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| Title | Attribute-invariant orientation discrimination at an early stage of processing in the human visual system |
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| Citation | Vision Research, 47(2), 203-209 https://doi.org/10.1016/j.visres.2006.09.023 |
| Issue Date | 2007-01 |
| Doc URL | http://hdl.handle.net/2115/19103 |
| Type | article (author version) |
| File Information | VR47-2.pdf |



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Attribute-Invariant Orientation Discrimination at an Early Stage of Processing
in the Human Visual System

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Keywords: Cue Integration; Form; Orientation Discrimination; Attention; Event-Related
Potentials

Note

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Abstract

This study investigated event-related brain potentials (ERPs) during selective attention to the orientation of a bar comprised of two squares, which were defined by only color or motion (intra-attribute conditions) or both (interattribute condition). An early positive potential in association with orientation selection was elicited for all conditions in similar latency ranges but with different scalp distributions. These results suggest that attribute-invariant orientations can be discriminated at an early stage of processing in the human brain, which fills a gap between monkey electrophysiology and human psychophysics, while attribute-specific orientations are also available in a given context.

Attribute-Invariant Orientation Discrimination at an Early Stage of Processing
in the Human Visual System

The visual system processes feature dimensions, such as color or motion, in their respective channels or modules (Zeki, 1993), which indicates that the different attributes of an image are separately detected in the initial stage of processing. However, it has been suggested that contour or edge information for different attributes is converged beginning in an early stage of processing. In behavioral studies, tilt effects and illusory contours occur across stimuli defined by luminance, motion, and disparity cues (Poom, 2000, 2001). In addition, orientations defined by different feature dimensions show similar discrimination thresholds (Regan, 2000) and search efficiency (Cavanagh, Arguin, & Treisman, 1990). These results suggest that common attribute-invariant representations are formed and perception or task performance is then achieved based on these representations.

Neurophysiological studies in monkeys have provided neural bases for common form representations: there are neurons that selectively respond to orientation or shape, regardless of the defining attributes, in cortical areas V2 (Leventhal, Wang, Schmolesky, & Zhou, 1998; Marcar, Raiguel, Xiao, & Orban, 2000) and IT (Sary, Vogels, & Orban, 1993; Sary, Vogels, Kovacs, & Orban, 1995).

However, it remains unclear how common representations are involved in shape discrimination processes in the human brain. Although common and distinctive brain regions have been identified in response to forms defined by different feature dimensions (e.g., Dupont et al., 1997; Mendola, Dale, Fischl, Liu, & Tootel, 1999; Orban, Dupont, Bruyn, Vogels, & Vandenberghe, 1995), no overlapping brain regions were activated in the discrimination of color- and motion-defined forms (Gulyas, Heywood, Popplewell, Roland, & Cowey, 1994). Thus, shape discrimination seems to be based on attribute-dependent representations rather than attribute-invariant representations. However, the slow time

course of the hemodynamic response in neuroimaging techniques may mask slight transient neural responses, and experimental tasks that require common representations have not been examined.

Scalp-recorded, event-related brain potentials (ERPs) are a useful tool for examining fine temporal information in the brain. Previous ERP studies on visual selective attention have identified several components associated with discrimination or selection processes in separate feature dimensions such as color, motion, and shape/orientation (for reviews, Harter & Aine, 1984; Hillyard & Anllo-Vento, 1998; Näätänen, 1992). Stimuli with an attended feature value (i.e., red or circle) typically evoked selection negativities (SNs) over posterior regions with an onset latency at around 150-300 ms post-stimulus, relative to those with an unattended feature. Earlier selection positivities (SPs) at around 100-200 ms post-stimulus have also been identified for color, motion, and shape/orientation, although these have been reported relatively infrequently because of the small amplitude (Anllo-Vento, Luck, & Hillyard, 1998; Kenemans, Lijffijt, Camfferman, & Verbaten, 2002; Martinez, Di Russo, Anllo-Vento, & Hillyard, 2001; Martin-Loeches, Hinojosa, & Rubia, 1999; Proverbio, Esposito, & Zani, 2002). The selection potentials are clearly distinguished from the early stimulus-evoked P1 and N1 components that are associated with a gain control mechanism of sensory-evoked responses by spatial attention (for a review, Hillyard & Anllo-Vento, 1998). In contrast, scalp distributions of SPs and SNs can vary according to the feature dimension to be attended, which indicates that these may reflect neural activities in specialized brain regions for processing particular attributes (Anllo-Vento & Hillyard, 1996; Anllo-Vento et al., 1998; Martin-Loeches et al., 1999; Previc & Harter, 1982). Furthermore, the scalp distributions and neural origins of SPs differ from those of SNs, which suggests that the selection potentials reflect a processing sequence in particular feature dimensions (Anllo-Vento et al., 1998): early processing for SPs and later processing for SNs.

In the present study, we examined ERPs during selective attention to the orientation of stimuli similar to those used by Morita, Morita, & Kumada (2003), where the orientation was determined by the spatial arrangement of two squares, as shown in Figure 1. In the interattribute condition, one of the squares was segregated from the background by motion and the other was segregated by color. Therefore, the integration of information across these two attributes would be required to discriminate the orientation. Morita et al. (2003) showed that visual search became more difficult as the number of items increased in the interattribute condition relative to when the two squares were defined by the same attribute (intra-attribute conditions), which suggests that attribute-specific representations are involved in visual search processes. In contrast, the present study examined only a single item to elucidate neural substrates of form discrimination processes based on attribute-invariant representations. If common representations found in single-unit studies in the early visual cortex are available for the discrimination of orientation defined by different attributes, orientation SP should be observed in the interattribute condition. In addition, we compared ERPs associated with orientation discrimination in the interattribute condition with those in the intra-attribute conditions to explore how attribute-specific representations are integrated into common representations.

[Insert Figure 1 around here]

Methods

Participants

Eighteen volunteers (5 females; 19-36 years old, mean 23.2 years) participated in this experiment. All had normal or corrected-to-normal visual acuity and color vision. One male was left-handed. Written informed consent was obtained from each participant after the nature of the study had been fully explained.

Apparatus and stimuli

Stimuli were presented on a color video monitor (NANA O FlexScan 56 T/S) controlled by a computer (Genuine Intel Pentium II) equipped with a Visual Stimulus Generator (Cambridge Research Systems, VSG2/3) at a viewing distance of 57 cm. Schematic illustrations of the stimuli are shown in Figure 1. A bar was presented at the center in one of the quadrants of the background ($8.14^\circ \times 8.14^\circ$ in visual angle) filled with a yellow-and-black random-dot pattern; each dot ($0.03^\circ \times 0.03^\circ$) was randomly assigned yellow (26 cd/m^2) or black (0 cd/m^2). The bar consisted of a pair of squares ($1.49^\circ \times 1.49^\circ$) adjacent to each other with a small gap between them. The size of the gap was 0.75° for targets or 0.15° for non-targets (standards). The bar appeared with an orientation of 45° or 135° at a distance of 2.3° from a fixation point at the center of the background. The fixation point was a small white circle ($0.2^\circ \times 0.2^\circ$) and was always visible during experimental blocks.

There were two intra-attribute conditions. Under the intra-color condition, the bar consisted of two color-defined squares; one was filled with a random-dot pattern of red and black, and the other was filled with a random-dot pattern of green and black. The red and green stimuli were set to be equiluminant with yellow in the background using a minimum flicker technique for each participant. Under the intra-motion condition, the bar consisted of two motion-defined squares; one was filled with random dots of yellow and black that moved coherently to the left at $2.29^\circ/\text{sec}$, and the other was filled with the same dots moving to the right at the same speed. The positions (upward and downward) of different feature values were varied randomly. The most relevant condition in the present study was the interattribute condition, in which the bar consisted of a color-defined square and a motion-defined square. To use two feature values as in the intra-attribute conditions, one of the colors and one of the motion directions were selected for each participant, counter-balanced across the participants.

Procedure

Participants were seated in a sound-attenuated, electrically shielded, and darkened room facing the video monitor. The three conditions (intra-color, intra-motion, interattribute) were administered in separate sessions on a single day. Each session consisted of two blocks, each consisting of a sequence of 160 stimulus presentations randomly sampled from 16 stimulus classes defined by type (target, standard), orientation (45, 135), and location (four quadrants). The presentation probabilities were 0.2 for target, 0.8 for standard, and both orientations and the four locations were equiprobable. The duration of each stimulus was 200 ms and inter-stimulus intervals were varied at random between 1000 -1500 ms (6 steps, rectangular distribution).

The participants were instructed to pay attention to a particular orientation and to press a button with the right hand every time they detected a target with the orientation regardless of the location. The location was varied across trials to avoid having the participants use a strategy of attending only to a local change in feature contrast rather than orientation. We emphasized that they should respond as quickly as possible, to maintain ocular fixation on the fixation point and not to move their eyes during the experiment. The order of the cue-attribute condition and the attended orientation was counter-balanced across the participants. In this task, all stimuli were assigned as having either an attended orientation (O+) or unattended orientation (O-) for both target (T+) and standard (T-). Prior to each session, the participants performed at least 80 trials of practice blocks until fixation had stabilized during the task. They also practiced the task before new target orientation blocks (40 trials). Each block included a rest period in the middle.

Recording and analyses

The electroencephalogram (EEG) was recorded from 19 scalp sites according to the International 10-20 System (Fp1, Fp2, F7, F8, F3, F4, Fz, T3, T4, C3, C4, Cz, P7, P8, P3, P4,

Pz, O1, O2) using Ag-AgCl electrodes mounted on an elastic cap (Neuroscan). All electrodes were referenced to the average of ear lobes. Eye movements were monitored with electrodes at the outer canthi of both eyes (horizontal EOG) and above and below the right eye (vertical EOG). The impedance of the scalp electrodes was kept below 5 kOhm and that of EOGs was kept below 15 kOhm. EEGs were filtered with a bandpass of 0.16-30 Hz and sampled at 200 Hz. Averaging epochs were 800 ms, starting 100 ms before the onset of the stimulus and ending 700 ms post-stimulus. Automatic artifact rejection was performed to eliminate data epochs that were contaminated by blinks, saccades, excessive muscle activity, or amplifier saturation (with a criterion of 50 μ V). Epochs that included incorrect behavioral responses were also excluded from ERPs. On average, 20 % of the trials were rejected.

Behavioral performance was measured, including the percentage of correct target detections (hits) and reaction times (RTs) for hits. Responses were scored as correct if they occurred within 200-1000 ms after a target stimulus with the attended orientation. Responses to other stimuli were classified as false alarms (FAs).

ERPs were calculated separately for the type and attentional relevance of orientation in each cue condition, collapsing over the stimulus locations. Further ERP analyses were conducted only for the standard trials to examine ERP components associated with feature selection, separating those associated with terminal decision and motor processes (Hillyard & Münte, 1984). Grand-averaged ERPs were examined for each cue-attribute condition to identify orientation selection effects, and identified ERPs were estimated by the mean amplitudes with respect to a 100-ms prestimulus baseline voltage, which were subjected to a repeated-measures analysis of variance (ANOVA). The Huynh-Feldt correction was used to reduce the positive bias resulting from repeated factors with more than two levels.

Results

Behavioral results

Behavioral data are shown in Table 1. RTs were shortest for the intra-color condition, longest for the intra-motion condition, and intermediate for the interattribute condition, $F(2, 34) = 50.2, p < 0.0001$. The percentage of hits for the intra-color condition was higher than that for the intra-motion and interattribute conditions, $F(2, 34) = 11.2, p < 0.001$. The percentage of FAs was generally low, although it was higher for standards with an attended orientation (O+T-) than for targets and standards with an unattended orientation (O-T+, O-T-), $F(2, 34) = 8.1, p < 0.01$. This effect was the greatest in the interattribute condition, $F(4, 68) = 2.7, p < 0.05$.

[Insert Table 1 around here]

Electrophysiological results

Figure 2 shows grand-averaged ERPs at all electrode sites in response to standard stimuli in the interattribute condition. The ERPs were characterized by lateral parietal P1 (with a peak at approximately 150 ms), occipito-temporal N1 (200 ms), central parietal P2 (250 ms), and central N2 (300 ms). Orientation selection effects were observed as differences between ERPs in response to stimuli with attended orientation (O+) and unattended orientation (O-). A more positive potential was observed for O+ relative to O- at around 150 ms post-stimulus at the right occipital site (O2) and a more negative potential was observed for O+ at around 300 ms over central sites. The former was identified as SP.

[Insert Figure 2 around here]

Early orientation selection effect. Figure 3 shows the ERPs in the inter- and intra-attribute conditions at selected electrode sites and scalp distributions of the subtraction ERPs [(O+)-(O-)]. The right-occipital SP in the interattribute condition (see also Figure 4) was reflected by a significant Relevance x Hemisphere interaction at the occipital electrode sites (O1, O2) in a 125-175 ms time-window, $F(1, 17) = 5.3, p < 0.05$. SPs were also

observed in the intra-attribute conditions. In the intra-color condition, SP was elicited at the frontal sites, indicated by a significant main effect of Relevance in the 125-175 ms time-window at the frontal electrodes (F3, F4), $F(1, 17) = 7.4, p < 0.05$. SP in the intra-motion condition was elicited over the occipital sites at a later latency range, which was indicated by a main effect of Relevance in a 175-225 ms time-window at the occipital electrodes (O1, O2), $F(1, 17) = 7.4, p < 0.05$.

[Insert Figures 3 and 4 around here]

The scalp distributions of the SPs were compared, including data from all electrodes, and amplitude differences were eliminated by scaling (MacCarthy & Wood, 1985). The subtraction ERPs were subjected to ANOVA with factors of Cue-Attribute and Electrode: significant interaction was found between the intra-color and intra-motion condition [$F(18, 306) = 2.7, p < 0.05$] and between the interattribute and intra-color conditions [$F(18, 306) = 2.6, p < 0.05$], which indicate that different neural origins contributed to the scalp distributions in each comparison.

Later orientation selection effect. Subsequent orientation selection effects were broad negative potentials over posterior and central regions with a peak at around 300 ms for all of the cue-attribute conditions. The negativities showed a greater amplitude for the interattribute condition than for the intra-color and intra-motion conditions, which was reflected by a significant interaction of Cue Attribute and Relevance in a 275-325 ms window in an analysis that included the central and parietal electrodes (Cz, Pz, C3, P3, C4, P4), $F(1, 17) = 4.0, p < 0.05$.

Stimulus-evoked ERPs. Figure 5 shows the scalp distributions of ERPs in response to standards with unattended orientation (O-). Since the peak latencies of the stimulus-evoked responses in the intra-attribute conditions were equal to those in the interattribute condition, ERPs in the same latency ranges were compared: P1 (125-175 ms), N1 (175-225 ms), and P2

(225-275 ms). P1 was distributed over the lateral parietal sites and N1 was distributed over the occipital-temporal sites, similarly across the cue conditions. P2 for the intra-color condition was distributed maximally at the lateral parietal sites, while that for the intra-motion condition was distributed more centrally. P2 for the interattribute condition was distributed in a manner intermediate of those for the intra-color and intra-motion conditions. Significant interactions between Cue-Attribute and Electrode revealed that different neural origins contributed to the scalp distributions in the P2 latency range between the intra-color and intra-motion conditions [$F(18, 306) = 11.2, p < 0.0001$] and between the intra-color and interattribute conditions [$F(18, 306) = 5.7, p < 0.005$].

[Insert Figure 5 around here]

Discussion

The purpose of the present study was to elucidate the neural processes of the orientation discrimination based on attribute-invariant form representations, which has been suggested in behavioral studies in humans (Cavanagh et al., 1990; Poom, 2000, 2001; Regan, 2000) and in neurophysiological studies in monkeys (Leventhal et al., 1998; Marcar et al., 2000; Sary et al., 1993, 1995). We found an orientation SP at around 150 ms post-stimulus over the occipital region in the interattribute condition, which defined an orientation by spatial arrangement of color- and motion-defined forms. This SP was the difference between ERPs in response to stimuli with attended and unattended orientations, and thus indicates that attribute-invariant orientations can be discriminated in this latency. Moreover, the SP could reflect the selective enhancement of neural activities representing attribute-invariant orientations, distinguished from activities in response to the defining attributes themselves. To our knowledge, the present SP in the interattribute condition is the first indication of the neural activities involved in attribute-invariant orientation discrimination in the human brain.

The present results reveal some properties of attribute-invariant orientation discrimination processes. We also found an orientation SP in the intra-color condition, which was distributed over the frontal region, similar to the SP associated with color selection that have been observed previously (Anllo-Vento et al., 1988; Martin-Loeches et al., 1999). Interestingly, the orientation SP in the intra-color condition was elicited at the same latency range as that in the interattribute condition. Moreover, we found that the orientation SP in the intra-motion condition at a later latency had a scalp distribution different from that in the intra-color condition. These results suggest that attribute-invariant orientation is available as early as attribute-dependent orientation, although an attribute-dependent representation is used for orientation selection when the orientation is defined by only one attribute. This notion is similar to ‘dimensional weighting’, where the participant’s knowledge of the upcoming target biases the processing in a specific dimensional analyzer (Kumada, 2001), and can explain why it has been proposed that attribute-dependent brain regions are involved in shape discrimination of color- or motion-defined forms in a blocked design (Gulyas et al., 1994). It would be interesting to examine whether an attribute-dependent representation is available when the intra- and interattribute conditions are randomized within blocks rather than given in separate blocks.

The orientation SP in the intra-motion condition was elicited later than that in the intra-color and interattribute conditions, which is consistent with the fact that response latencies were longer in kinetic-contour-selective cells in V2, due to feedback projection from higher areas for motion processing (Leventhal et al., 1998; Marcar et al., 2000) and with the fact that motion contrast is generally less salient than color contrast (Nothdurft, 2000). Behavioral performance (RTs, Hits) was also the worst in the intra-motion condition. However, since the behavioral performance also involved target (gap size) discrimination, we conducted an additional behavioral test to discriminate only orientation, and observed a

similar RT trend (462.5 ms for interattribute; 431.6 ms for intra-color; 489.4 ms for intra-motion, $F(2,22)=55.5$, $p<0.0001$). The behavioral results also support the notion that attribute-invariant orientations are unnecessarily formed after attribute-specific orientations.

In the later orientation selection effects, the broad negative potentials over the posterior sites seemed less clear than typical occipito-temporal shape/orientation SNs (e.g., Kasai & Morotomi, 2001; Martin-Loeches et al., 1999; Proverbio et al., 2002). Since SNs are associated with the integration of features into a coherent object (Kasai & Morotomi, 2001; Previc & Harter, 1982; Smid, Jakob, & Heinze, 1999), the SN for orientation defined by two squares or objects might have been decreased. On the other hand, the enlargement of the negativities in the interattribute condition may be due to overlapping vertex N2b, which has been postulated to reflect a binding of separate feature dimensions (Kenemans et al., 2002; Lange, Wijers, Mulder, & Mulder, 1998; Smid et al., 1999). This may suggest that the integration of different attributes is required to discriminate orientations at a higher stage of processing in the interattribute condition, consistent with the fact that a visual search of orientation was more attention-demanding in the interattribute condition (Morita et al., 2003). However, N2b may also reflect the binding of task-relevant dimensions, i.e., orientation and gap size. This seems to be consistent with the present results for FAs, which indicate that orientation discrimination preceded gap-size discrimination, and this trend was the greatest in the interattribute condition. Thus, an alternative account for the enlarged N2b would be that the binding of information on orientation and gap size was more demanding in the interattribute condition than in the intra-attribute conditions.

Finally, it would be important to consider what types of signals were used for the orientation discrimination in the present study. Previous studies have suggested that orientation discrimination may be based on the axis of symmetry or elongation in global shapes, rather than on local contours (e.g. Boutsen & Marendaz, 2001). Since the two

squares were defined by different values of features even in the intra-attribute conditions (i.e., red vs. green for color; left vs. rightward for motion), the appearance in the present study was not of a single bar with a continuous contour. Therefore, the orientation SPs may also indicate that orientations based on the axis of symmetry or elongation are also available at an early stage of visual processing and can be attribute-invariant. To examine this issue, it would be useful to compare the present results with those obtained when two adjacent squares are defined by the same color or direction and contours are completed.

In conclusion, the present study provided evidence that attribute-invariant orientations are available at an early stage of processing in the human brain. These electrophysiological results bridge the gap between monkey electrophysiology and human psychophysics. However, attribute-specific orientations are also available at the same early stage, indicating that task-relevant channels or modules can be selected according to a given context. The orientation discrimination processes at higher stages of processing seemed to involve the integration of objects and features. These multiple discrimination processes of orientation may contribute to a better understanding of the functional organization of form representations in the visual system.

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Figure legends

Figure 1. Schematic illustrations of stimuli used in the present experiment. Black outlines indicate motion-defined contours. Blue arrows indicate directions of motion.

Figure 2. Grand-averaged ERPs in response to standard stimuli with an unattended orientation (O-) and an attended orientation (O+) in the interattribute condition.

Figures 3. Grand-averaged ERPs at selected electrodes in response to standard stimuli in the interattribute, intra-color, and intra-motion conditions (ERPs at the left and right hemispheres were averaged) and scalp distributions of the orientation selection effects calculated by subtracting ERPs in response to stimuli with an unattended orientation (O-) from those with an attended orientation (O+) in each condition.

Figure 4. Mean amplitudes of SPs in the interattribute, intra-color, and intra-motion conditions. Error bars indicate \pm standard errors of the mean.

Figure 5. Scalp topographies of ERPs in response to standard stimuli with unattended orientation (O-).

Figure 1

Interattribute Intra-color Intra-motion

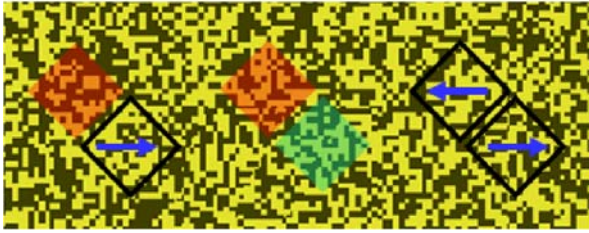


Figure 2

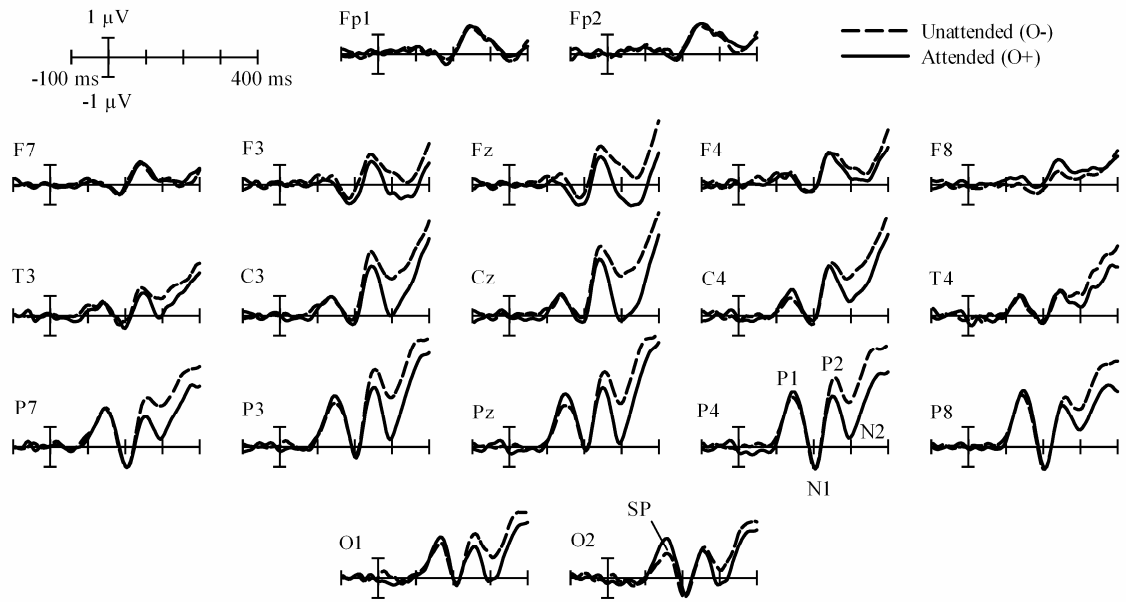


Figure 3

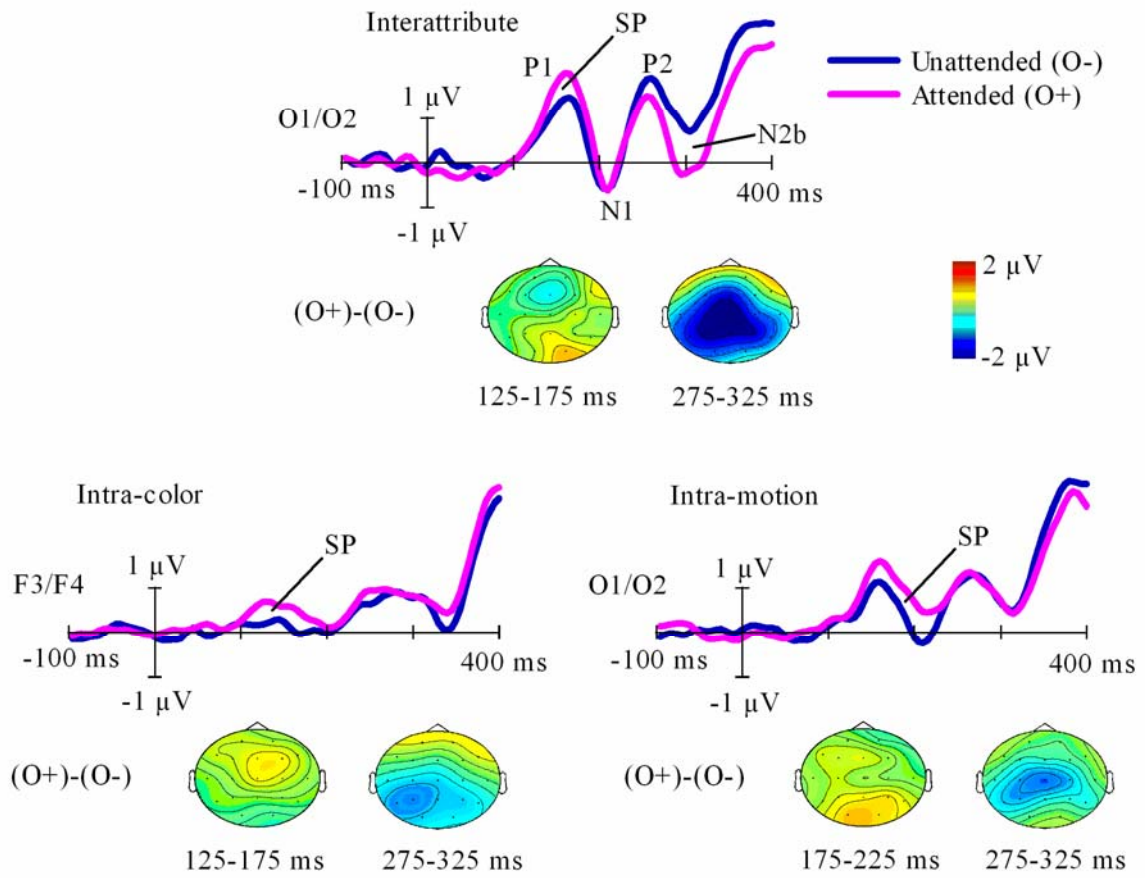


Figure 4

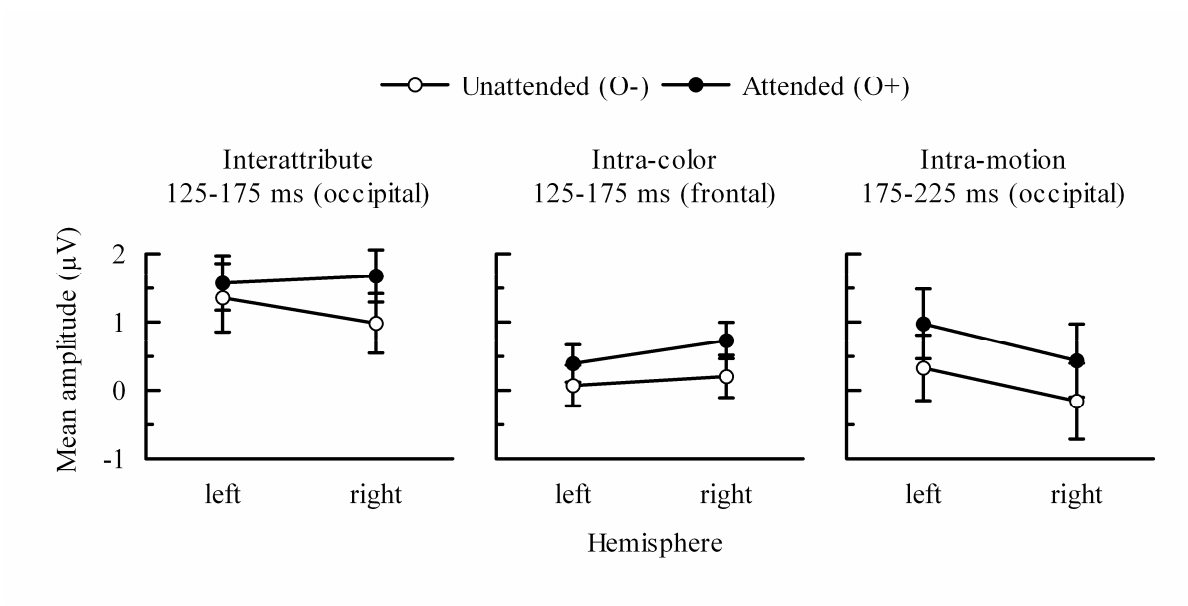


Figure 5

