

Published in final edited form as:

Psychophysiology. 2012 August ; 49(8): 1101–1108. doi:10.1111/j.1469-8986.2012.01385.x.

The Spotlight of Attention Illuminates Failed Feature-based Expectancies

Jesse J. Bengson^a, Javier Lopez-Calderon^{a,b}, and George R. Mangun^{a,b,c}

^aCenter for Mind and Brain, University of California-Davis

^bDepartment of Psychology, University of California-Davis

^cDepartment of Neurology, University of California-Davis

Abstract

A well-replicated finding is that visual stimuli presented at an attended location are afforded a processing benefit in the form of speeded reaction times and increased accuracy (Posner, 1979; Mangun 1995). This effect has been described using a spotlight metaphor, in which all stimuli within the focus of spatial attention receive facilitated processing, irrespective of other stimulus parameters. However, the spotlight metaphor has been brought into question by a series of combined expectancy studies which demonstrated that the behavioral benefits of spatial attention are contingent upon secondary feature-based expectancies (Kingstone, 1992). The present work used an event-related potential (ERP) approach to reveal that the early neural signature of the spotlight of spatial attention is not sensitive to the validity of secondary feature-based expectancies.

The notion of modularity has been a fundamental point of interest throughout the history of psychology and neuroscience (Fodor, 1983; Gall & Spurzheim, 1809; Pyshlyyn 1999). Within the visual system, evidence has accrued pointing to localized brain regions that preferentially process certain kinds of visual input, such as faces or objects (Kanwisher, McDermott & Chun, 1997). In a corresponding fashion, the visual attention system can be defined with reference to the category of the attended stimulus of interest (Anllo-Vento & Hillyard, 1996; Bengson & Mangun 2011; Fink & Dolan 1997; Hayden & Gallant, 2005). The notion of attentional modularity is not a settled issue however. Many prominent theories posit a domain-general attentional process that exists without reference to the perceptual category of interest (Bundesen, 1990; Cowan, 2001). A specific point of contention has been whether spatial attention is unique from other forms of attention (Andersen, Fuchs & Muller, 2009; Duncan 1984; Kingstone, 1992).

Duncan (1984) hypothesized that the justification of a unique spatial attention system requires evidence that spatial attention has a unique property not shared by other forms of attention. Given that attention to form (Kingstone, 1992), color (Humphreys, 1981), semantic category (Neely, 1977) and location all have beneficial behavioral effects, it is reasonable to posit that advance knowledge of location is not distinct from other kinds of expectancies. Furthermore, evidence against a unique spatial attention system also comes from studies that have simultaneously combined feature-based expectancies with location-based expectancies (Kingstone, 1992; Lambert, 1987; Lambert & Hockey, 1986). The general finding from these studies is that the effect of speeded reaction times to stimuli presented at attended locations is contingent upon the validity of other stimulus expectancies

such as form or color. Specifically, an interaction is observed in which reaction times are slowed for unexpected forms when presented within the focus of spatial attention. This finding suggests an interdependency between spatial attention and feature-based attention and draws into question the spotlight metaphor of spatial attention: that all stimuli falling within its focus are afforded processing benefits.

One combined expectancy study relevant to the present exploration was that of Kingstone (1992) who combined spatial expectancies with other feature-based expectancies in a trial by trial cuing paradigm. Kingstone cued participants to simultaneously expect both the location and form of target stimuli. These target stimuli were then briefly flashed and subjects were instructed to make an orientation discrimination that was unrelated to the cued aspect of the target form, thus ensuring the cues did not provide information concerning the anticipated response. Importantly, target stimuli could appear in one of 4 conditions (2x2 design): 1.) both spatial and form dimensions validly cued, 2.) only space validly cued (invalid target form) 3.) only form validly cued (invalid location), or 4.) both location and form invalidly cued. Such a design allows the examination of the behavioral effect of form validity within attended locations. The question was: Are the benefits of valid spatial expectancies mitigated by the presentation of uncued target forms at attended locations? Surprisingly, Kingstone observed a robust slowing of reaction times to un-cued forms that was primarily restricted to attended locations. This pattern of results suggests that spatial attention might not operate as a spotlight and is in fact dependent upon the confirmation of other forms of advance stimulus knowledge. A specific mechanism for this interdependency between different forms of attention could possibly be modeled according to an interactive race model (Mordkoff & Yantis, 1991) in which inter-channel crosstalk from correlated dimensional signals (typical of combined expectancy paradigms) produces interactive behavioral effects that can be interpreted as “spotlight failure”. Kingstone did note however that this pattern could be reconciled with a unique spotlight of spatial attention if spatial attention has an early neural signature of facilitated processing that is independent of other form-related expectancies (as suggested by the sustained attention study of Hillyard and Munte, 1984). Such a proposition implies that the neural locus of the slowing of reaction times for un-cued forms at attended locations occurs after the early visual-cortical processing stage at which spatial attention might operate. Because reaction times only index the endpoint of perception and cognition, the neural locus of the effect of form validity at attended locations observed in the Kingstone study is still a point of contention.

In a trial by trial cuing design similar to Kingstone (1992), Handy, Green, Klein & Mangun (2001) employed an event-related potential (ERP) technique in order to examine the neural locus of slowed reaction times to invalid non-spatial expectancies. Handy, et al. replicated the general design of previous combined cuing studies by presenting a left or right pointing arrow at fixation with either the letter “V” or “H” above it. Individuals were instructed on a trial by trial basis to use this cue to expect both the impending orientation (“V” for vertical and “H” for horizontal) and location of a target stimulus. Upon target presentation, subjects were instructed to respond to the orientation as quickly and as accurately as possible. Importantly, as with the Kingstone study, the targets could appear with both dimensions validly cued, only one dimension validly cued (orientation or location), or with both dimensions invalidly cued. Handy, et. al. recorded averaged evoked responses to the target stimuli and showed that an early perceptual neural signature of spatial attention, the evoked P1 component (Mangun & Hillyard, 1991), is robust even when uncued orientations appear at an attended location. Handy concluded that the reaction time slowing to uncued orientations at attended locations was a post-perceptual spotlight masking effect, because the early neural index of spatial attention, the P1 component, was not sensitive to the validity of secondary response-related orientation expectancies. However, because the Handy et al (2001) study cued both the upcoming response as well as orientation of target stimuli, the

finding cannot be generalized to a paradigm akin to the Kingstone study, in which the anticipated form of a stimulus was cued and the response –relevant dimension of the target was dissociated from the form-related expectancy. Although this difference is subtle, we could expect that the P1 component might be sensitive to a pure form-based validity manipulation for a number of reasons when combined with spatial expectancies: 1.) The neural locus of the site of selection for feature-based attention is more spatio-temporally proximal to the locus of selection for spatial attention than response related expectancies, thus increasing the probability of early perceptual interdependence, and 2.) we have recently observed that combining response related expectancies with spatial attention does not tax capacity limits, whereas combining feature-based expectancies with spatial attention depends heavily on limited capacity resources related to working memory (Bengson & Mangun, 2010). This finding suggests that response related expectancies are qualitatively distinct from form-related expectancies. Thus, we aim to replicate the behavioral findings of Kingstone (1992) and use the ERP technique employed by Handy et al. (2001) to examine if the P1 component is sensitive to feature-based expectancies within the spotlight of attention.

Methods

Participants

Data from 17 undergraduate students from the University of California-Davis were analyzed. All participants had normal or corrected-to-normal vision. All artifact-free trials with correct behavioral performance were entered into statistical analysis of the EEG.

Apparatus & Stimuli

All stimuli were presented on a 19" Viewsonic VX922 color monitor that was placed 60 cm from each participant's nasion. Each trial was initiated by the presentation of an arrow that pointed to the left or right (1.8° long) for 200ms at fixation with the letter V or H directly above it. Following a randomly distributed Stimulus-Onset-Asynchrony (SOA) of 1500 ± 150 ms, vertically or horizontally aligned $5^\circ \times 5^\circ$ square target gratings were presented for 100 ms at location markers 11.5° to the left or right of a white dot placed at fixation and 3.5° below the horizontal mid-line at a ratio of .50. The spatial frequency of each grating subtly uniformly varied by chance and within each condition and hemi-field at a ratio of .50 between high (.53° per cycle) and low (.59° per cycle) spatial frequencies of alternating black and white square waves. Stimuli were presented on a gray background (rgb intensities of 60,60,60) with an inter-trial interval of 2000 ms with each trial proceeding automatically. Figure 1 illustrates an example trial sequence and target gratings and Figure 2 illustrates the response-relevant distinction between low and high spatial frequencies of gratings.

Procedure

Participants were instructed to make a 2-Alternative-Forced-Choice (AFC) response to indicate the low or high spatial frequency aspect of the target gratings. Participants were also instructed to sustain gaze at fixation for the length of each trial block. Participants were instructed to use the combined cue to anticipate the location and orientation of the to-be-presented target grating and to respond as quickly and as accurately as possible to the spatial frequency of the gratings.

Trials were presented in four minute blocks of 60 trials each. There were 16 blocks and each one contained 48 trials in which both orientation and location were validly cued; 4 trials with only validly cued orientation (invalid location); 4 trials with only validly cued spatial location (invalid orientation), and 4 trials in which both location and orientation were invalidly cued. This resulted in within-subjects 2×2 spatial by orientation validity factorial design where each cue was .867 predictive of its particular dimension. Targets were

presented with equal probability (.50) in the left and right visual field and orientation of targets varied randomly between vertical and horizontal at a ratio of .50 within each cueing condition and spatial hemi-field. A mersene twister algorithm was used to randomize trial order.

Electrophysiological Recording

Scalp potentials (EEGs) were recorded using a 64-channel Electro-cap from sites: FPZ, FZ, FCZ, CZ, CPZ, PZ, POZ, OZ, INZ, FP1, FP2, F7, F8, F3a, F4a, F3, F4, F7p, F8p, F3i, F4i, C3a, C4a, C3, C4, FC1, FC2, PA1, PA2, C5, C6, C1a, C2a, T3, T4, C1p, C2p, C5p, C6p, P3a, P4a, P1, P2, P3i, P4i, PO1, PO2, O1, O2, T3i, T4i, TO1, TO2, T1i, T2i, O1i, O2i, I1, I2, M1, M2. All scalp channels were referenced to the right mastoid for online recording and impedances were kept below 5 k Ω for all participants. Data were recorded in DC with an online band-pass filter of .1 to 100Hz using a Synamps II amplifier with Scan 4.2 software. Data were digitized at a rate of 1000 Hz and a post-recording band-pass filter of .3 (6db/oct forward slope) to 35 (24db/oct zero phase slope) Hz was applied. Data were re-sampled to 250 Hz offline. To monitor eye position, bipolar electrodes were placed on the outer left and right canthus and referenced to each-other. Blinks were also monitored with a bipolar electrode above and below the left eye.

Analysis

Each subjects EEG was epoched with a –200ms pre-stimulus baseline and a 500 ms post target stimulus interval. Artifacts were detected and eliminated using BESA software's artifact scan tool with a 120 μ V amplitude difference threshold, within any given trial, a 75 μ V gradient threshold between time samples, and a .10 μ V variance gradient threshold to detect trials in which the signal was low relative to noise. Channels (n=4) that were consistently bad across participants were removed from the grand-averaged analysis as well (Channels F7, PA1A, T3 and T4). Prior to statistical analysis, participants were removed from the dataset if the cue locked electro-oculogram revealed a difference greater than 3.0 μ V between left and right pointing cues at any time-point during the cue-to-target interval (see Lins, Picton, Scherg & Berg, 1993; Mangun & Hillyard, 1991) and if less than 70% of trials were accepted following the artifact rejection procedure. The result was that 17 of the 30 subjects were accepted for final analysis (9 subjects removed due to eye movements and 4 due to excessive blinks). Our overall pattern of behavioral and ERP results persists when all 30 subjects were included.

Results

Behavior

Table 1 displays mean reaction times and error rates for each condition. Reaction times for correct responses were entered into a repeated-measures ANOVA with location validity and orientation cue validity as factors. Results revealed a main effect of location validity, $F(1,16) = 26.166$, $p < .001$, $\eta^2 = .621$, a main effect of orientation validity, $F(1,16) = 20.517$, $p < .001$, $\eta^2 = .562$, and a significant spatial by orientation validity interaction on reaction times, $F(1,16) = 6.552$, $p = .021$, $\eta^2 = .291$. Proportions correct for each participant were also entered into a 2×2 repeated measures ANOVA with the factors of location validity (2 levels) and orientation validity (2 levels). Results revealed a main effect of location validity on proportion correct, $F(1,16) = 15.497$, $p < .001$, $\eta^2 = .492$ and no main effect of orientation validity, $F(1,16) = .063$, $p = .805$, $\eta^2 = .004$. Accuracy did not vary as a function of spatial or orientation validity either as revealed by a non-significant spatial by feature validity interaction, $F(1,16) = 1.446$, $p = .247$, $\eta^2 = .083$. Of particular note is the slowing of reaction times to the un-cued orientations within the validly cued spatial location, suggesting

a failure of spatial attention to facilitate processing of all stimuli under its focus ("spotlight failure").

Electrophysiology

P1 Component—A repeated measures ANOVA was performed on the contra-lateral occipital electrode sites (see Figure 3) over the classically defined 92–132ms¹ peak time window with the main factors of spatial validity (valid vs. invalid cued location), feature-based validity (invalid vs. valid orientation), and hemi-field of target stimulus presentation (left vs. right side of screen). For each participant, mean amplitude voltages were computed for this interval relative to a 200ms pre-stimulus baseline and these values were subsequently entered into statistical analysis. For E54/55 (T01/T02), we observed a main effect of spatial attention, $F(1,16) = 11.536$, $p = .004$, $\eta^2 = .420$ with higher mean P1 amplitude evoked over the contra-lateral visual cortex for targets falling within the focus of spatial attention (see Figure 3). Importantly however, this effect of spatial attention was not influenced by the validity of the feature-based expectancy, with no significant spatial by feature validity interaction, $F(1,16) = 1.117$, $p = .306$, $\eta^2 = .065$. In fact from viewing Figure 4, we can see nearly equivalent mean P1 voltages for both validly and invalidly cued orientations even though a robust slowing of reaction times is observed. Furthermore, Figure 5 displays the evoked averages for all 4 validity conditions for left and right hemifield targets. There was also a main effect of hemi-field with a greater overall mean amplitude observed over the contra-lateral visual cortex for stimuli presented in the left vs. right hemi-field, $F(1,16) = 7.603$, $p = .014$, $\eta^2 = .322$. No other main effects or interactions were significant (all p 's $> .05$). The same general pattern persisted for electrode sites, E55/E56 (P3/P4) and E43/E44 (O1/O2) for which we also observed main effects of spatial attention (both p values $< .05$) with no spatial X feature based attention interactions (both p values $> .400$)².

N1 Component—A similar repeated measures ANOVA was performed on the contra-lateral occipital E43/44 (O1/O2) N1 component over 150–180ms time window with the same factors as the P1 analysis. This analysis revealed a main effect of spatial attention, $F(1,16) = 5.031$, $p = .039$, $\eta^2 = .239$ that again did not interact with feature based validity, $F(1,16) = .094$, $p = .763$, $\eta^2 = .006$. There was a marginally significant main effect of hemi-field with a greater overall mean amplitude observed over the contra-lateral visual cortex for stimuli presented in the left vs. right hemifield, $F(1,16) = 4.182$, $p = .058$, $\eta^2 = .207$. No other main effects or interactions were significant (all p 's $> .250$). For electrode sites E53/54 (TO1/TO2), a marginally significant main effect of spatial attention was observed, $F(1,16) = 3.113$, $p = .097$, $\eta^2 = .163$. No other main effects or interactions were significant (all p 's $> .250$). For electrode sites, E55/E56 (P3/P4), only a main effect of hemi-field was observed, $F(1,16) = 5.176$, $p = .037$, $\eta^2 = .244$. No other main effects or interactions were significant (all p 's $> .160$).

300–400ms Component—Although our intent was to test the spotlight failure hypothesis and explore the possible sensitivity of the P1 component to feature-based attention, we also engaged in a post-hoc exploratory analysis of the effects of feature-cue validity and found a robust effect of feature based attention beginning 300ms after target presentation. Figure 6 plots the difference waves for a representative electrode site (E38 CpZ) and the associated topographical difference maps between validly and invalidly cued orientations for targets at

¹The pattern of results we present here persists under a number of different time windows (ie 70–100ms, 90–120, etc.). We chose the 92–132 ms window because it was the exemplar window in a classic study of spatial attention (Mangun & Hillyard, 1991).

²We chose this group of 3 electrode sites because these showed the maximal lateralized P1 mean amplitude (averaged across conditions).

the attended locations. From viewing Figure 6, we can see a distributed effect of feature based attention over the anterior electrode sites that interacts with hemi-field of target presentation. For each electrode site, we conducted a repeated measures ANOVA with spatial validity (valid vs. invalid cued location), feature-based validity (invalid vs. valid orientation), and hemi-field of target stimulus presentation (left vs. right side of screen) as the factors. The pattern of activation in Figure 6 is confirmed by spatial X feature X hemi-field interaction, in which the effects of feature based attention are different as a function of hemi-field and that this effect only occurs at the attended locations. The p-values of this spatial by feature by hemi-field interaction are plotted in the top right of Figure 6, showing an anterior distribution of activity sensitive to feature-based attention for this 300–400ms time interval. Because of its anterior distribution, we further explored whether this effect was specific to eye movements and conducted the same ANOVA on the horizontal electro-oculograms. The spatial by feature by hemi-field interaction was not significant ($p > .70$) suggesting that differences in eye movements between conditions is not driving our effect.

400–500ms Component—Figure 6 also plots the effect of feature based attention within the 400–500ms time interval. The overall pattern of activation is similar to the 300–400ms time window with the exception that it was not localized to the attended hemi-field. This was observed as an effect of feature based attention that interacted with hemi-field irrespective of spatial validity. We calculated a repeated measures ANOVA for each electrode site within this time interval and plotted the p values of the feature X hemi-field interaction in Figure 6. Upon observing the lower right part Figure 6, we can see a distributed pattern of feature based sensitivity in this time-window that does not interact with spatial attention.

Discussion

Our data demonstrate that the effect of spatial attention on the P1 response is not affected by the validity of feature based expectancies, even though a slowing of reaction times is observed to invalidly cued orientations. With direct reference to the pattern of behavior observed by Kingstone, (1992), our finding of a robust effect of spatial attention on the P1 component that is not sensitive feature-based validity reinforces the notion of a spotlight of attention that operates to illuminate a region of space irrespective of other forms of attention. Such a finding suggests that the interpretation of the slowing of reaction times to uncued features depends on the stage of information processing at which the effects of attention are observed. Our application of a measure with high temporal resolution reveals the early stage at which spatial attention independently operates to facilitate target processing.

We further explored the later processing stages at which the effects of feature-based attention manifest and observed an anterior distribution of activity at the 300–400ms time window that is sensitive to the validity of feature-based expectancies within the spotlight of attention. It is interesting to note that this time window occurs in the temporal window of the P300 component, which has been associated with the updating of working memory (Linden, 2005; McEvoy, Smith & Gevins, 1998; Polich, 2003). Prior work from our lab has shown that feature-based attention uniquely interacts with individual working memory capacity only within the spotlight of spatial attention (Bengson & Mangun, 2011). Interestingly, the ERP effect of feature based attention for the 300–400ms time window shown in Figure 6 is localized specifically to attended locations. Although speculative, this activity may be the neural signature of a common mechanism by which working memory and feature-based attention interact. Alternatively, the later interactive components at the 300–400ms time-windows might index the point at which interchannel crosstalk may occur whereby correlated signals from the spatial cue and feature based cue interact in to differentially process the target as a function of feature-validity. Because cuing conditions are typically

correlated in combined expectancy designs, interactive race models of divided attention might account for our findings whereby probabilistic inter-channel contingencies determine the degree of inter-channel interaction (Mordkoff & Yantis, 1991). The later interactive components we observe in the 300–400ms window may index the neural locus of such crosstalk and that the “spotlight failure” observed in many combined expectancy studies may be sensitive to probabilistic information (Mordkoff & Yantis, 1991). However, the fact that our interactive components occur during a post-perceptual locus more closely linked with the updating of working memory suggests that such implicit and purely probabilistic cross-talk is not a likely candidate for our observed interactions in the ERP waveforms because the interactive race models positing such crosstalk operate at the level of implicit perceptual processing and not later attentional or working memory stages (Mordkoff & Yantis, 1991). Our ERP results are more in line with a post-perceptual locus of interaction between spatial and feature based attention in the 300–400ms post-target interval. However, the effects we observe could still be derived from a different kind of post-perceptual probabilistic crosstalk related to working memory updating (Bengson & Mangun, 2011). Further work is needed to dissociate the exact mechanism by which feature based attention and spatial attention interact at the later stages of processing.

Conclusion

In general, the present data are informative with respect to a fundamental point of contention within cognitive neuroscience. Underlying many influential theories of attention is the assumption that attention is a domain general construct (Broadbent, 1958; Bundesen, 1990; Kahneman, 1973; Norman and Bobrow, 1975). A form of this assumption can be found in a hypothesis put forward by Duncan (1984), who suggested that spatial attention may be a manifestation of a domain general attention mechanism that is not unique from other forms of attention. This was supported to some degree by the behavioral work of Kingstone (1992) and others (Lambert, 1987; Lambert & Hockey, 1986) who demonstrated that the benefits of spatial attention are sensitive to non-spatial expectancies. Our results show that the interpretation of this pattern depends on the stage of information processing at which the effects of attention are measured. We find that early in the visual processing stream, spatial attention operates to independently enhance the representation of visual stimuli. However, because our measurements are taken over the visual cortex at the site of attentional selection, it is still conceivable that selection can occur via a multi-level selection process that is controlled by a domain-general mechanism. Nonetheless, we still observe a unique pattern of cortical activation with respect to the expression of spatial attention. This pattern is in line with other recent experimental work demonstrating that feature-based attention and spatial attention have unique properties (Hayden and Gallant, 2005; Andersen, et al., 2009) and further supports the notion that attention is a multidimensional phenomenon that varies according to task demands and the stage of information processing at which it is measured (Spelke, et al. 1976; Woodman, Vogel, Luck, 2001).

Acknowledgments

This work was supported by NIMH grant MH055714 to G.R.M.

We would like to thank Dr. Steve Luck for his help.

References

- Anllo-Vento L, Hillyard SA. Selective attention to the color and direction of moving stimuli: Electrophysiological correlates of hierarchical feature selection. *Perception & Psychophysics*. 1996; 58:191–206. <http://dx.doi.org/10.3758/BF03211875>. [PubMed: 8838164]

- Andersen SK, Fuchs S, Müller MM. Effects of feature-selective and spatial attention at different stages of visual processing. *Journal of Cognitive Neuroscience*. 2010; 23:238–246. <http://dx.doi.org/10.1162/jocn.2009.21328>. [PubMed: 19702461]
- Bengson JJ, Mangun GR. Individual working memory capacity is uniquely correlated with feature-based attention when combined with spatial attention. *Attention, Perception & Psychophysics*. 2011; 73:86–102. <http://dx.doi.org/10.3758/s13414-010-0020-7>.
- Bundesen C. A theory of visual attention. *Psychological Review*. 1990; 97:523–547. <http://dx.doi.org/10.1037/0033-295X.97.4.523>. [PubMed: 2247540]
- Cowan N. The magical number 4 in short-term memory: a reconsideration of mental storage capacity. *Behavioral and Brain Sciences*. 2001; 24:87–114. <http://dx.doi.org/10.1017/S0140525X01003922>. [PubMed: 11515286]
- Duncan J. Selective attention and the organization of visual information. *Journal of Experimental Psychology: General*. 1984; 113:501–517. <http://dx.doi.org/10.1037/0096-3445.113.4.501>. [PubMed: 6240521]
- Fodor, JA. *The modularity of mind: An essay on faculty psychology*. MIT Press/A Bradford Book; 1983.
- Fink GR, Dolan RJ, Halligan PW, Marshall JC, Frith CD. Space-based and object-based visual attention: shared and specific neural domains. *Brain*. 1997; 129:2013–2028. <http://dx.doi.org/10.1093/brain/120.11.2013>. [PubMed: 9397018]
- Gall, FJ.; Spurzheim, G. *Recherches sur le système nerveux en général et sur celui du cerveau en particulier*. Paris: Schoell; 1809.
- Handy TC, Green V, Klein RM, Mangun GR. Combined expectancies: Event-related potentials reveal the early benefits of spatial attention that are obscured by reaction time measures. *Journal of Experimental Psychology: Human Perception & Performance*. 2001; 27:303–317. <http://dx.doi.org/10.1037/0096-1523.27.2.303>. [PubMed: 11318049]
- Hayden BY, Gallant JL. Time course of attention reveals different mechanisms for spatial and feature-based attention in area V4. *Neuron*. 2005; 47:637–643. <http://dx.doi.org/10.1016/j.neuron.2005.07.020>. [PubMed: 16129394]
- Hillyard SA, Münte TF. Selective attention to color and location: an analysis with event-related brain potentials. *Perception & Psychophysics*. 1984; 36(2):185–198. <http://dx.doi.org/10.3758/BF03202679>. [PubMed: 6514528]
- Humphreys GW. Flexibility of attention between stimulus dimensions. *Perception & Psychophysics*. 1981; 30:291–302. <http://dx.doi.org/10.3758/BF03214285>. [PubMed: 7322805]
- Kanwisher N, McDermott J, Chun MM. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*. 1997; 17:4302–4311. PMID:9151747. [PubMed: 9151747]
- Kingstone A. Combining expectancies. *Quarterly Journal of Experimental Psychology*. 1992; 44A:69–104.
- Lambert AJ. Expecting different categories at different locations and spatial selective attention. *Quarterly Journal of Experimental Psychology*. 1987; 39A:61–76. [PubMed: 3615941]
- Lambert AJ, Hockey R. Selective attention and performance with a multidimensional visual display. *Journal of Experimental Psychology: Human Perception and Performance*. 1986; 12:484–495. <http://dx.doi.org/10.1037/0096-1523.12.4.484>. [PubMed: 2946805]
- Linden DE. The p300: where in the brain is it produced and what does it tell us? *Neuroscientist*. 2005; 11:563–576. <http://dx.doi.org/10.1177/1073858405280524>. [PubMed: 16282597]
- Lins OG, Picton TW, Berg P, Scherg M. Ocular artifacts in EEG and event-related potentials. I: Scalp topography. *Brain Topography*. 1993; 6:51–63. <http://dx.doi.org/10.1007/BF01234127>. [PubMed: 8260327]
- Mangun GR, Hillyard SA. Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual-spatial priming. *Journal of Experimental Psychology: Human Perception & Performance*. 1991; 17:1057–1074. <http://dx.doi.org/10.1037/0096-1523.17.4.1057>. [PubMed: 1837297]
- Mangun GR. Neural mechanisms of visual selective attention. *Psychophysiology*. 1995; 32:4–18. <http://dx.doi.org/10.1111/j.1469-8986.1995.tb03400.x>. [PubMed: 7878167]

- McEvoy LK, Smith ME, Gevins A. Dynamic cortical networks of verbal and spatial working memory: effects of memory load and task practice. *Cerebral Cortex*. 1998; 8:563–574. <http://dx.doi.org/10.1093/cercor/8.7.563>. [PubMed: 9823478]
- Mordkoff JT, Yantis S. An interactive race model of divided attention. *Journal of Experimental Psychology: Human Learning & Performance*. 1991; 17:520–538.
- Neely J. Semantic priming and retrieval from lexical memory: Roles of inhibitionless spreading activation and limited-capacity attention. *Journal of Experimental Psychology: General*. 1977; 106:226–254.
- Polich, J. Theoretical overview of P3a and P3b. In: Polich, J., editor. *Detection of change: event-related potential and fMRI findings*. Boston, MA: Kluwer Academic; 2003. p. 83-98.
- Posner, M. *Chronometric explorations of mind*. Hillsdale, N.J: Erlbaum; 1979.
- Pylyshyn Z. Is vision continuous with cognition? The case for cognitive impenetrability of visual perception. *Behavior and Brain Sciences*. 1999; 22:341–365. <http://dx.doi.org/10.1017/S0140525X99002022>.
- Spelke E, Hirst W, Neisser U. Skills of divided attention. *Cognition*. 1976; 4:215–230. [http://dx.doi.org/10.1016/0010-0277\(76\)90018-4](http://dx.doi.org/10.1016/0010-0277(76)90018-4).
- Woodman G, Vogel E, Luck. Attention is not unitary. Commentary on Cowan. N. The magical 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences*. 2001; 24:153–154. <http://dx.doi.org/10.1017/S0140525X01603923>.

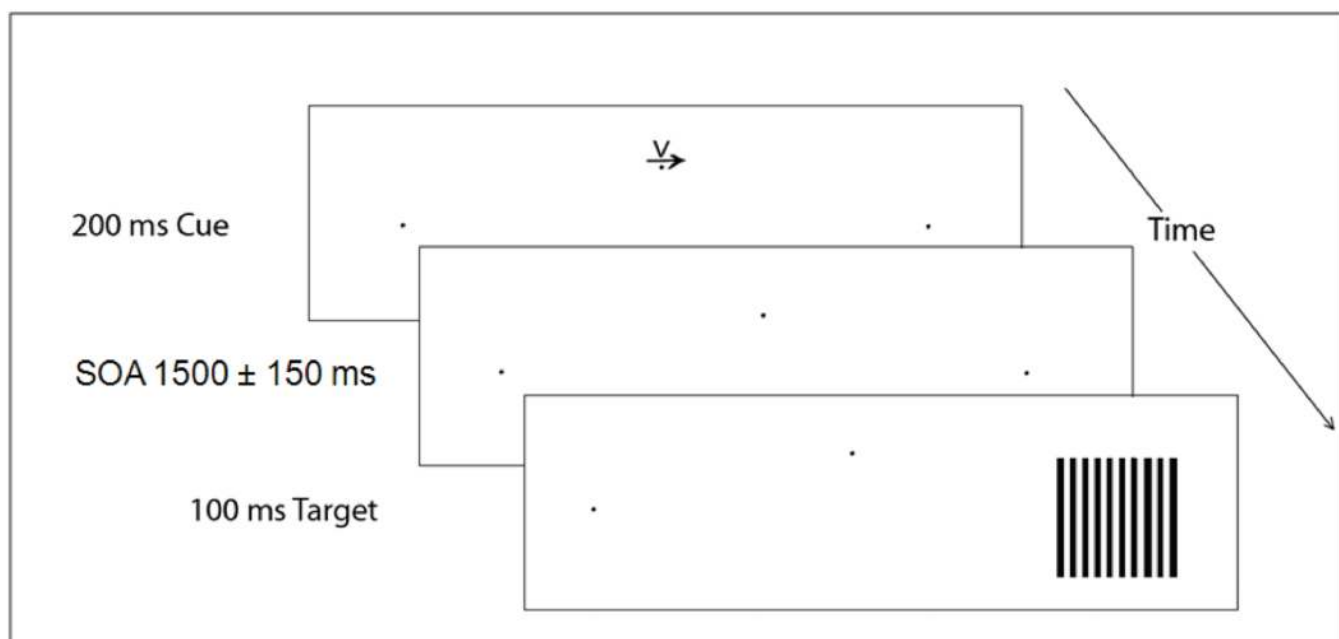


Figure 1.
Displays an exemplar trial sequence.

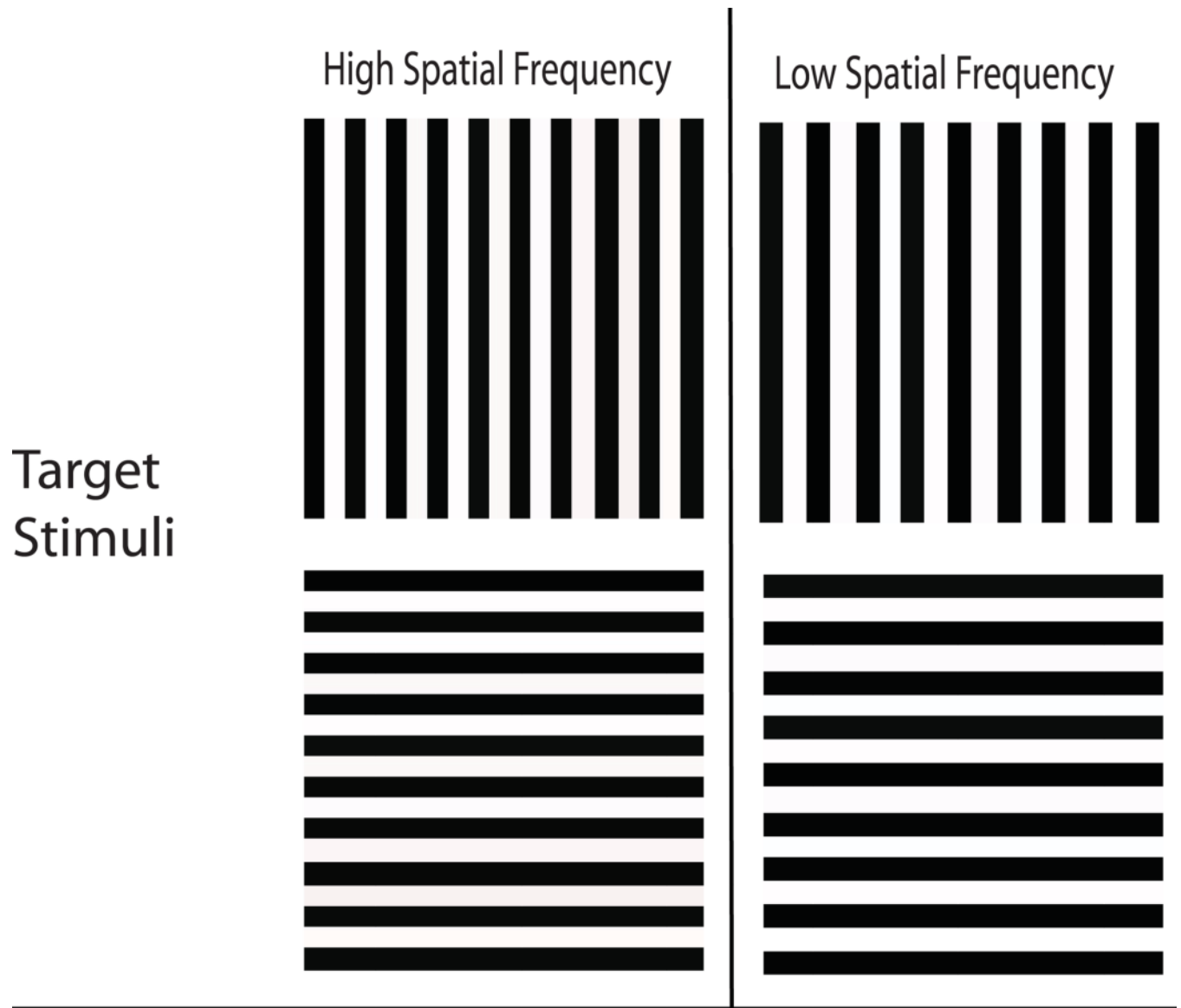
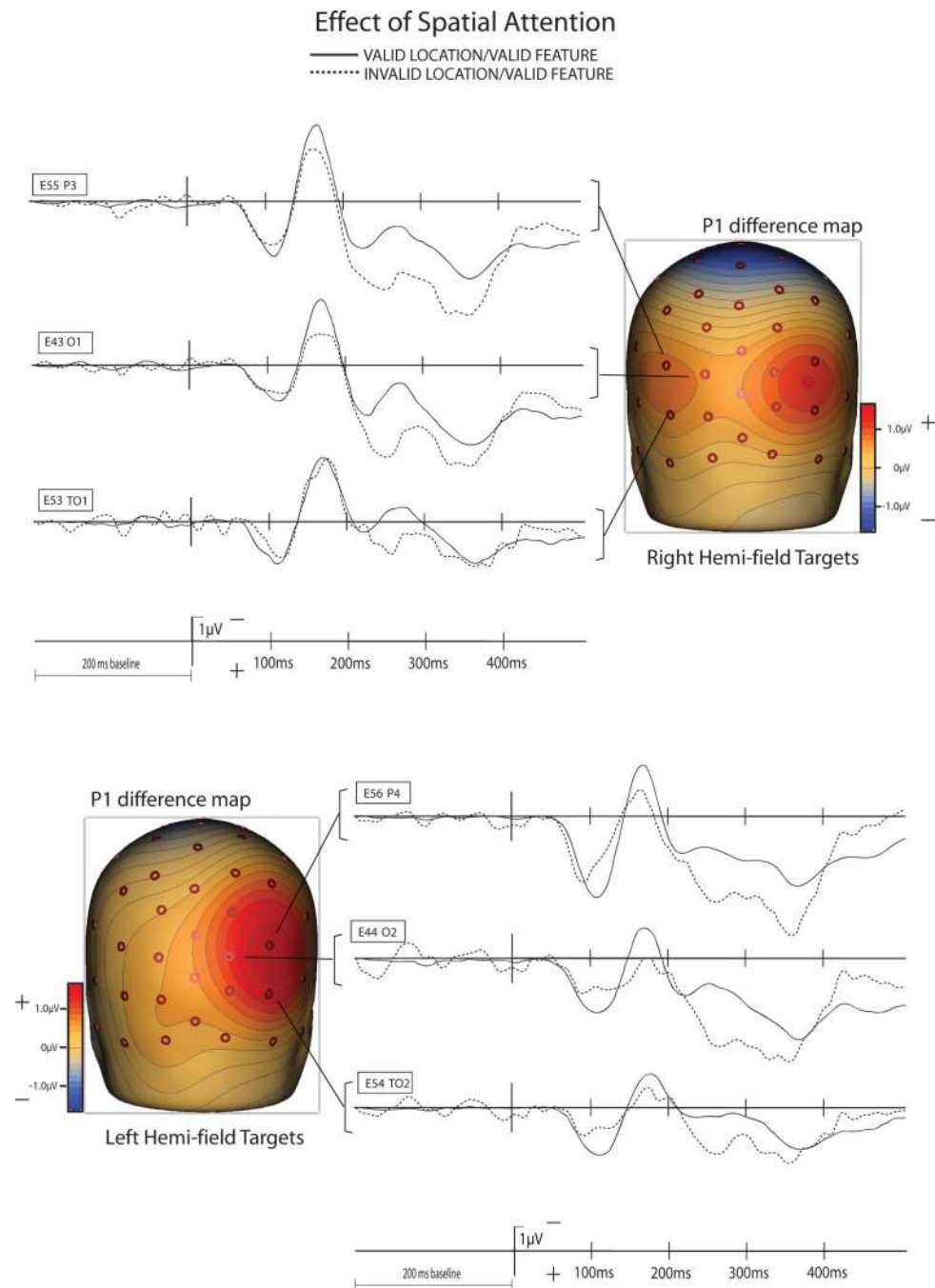


Figure 2. Illustrates the response relevant distinction between the high and low frequency target gratings.

**Figure 3.**

Displays the topographic maps of the difference between attended and unattended locations in the 92–132ms interval and the associated contra-lateral Event Related Potentials for targets at attended and unattended locations over the 500ms post-target interval.

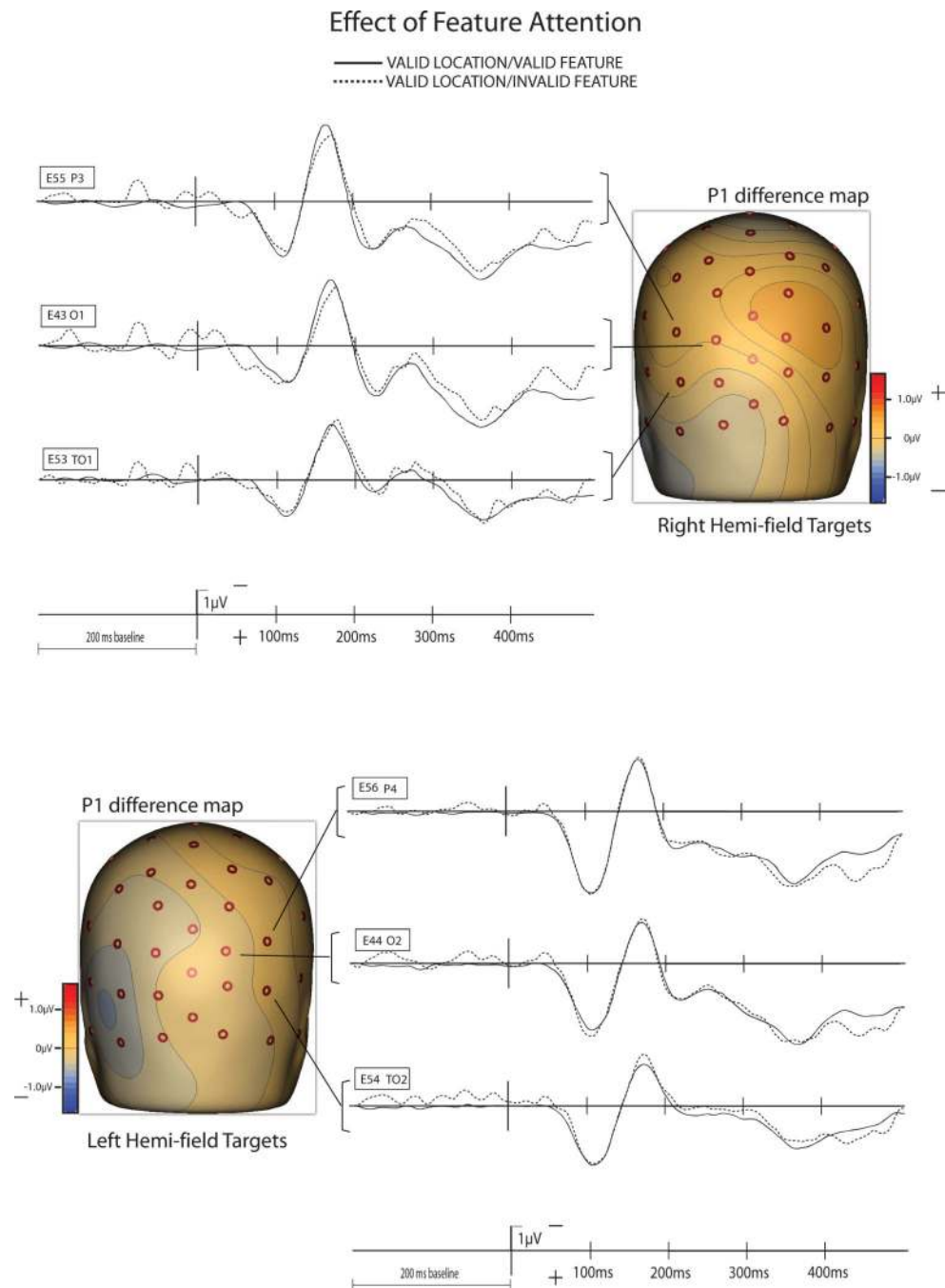


Figure 4.

Displays the topographic maps of the P1 difference (92–132ms) between expected and unexpected oriented targets for attended locations and the associated contra-lateral occipital Event Related Potentials for validly cued and invalidly cued orientations over the 500ms post-target interval.

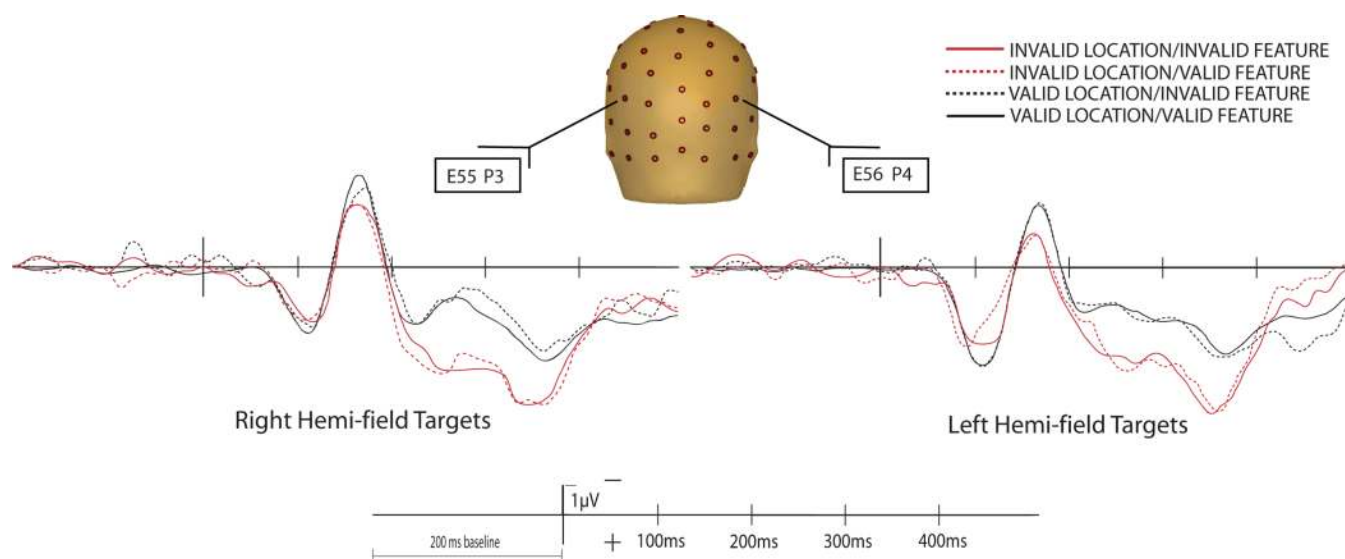
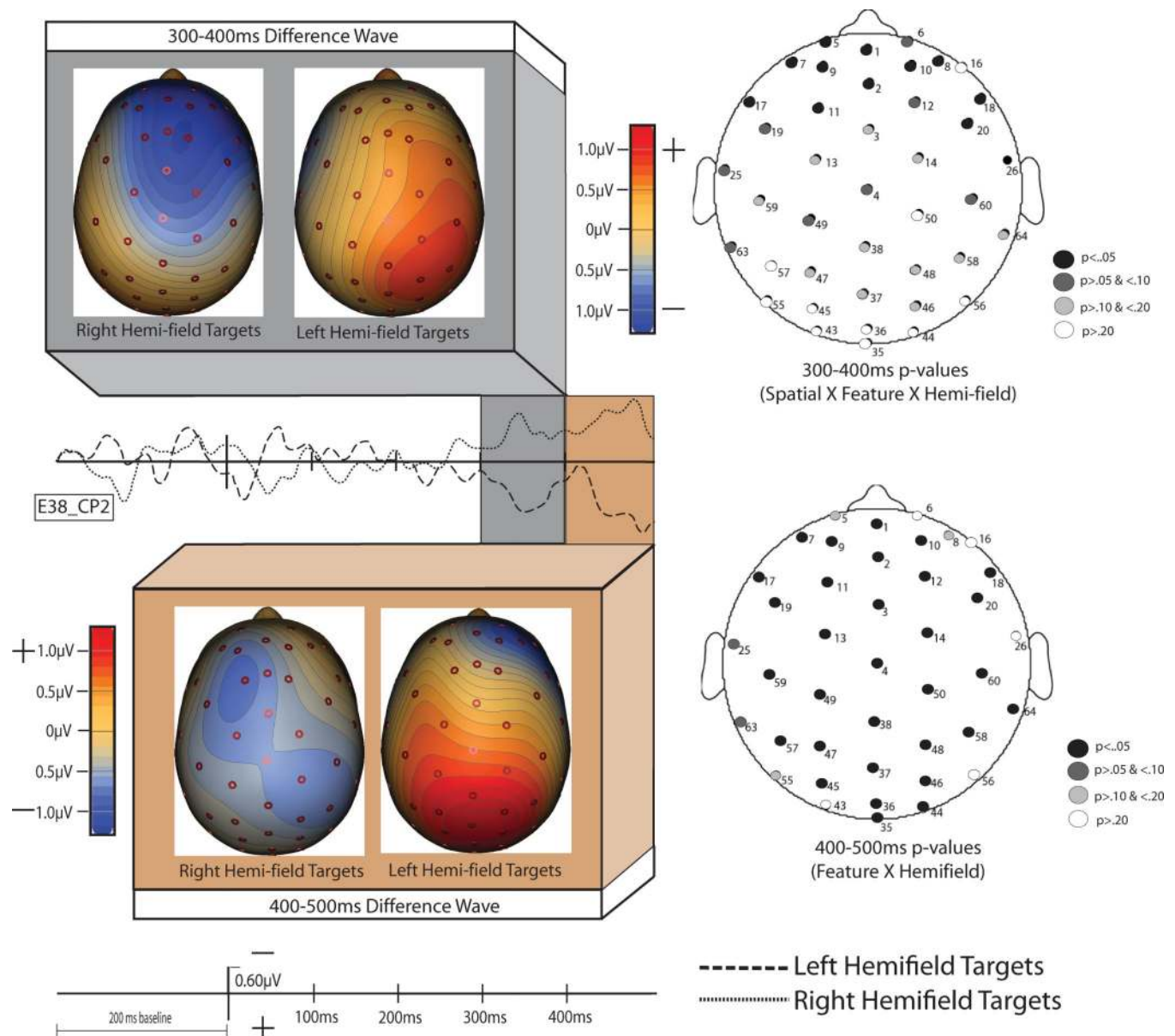


Figure 5.
Displays the mean voltages over the 500ms post-target interval for all four target validity conditions for electrodes P3/P4.

**Figure 6.**

Displays a representative electrode site and the associated topographic maps of the difference waves between expected and unexpected oriented targets (expected – unexpected) at the cued locations for the 300–400ms and 400–500ms time windows. To the right of the figure are the respective maps of p-values for the feature based attention effect for the 300–400ms and 400–500ms time windows.

Table 1

Mean RT and Error Proportions (N=17)

	Valid Location		Invalid Location	
	RT	(ACC)	RT	(ACC)
Valid Orientation	710	(.24)	811	(.30)
Invalid Orientation	772	(.23)	839	(.30)