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Task relevance effects in electrophysiological brain activity: Early, but not first

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ABSTRACT

A current controversy surrounds the question whether high-level features of a stimulus such as its relevance to the current task may affect early attentional processes. According to one view abruptly appearing stimuli gain priority during an initial feedforward processing stage and therefore capture attention even if they are irrelevant to the task. Alternatively, only stimuli that share a relevant property with the target may capture attention of the observer. Here, we used high-density EEG to test whether task relevance may modulate early feedforward brain activity, or whether it only becomes effective once the physical characteristics of the stimulus have been processed. We manipulated task relevance and visual saliency of distracters presented left or right of an upcoming central target. We found that only the relevance of distracters had an effect on manual reaction times to the target. However, the analysis of electrocortical activity revealed three discrete processing stages during which pure effects of distracter saliency (~80–160 ms), followed by an interaction between saliency and relevance (~130–240 ms) and finally pure effects of relevance (~230–370 ms) were observed. Electrical sources of early saliency effects and later relevance effects were localized in the posterior parietal cortex, predominantly over the right hemisphere. These findings support the view that during the initial feedforward stage only physical (bottom-up) factors determine cortical responses to visual stimuli, while top-down effects interfere at later processing stages.

Introduction

An object may become the focus of attention due to its particular physical properties such as brightness or unique shape (bottom-up signals), or because it matches current preferences and action goals of the observer (top-down signals; Egeth and Yantis, 1997; Fecteau and Munoz, 2006; Pashler et al., 2001). A central question for the study of attention is whether a salient stimulus may capture attention automatically by overriding observer's goals or intentions (Itti and Koch, 2000; Theeuwes, 2004; Van der Stigchel et al., 2009; Yantis and Jonides, 1984), or whether attention selects stimuli based on their relevance and compatibility with current action goals (Folk et al., 1992; Gibson and Jiang, 1998; Simons, 2000). Much of recent attention research focused on the distinction between bottom-up and top-down processing, whereas less is known about when and where in the brain these complementary modes of function converge and interact.

An influential model of visual processing proposes that neural activity evoked by a stimulus moves from occipital to parietal and frontal areas in a fast, feedforward sweep (Lamme and Roelfsema, 2000). This first sweep of activity lasts approximately 100–150 ms and is followed by recurrent processing of the stimulus in the occipito-temporal cortex through feedback projections from higher-order areas. Derived from this physiological model is the proposal that attentional processing during the feedforward sweep is only affected by physical saliency of the stimulus, whereas stimulus relevance affects selection later, during the recurrent processing stage (Theeuwes, 2010; Van der Stigchel et al., 2009). An argument put forward to favour this proposal is the observation that irrelevant distracters with a unique feature capture attention (Jonides and Yantis, 1988) or gaze (Theeuwes et al., 1999; van Zoest et al., 2004) and elicit electrophysiological responses preceding activity related to processing of the relevant target (Hickey et al., 2006). In contrast, other studies using similar paradigms found that stimulus relevance is a crucial determinant of attentional capture and may affect early cortical processing of visual stimuli (Eimer and Kiss, 2008; Leblanc et al., 2008; Ptak et al., 2011; Yantis and Egeth, 1999). For instance, the capture of attention by goal-relevant features modulates event-related potentials (ERPs) approximately 180 ms after stimulus onset (Leblanc et al., 2008). However, these studies aimed to show that relevant stimulus features influence early brain activity; therefore, the saliency of stimuli was kept constant, precluding the observation of competitive or interactive effects between bottom-up and top-down processes. For this reason, their findings do not answer the question

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whether stimulus relevance effects may precede effects of saliency in early brain activity.

Here, we conducted an electrical neuroimaging study in which the saliency and relevance of the stimuli were modulated independently. Visual distracters had high or low saliency (based on luminance contrast) and could be relevant (same colour as the target) or irrelevant (different colour than the target), yet never afforded a reaction. This design allowed us to isolate temporal windows in which brain activity either reflected effects of saliency, the interaction between saliency and relevance, or pure effects of relevance.

Methods

Participants

Twenty-two elderly healthy volunteers gave written informed consent according to the Declaration of Helsinki before participating to this study. Approval was obtained from the ethical committee of the University Hospital Geneva. The data of four subjects were excluded because of EEG artefacts (excessive muscle activity, eye movements and blinks) or failure to distinguish stimulus colours during a practice run. The remaining eighteen subjects (12 females) had a mean age of 62.6 ± 7.3 years, were all right-handed, had normal vision and had no history of neurological or psychiatric illness. This study was part of a larger project that included patients with focal brain damage, and the present results are based on an in-depth analysis of the data from the age-matched healthy control sample.

Stimuli and procedure

Stimuli were presented on a 21″ CRT screen (refresh cycle 85 Hz) at 70 cm viewing distance and were upright or rotated (90, 180, or 270°) L- and T-shapes made from identical horizontal and vertical elements (size: 3 × 3°). Their borders were blurred with a Gaussian filter in order to eliminate sudden changes of luminance between the stimulus and the grey background. The experiment was a go/no-go task in which participants reacted to a coloured target (e.g., red) presented centrally and withheld reactions to all other stimuli presented in the centre (non-targets, e.g., green and blue). Subjects were instructed to completely ignore peripheral distracters appearing 400 ms before the target at 5° eccentricity in the left or right hemifield. Since these peripheral distracters never afforded a response the EEG time-window that was analysed (0–400 ms) was not contaminated by processes related to a decision to react or to withhold reaction. The central target and non-target stimuli were either red (RGB: 222,80,80), green (0,180,0) or blue (10,150,250) and had slightly higher luminance (25 cd/m^2) than the background (15 cd/m^2). For each subject one of these colours was randomly defined as the target colour, in a counterbalanced way. The peripheral distracters were either relevant or irrelevant and had high or low saliency. Distracter relevance was defined as the similarity with the target regarding the target-defining feature (e.g., 'redness' when the target was red) and distracter saliency as the difference in luminance compared to the background. Thus, for each of the three colour dimensions one high-saliency colour (41 cd/m^2) and one low-saliency colour (9 cd/m^2) were used (Fig. 1A). The RGB-values for the three colours were as follows: red (high saliency: 255,199,199; low saliency: 162,68,68), green (high saliency: 95,255,95; low saliency: 0,138,0) and blue (high saliency: 0,254,254; low saliency: 0,94,188).

In order to make sure that the differences in saliency effectively influenced behaviour we conducted a control experiment in which we presented the distracter stimuli in the left or right visual field (at the same positions as in the main experiment) and asked nine healthy controls (7 females, mean age: 30.5 ± 3.3) to react as quickly as possible when they perceived a specific colour (three controls for each colour). We argued that a shape with high saliency should be detected faster than a low-saliency shape; hence, that reaction times to the former should be faster than to the latter. The stimuli were presented for 300 ms and a time-window of 2000 ms was given for the answer. A repeated-measures ANOVA with factors visual field (left-LVF, right-RVF) and saliency (high, low) only revealed a significant effect of saliency ($F_{(1,8)} = 7.86$, $p < 0.05$), with shorter RTs to high-saliency (307 ms) than low-saliency stimuli (316 ms). Thus, the stimuli used as distracters in the EEG experiment were perceived differently according to their level of saliency.

Fig. 1B shows a schematic representation of the sequence of events in the EEG experiment. On every trial participants first fixated a small white cross (0.5°) shown in the middle of the screen. After 1000 ms a distracter appeared in the left or right hemifield for 300 ms, followed by 100 ms blank screen. The target display then appeared for 2000 ms. Participants were asked to press a button with their right (dominant) hand when they detected the target-colour in the centre, irrespective of shape. It was emphasized that they should never react to the peripheral distracter stimulus. There were 64 trials in each experiment block, one third of which contained a target (go trials) and the remaining a non-target (no-go trials). Within each block the four distracter conditions (high saliency/relevant; high saliency/irrelevant; low saliency/relevant and low saliency/irrelevant) varied orthogonally. Every participant completed at least twenty blocks for a total of 1280 trials.

EEG acquisition and preprocessing

Continuous EEG was acquired with a sampling rate of 512 Hz through a 128-channel Biosemi ActiveTwo system (Biosemi V.O.F, Amsterdam, Netherlands) referenced to the common mode sense/

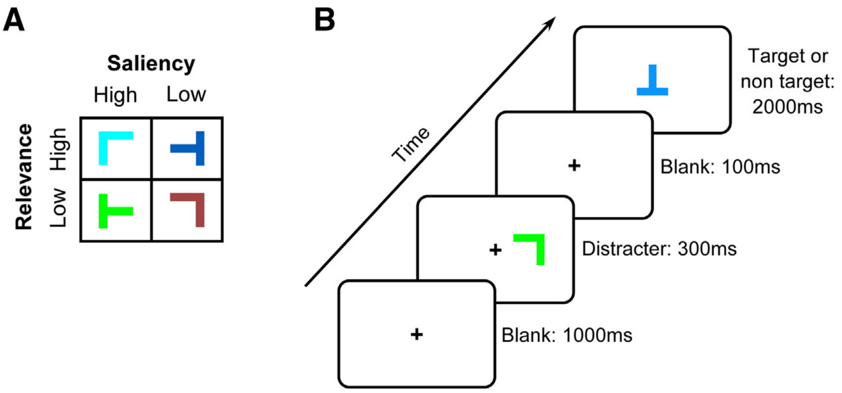

Fig. 1. A) Example stimuli used in the experiment. In this condition, the target and relevant distracters were blue while irrelevant distracters were red or green (relevance modulation). Distracters in each relevance condition either had high or low luminance contrast with the background (saliency modulation). B) Time-course of events presented in one experimental trial. The example shows a trial with an irrelevant, high-saliency distracter and a blue target. Note that in reality all stimuli were shown on a neutral grey background and that the size of the stimuli is exaggerated.

driven right leg (CMS-DRL) ground. EEG data pre-processing and analyses were conducted using Cartool software (https://sites.google.com/site/fbmlab/cartool; Brunet et al., 2011). The main interest of the study was to examine to what extent the level of relevance and saliency of peripheral distracters affected early visual processing, uncontaminated by response-related activity. For this reason only the first 400 ms of EEG data, time-locked to distracter onset was analysed, and electrophysiological responses beyond this time-point were not examined. Data were band-pass filtered (0.1–100 Hz) and recalculated against the average reference. Electrodes with artefacts were interpolated using 3D splines (Perrin et al., 1987) and artefact-free EEG epochs (100 ms pre- to 400 ms post-distracter onset) were averaged for each participant.

EEG Analyses

An ERP component analysis was conducted on activity measured at two posterior electrodes (PO7/PO8) where ERP components P1 (60–140 ms), N1 (140–240 ms) and P2 (240–400 ms) associated with early visual processing are known to be maximal. ERPs measured at electrodes contralateral to distracter position were averaged for each condition and each subject after baseline correction on the 100 ms pre-stimulus period.

Multivariate topographic pattern analyses were performed to confirm the timing of the main effects found in the component analyses and to determine whether the configuration of intracranial generators changed as a function of relevance and saliency. This approach is based on the evidence that ERP topography does not vary randomly across time, but remains quasi stable during functional microstates lasting 20–100 ms, before rapidly switching to other stable periods (Lehmann and Skrandies, 1980; Michel et al., 2004; Murray et al., 2008). A change in the topography of the scalp-recorded electric field is assumed to be a consequence of changes in the configuration of underlying generators of the brain's activity. Thus, topographic modulations can be directly interpreted as the engagement of distinct functional brain networks. This method is independent of the reference electrode and insensitive to pure amplitude modulations across conditions. Moreover, it requires no a-priori selection of electrodes or periods of interest, which represent a potential bias in the statistical analysis of traditional ERP component analysis (Murray et al., 2008).

The most dominant scalp topographies appearing in the group-averaged ERPs from each condition over time were found using a K-means cluster analysis (Pasqual-Marqui et al., 1995). The optimal number of clusters to describe the data set was identified using a modified Krzanowski–Lai criterion. Differences in the pattern of topographic maps observed between conditions were tested by computing the spatial correlation between these “template” maps from the group-averaged data and each time point of single-subject data (referred to as ‘fitting’). For this fitting procedure, each time-point of ERPs from each subject was labelled according to the map with which it best correlated spatially. The result is a measure of the duration of electrical maps, indicating the amount of time over a given interval that each map best accounts for the response from a given individual subject and condition. Thus, the fitting procedure reveals whether a given experimental condition is characterized by a particular map, and therefore whether the same or different generator configurations best account for specific experimental conditions.

Electrical source estimations

We estimated electrical sources in the brain using a distributed linear inverse solution and the local autoregressive average (LAURA) regularization approach (Grave de Peralta Menendez et al., 2004; see also Michel et al., 2004 for a comparison of inverse solution methods). LAURA selects the sources of configuration that follow best the biophysical behaviour of electric fields (i.e., activity at one point depends on the activity at neighbouring points according to electromagnetic law). We used homogenous regression coefficients in all directions and within the whole solution space. We applied the Spherical Model with Anatomical Constrains method to calculate the lead field (Spinelli et al., 2001). This method first transforms a template MRI to the best fitting sphere using homogenous transformation operators. It then defines a regular grid of 3005 solution points in the grey matter of this spherical MRI and computes the lead field matrix using the analytical solution for a spherical head model with three shells or different conductivities.

For each time-window corresponding to P1 (60–140 ms), N1 (140–240 ms) and P2 (240–400 ms) ERP-components, time-point wise 2 × 2 ANOVAs were computed with factors saliency and relevance for the 3005 solution points. To correct for multiple testing and temporal auto-correlation, we applied a temporal criterion of 20 consecutive time-frames, and a spatial criterion of 20 contiguous solution points to reach statistical threshold ($p < 0.05$; see Knebel and Murray, 2012; and Toepel et al., 2012 for a similar approach).

Results

Behavioural results

Fig. 2 shows average RTs as a function of the position of the distracter. A repeated-measures ANOVA with factors visual field (left, right), distracter relevance (relevant, irrelevant) and distracter saliency (high, low) only revealed a significant effect of relevance ($F_{(1,17)} = 15.5$, $p < 0.01$). Subjects were significantly faster with high- compared to low-relevance distracters, irrespective of their saliency and of the visual field. Omission rates (mean percentage: 2.7% ± 1.6) and false positive reactions (mean percentage: 2.8% ± 1.8) were low and were therefore not analysed further.

EEG results

ERP component analysis

Fig. 3 displays the grand average waveforms and the absolute peak amplitude values for the P1, N1 and P2 ERP components recorded at parietal electrodes PO7/PO8 contralateral to the distracter and time-locked to distracter-onset. Repeated-measures ANOVAs with the factors visual field (left/right), saliency (high/low), and relevance (high/low) were run for the three ERP components (P1, N1, P2). Analysis of the peak amplitude in the time-window corresponding to the P1-component (60–140 ms) revealed a main effect of saliency ($F_{(1,17)} = 10.19$, $p < 0.01$) and of visual field/electrode ($F_{(1,17)} = 6.14$, $p < 0.05$), indicating that distracters with high saliency elicited a P1 of greater amplitude than distracters with low saliency. Moreover, contralateral P1-amplitudes were greater for distracters shown in the LVF compared to RVF-distracters. A main effect of saliency was also found in the N1 period (140–240 ms; $F_{(1,17)} = 4.77$, $p < 0.05$), revealing a more negative

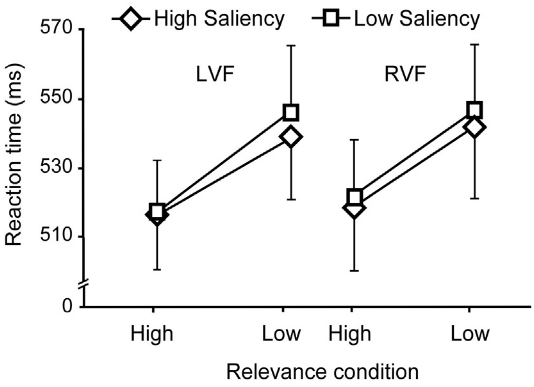

Fig. 2. Reaction time data as a function of distracter condition (high/low relevance; high/low saliency) and the visual field of apparition of the distracter (LVF, left; RVF, right visual field).

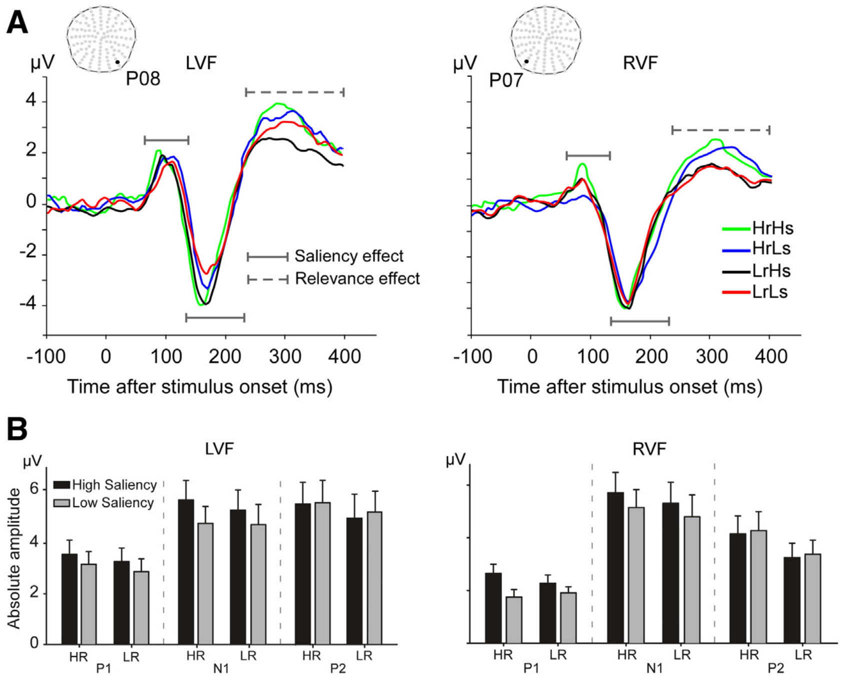

Fig. 3. Results of the ERP-component analysis. A) Grand-average ERPs registered at posterior electrodes P07/P08 contralateral to the position of the distracter (LVF/RVF), as a function of the four distracter conditions. Horizontal bars show the time windows in which significant effects of saliency (60–140 ms; 140–240 ms) and relevance (240–400 ms) were identified. B) Box plots showing the peak amplitudes (absolute values) of P1, N1 and P2 at posterior electrodes P07/P08 contralateral to the position of the distracter, as a function of the four distracter conditions. Error bars show SEM. *Abbreviations*: HrHs: high relevance/high saliency; HrLs: high relevance/low saliency; LrHs: low relevance/high saliency; LrLs: low relevance/low saliency, LVF: left visual field, RVF: right visual field; HR: high relevance; LR: low relevance, LVF: left visual field, and RVF: right visual field.

trace for high- than low-saliency distracters. In contrast, analysis of the amplitude of the P2-component (240–400 ms) revealed a main effect of relevance ($F_{(1,17)} = 6.8$, $p < 0.05$), with greater amplitude for relevant than irrelevant distracters. In addition, there was also a significant effect of hemifield ($F_{(1,17)} = 9.99$, $p < 0.01$) reflecting the fact that LVF distracters elicited a contralateral P2 of higher-amplitude than RVF distracters. No significant interactions between visual field (left/right), saliency (high/low), and/or relevance (high/low) factors were found for P1, N1 and P2 components. Analyses of the latency of peak amplitudes did not reveal any significant effects with either of the three components.

Thus, the ERP component analysis showed differential effects of saliency and relevance for three early ERP-components that are sensitive to effects of attention. While P1 and N1 were sensitive to modulations by stimulus saliency, the later P2 was exclusively modulated by stimulus relevance. This temporal sequence of saliency and relevance effects suggested by the ERP-analysis was further explored using a topographic analysis of the entire electric field.

Topographic pattern analysis

A topographic pattern analysis was performed on group-averaged ERPs of each distracter condition (saliency/relevance) to identify the pattern of predominating topographies (maps) of the electric field at the scalp (Fig. 4). The entire scalp electric field was divided into stable temporal segments using cluster analysis. The cluster analysis was performed for each visual field separately and accounted for 92% of global explained variance for LVF distracters and 92.1% for RVF distracters. The analysis identified a similar sequence of stable maps across conditions, with the exception of three time-periods in which distinct maps were observed as a function of condition. The fitting procedure applied over these three periods of topographic modulation observed in the averaged ERPs quantified how well each map accounted for single-subject ERPs. In the first time window (LVF: 110–158 ms; RVF: 116–144 ms), there was a significant interaction between saliency and map (LVF: $F_{(1,17)} = 24.67$, $p < 0.001$; RVF: $F_{(1,17)} = 13.9$, $p < 0.01$) indicating that differences in topographic configurations were only due to modulations of distracter saliency. In the second time window (LVF: 138–242 ms; RVF: 120–190 ms) we also found an interaction saliency × map ($F_{(1,17)} = 9.37$, $p < 0.01$), but only for RVF distracters. However, in both hemifields the presence of different topographies was also explained by a significant interaction between saliency and relevance (LVF: $F_{(1,17)} = 6.31$, $p < 0.05$; RVF: $F_{(1,17)} = 4.49$, $p = 0.05$). Finally, in the third time window (LVF: 230–290 ms; RVF: 230–350 ms), we observed a significant interaction between relevance and map in the RVF ($F_{(1,17)} = 9.54$, $p < 0.01$), and a statistical trend for the same interaction in the LVF ($F_{(1,17)} = 3.28$, $p < 0.05$). Thus, over the third period different topographical configurations were observed for high compared to low relevance conditions.

These findings indicate that the configurations of intracranial generators changed significantly across time as a function of distracter saliency and relevance. Complementing the ERP-component analysis, the topographic pattern analysis revealed early effects of saliency while relevance effects appeared later in time; additionally, the interaction of both factors determined electrocortical activity in an intermediate time-window.

Electrical source estimations

Source estimations were computed for time-windows corresponding to the effects of saliency and relevance found in the ERP component analysis. The first time-window encompasses the P1 and N1 component (60–240 ms) which was characterized by a saliency effect in the ERP component analysis. The second window corresponds to the P2 component (230–400 ms), where a main effect of relevance was observed. LAURA distributed source estimations for each of these time-windows were calculated, and the scalar value of each solution point was submitted to a time-wise repeated-measures ANOVA with saliency and relevance as within-subject factors. Follow-up analyses of the peak scalar value were performed to confirm the directionality of each effect.

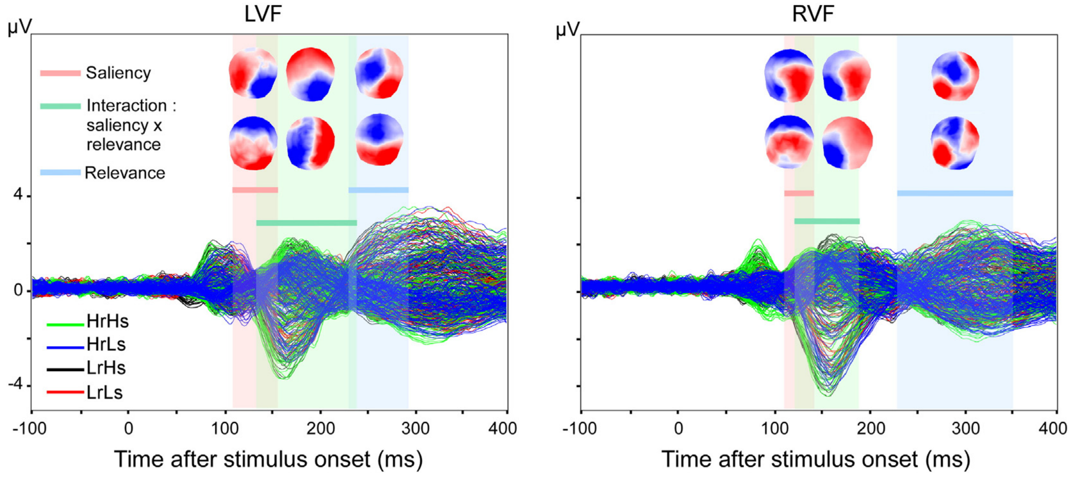

Fig. 4. Group-averaged ERPs and results of the temporal segmentation. ERP waveforms in response to the four distracter conditions (HrHs: high relevance/high saliency; HrLs: high relevance/low saliency; LrHs: low relevance/high saliency; LrLs: low relevance/low saliency) are displayed separately for left and right visual field distracters. The transparent, coloured columns represent the three periods of stable electric field topography that were identified in the topographic pattern analysis. These columns indicate the duration of a pure effect of saliency (light red), the interaction between saliency and relevance (light green) and a pure effect of relevance (light blue). Scalp distributions of the electric field for each of these effects are shown in the upper part of the figure (nasion is shown up and left is shown on the left). The colours shown in these electric field distributions represent positive (red) and negative (blue) voltages on the scalp (e.g., upper left—high saliency, lower left—low saliency).

The time-wise analysis revealed a significant main effect of saliency within 85–151 ms in the LVF condition ($F_{(1,17)} > 4.45$, $p < 0.05$), reflecting bilateral activations over posterior parietal areas (Fig. 5). The activation peak for this effect of saliency was localized in the right intraparietal sulcus (IPS; Talairach-coordinates: $x = 28$, $y = -52$, $z = 53$) and exhibited stronger activity for distracters with high saliency compared to distracters with low saliency ($F_{(1,17)} = 16.8$, $p < 0.001$). For distracters appearing in the RVF the effect of saliency appeared slightly earlier (60–103 ms; $F_{(1,17)} > 4.45$, $p < 0.05$), and electrical sources were localized in left inferior occipital areas with an activation peak in the left lingual gyrus (−9, −71, 1; Fig. 5). Again, activation strength was greater with high-saliency distracters than low-saliency distracters ($F_{(1,17)} = 18.42$, $p < 0.001$).

Time-wise analysis over the second time-window revealed significant relevance effects between 269 and 400 ms for distracters in the LVF ($F(1,17) > 4.45$, $p < 0.05$). Electrocortical activity associated with

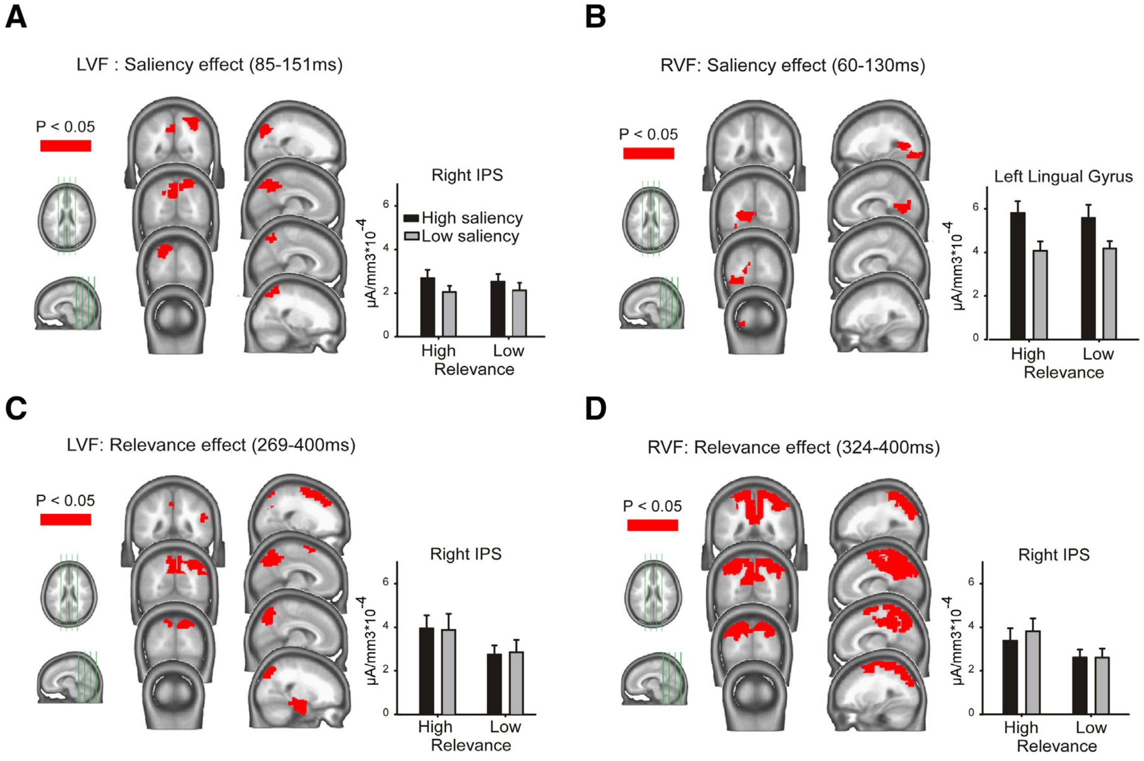

Fig. 5. Results of analyses of electrical current sources (LAURA inverse solutions). The bar plots next to each brain image show the current flow density per volume at the cortical location where it reached peak value, as a function of condition. A) Main effect of saliency for distracters presented in the LVF. The peak current flow was located in the right intraparietal sulcus (IPS). B) Main effect of saliency for distracters shown in the RVF. The peak current flow was located in the left lingual gyrus. C) The main effect of relevance for distracters presented in the LVF. The peak current flow was located in the right IPS. D) The main effect for relevance for distracters in the RVF. The peak current flow was located in the right IPS.

these effects involved posterior parietal areas and additionally regions within the dorsal premotor cortex, the peak of activity being located in the right IPS (21, −70, 47) reflecting higher activation for relevant than irrelevant distracters ($F(1,17) = 9.87$, $p < 0.01$). For distracters in the RVF significant relevance effects were observed 324–400 ms post-onset of the distracter ($F(1,17) > 4.45$, $p < 0.05$) bilaterally over the frontoparietal convexity. As in the LVF condition the activation peak reflecting higher activation of relevant than irrelevant distracters was located in the right IPS (34, −64, 53; $F(1,17) = 9.13$, $p < 0.01$).

Discussion

The purpose of the present study was to investigate the timing and neural origin of electrophysiological responses related to visual saliency and relevance effects in early visual processing. Based on contrasting theoretical positions two alternative time courses of early cortical processing were hypothesized: according to the model of Lamme and Roelfsema (2000, see also Theeuwes, 2010) a first processing wave is exclusively influenced by bottom-up factors, which predicts an early modulation of electrophysiological responses by stimulus saliency and the onset of relevance effects only once the purely feedforward sweep of processing is terminated. The contrasting view is that stimulus features that are contingent with a current behavioural goal (e.g., redness when the target is red) have an effect on these early processing stages (Folk and Remington, 2006). Based on this position we predicted that relevance factors (e.g., distracter-target contingency) affect early ERP components simultaneously or even prior to visual saliency (e.g., luminance contrast) (Leblanc et al., 2008).

Behavioural results of our experiment support the second prediction: RTs to central targets were influenced exclusively by distracters sharing the task-relevant property (colour) with the target. The effect was comparable for distracters shown in the left and right hemifield. However, given the length of average RTs (>500 ms) this finding does not exclude an early effect of stimulus saliency that is overridden by later appearing, but stronger effects of relevance. Indeed, EEG results demonstrated that whereas electrophysiological responses were initially modulated by saliency (>80–100 ms), at later processing stages (>230 ms) relevance factors prevailed. This was found although participants were not required to make any perceptual decision concerning the distracters. The modulation by saliency suggests an effect of attention, rather than purely sensory effects of the stimulus, as the latter influence ERP latency and may result in relatively flat ERPs where early components are difficult to differentiate (Johannes et al., 1995). According to Hillyard et al. (1998) attention has relatively pure effects on ERP amplitude that reflect its role as a gain control mechanism on early sensory responses. The fact that saliency and relevance only modulated ERP amplitude (not latency) supports an interpretation in terms of relatively pure attention effects. The finding of temporally distinct processing stages was based on classic ERP component analyses, as well as on the examination of distributed electrical activity at the scalp. Instead of focusing on a priori selected electrodes (which is influenced by experimenter bias), the latter analysis takes into account data from the entire electrode set and therefore provides additional information that otherwise might be overlooked (Murray et al., 2008). Importantly, in the present case both methods of analysis provided converging information about the time-course of saliency and relevance effects.

Our results contribute to a better comprehension of some divergent findings from previous ERP studies investigating automatic attentional capture. Though they are consistent with some previous studies examining capture by salient task-irrelevant stimuli (Belopolsky et al., 2008; Hickey et al., 2006), they appear to contradict several other studies. For example, Eimer and Kiss (2010)) found that a task-relevant, spatially uninformative cue modulated ERPs in the time-window 180–280 ms after cue onset. Using a rapid serial visual presentation task Leblanc et al. (2008) found that lateral flankers sharing a critical property with the target interfered with target detection. Similar to the findings of Eimer and Kiss (2008, 2010) this effect was accompanied by a modulation of the N2pc, an ERP component related to contralateral shifts of attention (Luck and Hillyard, 1994). However, though these studies support the view that task-relevance modulates early cortical processing, they do not argue against even earlier effects of stimulus saliency. Indeed, the finding of relevance effects from 180 ms post-stimulus onward is only slightly earlier to the timing of similar effects observed in our study. However, in contrast to these previous studies our paradigm varied saliency and relevance effects independently, allowing to track individual and combined effects of both factors across time. Consequently, the finding of early pure effects of distracter saliency, followed by later effects of distracter relevance, is not in contradiction with previous ERP studies. In addition, these results agree with the view that early attention effects are primarily driven by perceptual characteristics of the stimulus during fast feedforward processing, while top-down factors influence processing at later stages (Lamme and Roelfsema, 2000; Theeuwes, 2010). Interestingly, the early effect of stimulus saliency had no impact on behavioural responses, which were exclusively driven by the later effect of relevance. This finding is similar to that of a recent ERP study (Kiss et al., 2013) and supports the conclusion that attention might initially be captured, but then quickly withdrawn from the distracter.

Our findings provide evidence for discrete, sequential stages of cortical processing, starting with pure effects of stimulus saliency and ending with pure relevance effects. The topographic analysis of our data identified an additional, intermediate stage (~130–240 ms) at which these two factors interacted. Though a direct link between electrocortical processing and interactions between cortical areas remains hypothetical, this intermediate stage might be related to reentrant processing of incoming information. According to neurophysiological and cognitive models the first feedforward analysis of visual input creates a sensory representation that is highly ambiguous and inaccessible to conscious awareness (Di Lollo et al., 2000; Lamme and Roelfsema, 2000). Reentrant signals might provide the basis for top-down modulation of neural responses through expectations or action goals, and it is through these signals that initial representations become accessible to consciousness (Lamme and Roelfsema, 2000). The intermediate cortical processing stage identified in our study may reflect the interaction between top-down signals and initial sensory activity, during which relevant properties of the stimulus are enhanced and irrelevant properties are inhibited.

An important question is where in the brain bottom-up and top-down representations are integrated. Current source analyses of the early saliency effects suggested that stimulus saliency (as defined by luminance differences) generates different effects in the two cerebral hemispheres: stimuli projected to the RVF activated strongly left inferior occipito-temporal cortex while LVF distracters were associated with current sources in the right posterior parietal cortex (PPC). The inverse solution computed for the relevance effect localized sources of activity in the right intraparietal sulcus (IPS) and neighbouring regions of the PPC, as well as more anterior regions of the frontoparietal convexity. This distribution of activity is compatible with functional imaging and neuropsychological studies demonstrating the involvement of a frontoparietal network in voluntary aspects of attention (Corbetta et al., 2000; Ptak and Schnider, 2010; Serences and Yantis, 2007). However, the IPS also contained sources of activity related to the processing of saliency, in particular for distracters presented in the left hemifield. Though the hemifield differences should be interpreted with caution, they are in agreement with the known hemispheric asymmetry for spatial attention (Mesulam, 1981) and further supported by the results of the waveform analysis, which revealed greater amplitudes of the P1 and P2 components in the right hemisphere. Moreover, hemispheric differences in current sources suggest that while stimulus saliency and relevance have distinct effects on the left hemisphere the right hemisphere contributes more to the integration of both factors. The role of the IPS as integrator of saliency and relevance is supported by several findings. Neurophysiological, functional imaging and lesion studies suggest that attentional selection depends on a central interface where multiple inputs converge and relatively abstract signals within a priority map are computed (Bisley and Goldberg, 2010; Gottlieb, 2007; Ptak, 2012; Vandenberghe et al., 2012). Given its extensive connections with prefrontal cortex (where task-relevant signals are elaborated) and downstream visual areas, the IPS is the most likely candidate for such a function. For example, in a recent study the lateral intraparietal area (LIP) has been identified as the likely modulator of neural activity in the downstream area MT, suggesting that it might be a source of reentrant feedback to earlier visual areas (Saalmann et al., 2007). Interestingly, the LIP exhibits neuronal latencies to visual stimulation that are only slightly longer than in primary and secondary visual cortex and much shorter than in inferior temporal cortex, suggesting that it has privileged access to feedforward information (Bullier, 2001; Gottlieb et al., 1998). Thus, LIP shows a rapid on-response to any visual stimulus irrespective of its current relevance, followed by a later sustained activity which is sensitive to attentional modulations (Bisley et al., 2004). This pattern of response is reminiscent of the sequence of processing stages identified in our study. Also, the proposal that during feedforward processing visual representations are ambiguous and inaccessible to consciousness may explain why the pure saliency effect identified in our study did not influence behavioural responses. Together, these findings support the view that the PPC integrates sensory signals with high-level representations of behavioural goals into a priority map of the environment (Bisley and Goldberg, 2010; Ptak and Fellrath, 2013). The spatial distribution of computational weights in this priority map enables a quick orienting response toward the location with highest priority.

Conclusion

In conclusion, the present study provides evidence for the view that under competition, stimulus saliency and relevance effects manifest at different time points in early perceptual processing. Whereas saliency affects fast feedforward processing, relevance effects arise later and just after a processing stage during which both factors interact. These findings support the view that visual analysis proceeds in discrete stages, where a fast feedforward sweep of information precedes a stage of recurrent processing during which competition between bottom-up and top-down signals is resolved.

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