with the timing of effects found for the GFP analysis and the topographic pattern analysis. The ANOVA revealed a main effect of scalp region ($F_{(1.28,28.23)} = 10.78$; $p = 0.001$) and a main effect of cueing with greater positivity during the valid condition ($F_{(1,22)} = 5.77$; $p = 0.025$).

Discussion

In the current study, we recorded electrophysiological signals to identify which periods of object perception processes are modulated by the top-down influences of people's expectations about the colour of the objects. Previous studies have found that expectations alter ERPs around the time of the P2 or N2 (Melloni et al. 2011; Stojanoski and Niemeier 2011, 2014) but provided relatively complex cues to direct attention. In contrast, a number of studies probing feature-based attention with features such as colour or motion and in simple transient detection tasks show that early visual activity around the time of the P1 changes with attention (Andersen et al. 2011; Anllo-Vento et al. 1998; Bondarenko et al. 2012; Eimer 1995, 1997; Müller et al. 2006; Schoenfeld et al. 2007; Zhang and Luck 2009). Here we showed that colour expectations can yield similarly

early modulation of the ERPs during object perception; we found that valid cues produced a greater positivity at occipital electrodes at the P1/N1 transition, roughly coinciding with maps 7 and 8 of the cluster analysis. In addition, we found late effects: an intermitted increase in signal strength suggested modulations between maps 12 and 13, and several tests confirmed modulations during maps 14 and 15, and especially at central electrodes.

Our results, although for now based on achromatic colour cues alone, are consistent with the idea that a priori colour cues-biased expectations such that those lines in the stimulus that had the cued colour were preferably processed (e.g. Saenz et al. 2003) shortly after stimulus onset (Zhang and Luck 2009) or even before stimulus onset (e.g. Esterman and Yantis 2010; although the block-wise cueing in the current study prevents us from inspecting pre-stimulus times). In effect, it is feasible that during “valid trials” colour expectations aided foundational, “early” stages of object perception, such as boundary completion (Murray et al. 2006) or figure/ground segregation (Halgren et al. 2003), which are fundamental to identifying the shape of the cued object (see, e.g. Mihalas et al. 2011), for a model of equivalent effects of spatial attention. In agreement with this, it has been shown that transitions between P1 and N1 underlie important perceptual processes, such as integrating information crucial for object perception (Rousselet et al. 2008; Schyns et al. 2007). Furthermore, the timing of our results may arise from early aspects of object processing which makes it more likely that they are importantly mediated by a feed-forward sweep through the visual system (e.g. Lamme and Roelfsema 2000).

In contrast, during “invalid trials” lines of the wrong colour would be preferably processed. We argue that this should have several consequences: (a) perception is required to extract the object from poorly attended lines and might be slower or more effortful; (b) perception of the object might compete with erroneous attempts to extract objects from the lines of the cued colour, perhaps triggering decisional processes and even illusory object perception; (c) perception might abandon its initial colour expectation and enhance processing of the uncued colour.

All these hypothetical consequences of invalid cues arguably are more time-consuming. So, it is interesting that in addition to the early ERP effect, we also found two phases of later modulations that may relate to observations made elsewhere. For example, the intermediate modulation observed here could be consistent with Murray et al. (2006) results showing late ERP effect (~330–406 ms) only when the task required more effortful conceptual processing of shapes. As another possibility, especially the late modulation at central electrodes may be consistent with decisional processes such as in parietal cortex (Gold and Shadlen 2007). A third possible explanation could be that

the late effects reflect covert shifts of attention in search of the invalidly cued feature, which has been shown for both colour and form (Hickey et al. 2006) and is influenced by top-down, task-specific goals (Kiss et al. 2008) that delays target processing (Eimer et al. 2009; Hickey et al. 2010). Collectively, these possibilities suggest that the late effects result from differences in processing the invalidly cued stimuli. Future studies can directly examine this assumption by introducing a neutral condition.

In conclusion, we have shown that directing expectations to certain colours produced a significant behavioural cueing effect accompanied with a triphasic pattern of electrophysiological activity. We conclude that attending to colour influences aspects of object perception that are likely governed by early computations of figure/ground segregation and contour integration leading to rapid object perception. Several additional processes arguably triggered by invalid expectations will require further investigations. Together, our results illustrate the importance of systematically applying top-down expectations as a tool to understand processes of object perception.

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