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Time Course of Spatial and Feature Selective Attention for Partly-Occluded Objects

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Abstract

Attention selects objects/groups as the most fundamental units, and this may be achieved by an attention-spreading mechanism. Previous event-related potential (ERP) studies have found that attention-spreading is reflected by a decrease in the N1 spatial attention effect. The present study tested whether the electrophysiological attention effect is associated with the perception of object unity or amodal completion through the use of partly-occluded objects. ERPs were recorded in 14 participants who were required to pay attention to their left or right visual field and to press a button for a target shape in the attended field. Bilateral stimuli were presented rapidly, and were separated, connected, or connected behind an occluder. Behavioral performance in the connected and occluded conditions was worse than that in the separated condition, indicating that attention spread over perceptual object representations after amodal completion. Consistently, the late N1 spatial attention effect (180-220 ms post-stimulus) and the early phase (230-280 ms) of feature selection effects (target N2) at contralateral sites decreased, equally for the occluded and connected conditions, while the attention effect in the early N1 latency (140-180 ms) shifted most positively for the occluded condition. These results suggest that perceptual organization processes for object recognition transiently modulate spatial and feature selection processes in the visual cortex.

Keywords

Attention, Object, Perception, Amodal completion, Event-related potential, N1

Time Course of Spatial and Feature Selective Attention for Partly-Occluded Objects

1. Introduction

The visual scene is constructed from countless fragmented visual images, while coherent percepts and actions for objects are usually possible. This may be due to perceptual organization and attentional selection, the combination of which is referred to as object-based attention (for reviews, Driver & Baylis, 1998; Hopf, Schoenfeld, & Heinze, 2005; Scholl, 2001). Object-based attention may be achieved by an attention-spreading mechanism, in which the representations of task-irrelevant locations or features are obligatorily facilitated if they belong to the same object/group as task-relevant locations/features. For example, in most studies, behavioral performance in discriminating two features is better when they belong to the same object rather than to different objects (Duncan, 1984), and the shift in attention from a cued location to an uncued location is faster within an object than between two different objects in a spatial-cueing task with a two-rectangle display (Egly, Driver, & Rafal, 1994). Hemi-spatial neglect in brain-damaged patients can also be modulated by perceptual grouping with feature similarity, connectedness, or amodal completion for partly-occluded objects (Humphreys, 1999).

Event-related potentials (ERPs) with high temporal resolution are a particularly useful tool for exploring the mechanisms of mid-level perceptual operations, such as object-based attention. Previous studies have consistently found that the N1 spatial attention effect (at 140-190 ms post-stimulus) is object-based: the amplitude of N1 in response to stimuli that belong to an unattended region was enhanced when it belonged to an attended object (He et al., 2004; Martínez et al., 2006; Verleger et al., 2008). This indicates that object-based attention shares, at least in part, a common mechanism with early spatial selection, i.e., a sensory gain-control mechanism (e.g., Hillyard, Vogel, & Luck, 1999). Furthermore, the object-based modulation of the N1 spatial attention effect is considered to originate at the lateral occipital cortex (Martínez et al., 2006; 2007a, b).

By using a focal attention task for bilateral stimuli, we have shown that the N1 lateralization effect according to spatial attention is modulated by the extent of perceptual grouping for connected objects (Kasai, 2010), as with grouped elements with feature similarity (Kasai, Moriya, & Hirano, 2011). Note that it is difficult to distinguish attention-spreading due to perceptual grouping with task-irrelevant feature similarity from feature-based attention: attentional deployment occurs for stimuli with task-relevant or attended features over the whole visual field (Andersen, Fuchs, & Muller, 2011; Saenz, Buracas, & Boynton, 2002; Treue & Martínez-Trujillo, 1999). However, it is also possible that the global effect of feature-based attention is associated with perceptual grouping with feature similarity.

An interesting notion in object-based attention research is that attention-spreading may be the basis for the perceptual experience of object unity or perceptual grouping (Driver & Baylis, 1998). Therefore, the present study aimed to examine the links between the object-based N1 spatial attention effect and the visual experience of objects. According to Hulme & Zeki (2006), there are two types of object perception: awareness of the presence of an object and the direct perception of objects, which can both be examined by using occluded objects. Thus, we can perceive the presence of an object (i.e., awareness) even if it is partly occluded and invisible, which is called amodal completion. On the other hand, we can also perceive that the occluded object is fragmented by the other object and the occluded part is invisible (direct perception). Thus, we may have two perceptual experiences simultaneously. The present study focused on these two aspects of object perception, rather than consciousness itself, which is generally assessed in paradigms in which physical stimuli are held constant but the experience of the observer varies, such as with binocular rivalry (e.g., Blake, 2004). Previously, Martínez et al. (2007a, b) found that object-based modulation of the N1 attention effect occurred for illusory objects formed by inducers, suggesting that it is associated with perceptual object representations. However, this was the case for modal completion with subjective, but visible, contours, and thus it is unclear whether the results were associated with awareness or the direct perception of objects.

In the present study, we examined ERP spatial attention effects for partly-occluded objects or objects with amodal completion by using the same experimental paradigm as in our previous studies (Kasai, 2010; Kasai et al., 2011), which is basically a sustained-focal-attention task that involves bilateral stimulus arrays (Heinze et al., 1990, 1994; Woldorff et al., 2002). The task was to respond when an infrequent target was presented at an attended hemifield during a rapidly presented sequence of bilateral stimuli. Spatial attention was indexed by larger amplitudes of posterior ERPs over the hemisphere contralateral, rather than ipsilateral, to the attended hemifield. Here, object/group-based effects decrease the ERP attention effects, reflecting attention-spreading or guidance to the opposite side of the object/group (Figure 1a). This paradigm has some merits for examining object-based attention. First, analyses of the differences between ERPs at contralateral and ipsilateral electrode sites enable us to assess attentional operations, by dissociating them from ERPs evoked by physical stimulus properties themselves. Second, rapid presentation can lead to large numbers of ERPs, and thus systematic manipulations of object/grouping factors are possible. In addition, analyses of ERPs in response to infrequent targets may enable us to test object-based feature selection processes (Kasai & Kondo, 2007).

The present study set three stimulus conditions: separated condition, occluded condition, and connected condition (Figure 1b). In the separated condition, bilateral stimuli (rectangles) were presented separately from the central large occluder; in the connected condition, a line physically connected the bilateral stimuli, and in the occluded condition, the connecting line was perceived as being behind the occluder. Here, the occluded objects had more similarity or grouping factors than the separated objects, since the bilateral squares had interior short lines that were similar and aligned with respect to each other (although their lengths differed according to symmetry control). Thus, any differences between the occluded and separated conditions may involve similarity or grouping, rather than amodal completion. However, the connected objects had the same geometric properties as the occluded objects and also had unified connectedness, which should cause more object-based modulation for the N1 attention effect than ununified connectedness (Kasai, 2010). Therefore, it is critical to compare the occluded condition to the connected condition to reveal processes that are associated with amodal completion or the awareness of presence of objects. If the N1 spatial attention effect of ERPs is associated with selection based on unitary-object perception that overcomes physical discontinuities, those in the occluded and connected conditions should equally be smaller than those in the separated condition.

2. Methods

2.1 Participants

Fourteen volunteers (8 females), aged 21 to 36 years (mean = 24.2 years), participated in this study. Participants reported normal or corrected-to-normal vision, and provided their written informed consent.

2.2 Stimuli and Procedure

Stimuli were displayed on a Hitachi CRT monitor, at a viewing distance of 70 cm, and controlled by PsyScope on a personal computer (Macintosh G3) with a PsyScope button box (Cohen et al., 1993). A large green rectangle with curved corners (occluder) was extended at a visual angle of 3.9° x 3.0°, and was presented 0.8° (to the bottom edge) above a blue central fixation cross against a gray background throughout the experiment (Figure 1b). Black bilateral rectangles were displayed horizontally 4.2° to the left and right (to the center of the rectangles) and at the central height of the occluder. Each rectangle was 1.0° in height while the widths varied according to the type. Standards extended horizontally 0.7° or 1.4°, and targets extended 1.0° (i.e., square). The bilateral rectangles were connected by a line (0.8° wide) in front of the occluder in the connected condition, or behind the occluder in the occluded condition. There was no connecting line in the separated condition.

--------------------- Figure 1 about here ---------------------

Bilateral stimuli consisted of either two standard stimuli at 75 % probabilities or one standard and one target in the separate hemi-fields at 25 % probabilities. Stimuli of different widths (thin, thick) were selected in equal probabilities for the left and right sides to make an asymmetric display, since symmetry is also a grouping factor and may cause a ceiling effect (Kasai, 2010; Kasai & Kondo, 2007). As shown in Figure 1c, the bilateral stimuli were presented for 100 ms, and the inter-stimulus interval (offset to onset) was randomly varied between 300 and 650 ms (7 steps, rectangular distribution). While the ERPs in response to successive stimuli overlapped, due to the short ISI, this overlap should not differ among conditions due to the random order of stimulus presentation (Hillyard & Münte, 1984).

The participant was seated in a reclining chair in a sound- and electric- shielded room and instructed to attend to either the left or right hemi-field during the blocks and to press a button with the right thumb in response to the target (i.e., square) presented in the attended field as accurately and quickly as possible. It was emphasized that they had to maintain fixation and to try not to move their eyes during the block. The attend-left and attend-right conditions consisted of 12 blocks, respectively, each consisting of 100 trials, which were alternated. The initial visual field to be attended was counterbalanced across the participants. The experiment started with 1-2 practice blocks for each attention condition to stabilize task performance and eye movement.

2.3 Recordings and Analyses

The electroencephalogram (EEG) was measured using an electrocap (Neuroscan) with 25 Ag-AgCl electrodes (Fp1, Fp2, F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, T6, O1, Oz, O2, PO7, PO3, POz, PO4, and PO8 according to the International 10-20 System), which were referenced to the nose. Blinks and horizontal eye movements were monitored with electrodes at the outer canthi of the eyes (horizontal electrooculogram [EOG]) and Fp2 and below the right eye (vertical EOG). The impedance of the electrodes was kept below 10 kOhm. EEGs were filtered with a bandpass of 0.1-30 Hz and sampled at 200 Hz.

Behavioral performance was measured, including the percentage of correct target detections (hits) and RTs for hits. Responses were scored as correct if they occurred within 200-1000 ms after a target was presented in the attended location. Responses to other stimuli were classified as false alarms (FAs). The behavioral measures were subjected to repeated-measures analysis of variance (ANOVA): the factors considered were stimulus condition (separated, occluded, connected) and attention condition (attend left, attend right), and stimulus type (standard, unattended target) for FAs.

ERPs were averaged separately for each stimulus type, stimulus condition, and attention condition. Averaging epochs were 1000 ms, starting 200 ms before the onset of the stimulus and ending 800 ms post-stimulus, while correcting for differences in the 200-ms pre-stimulus baseline. Automatic artifact rejection was applied to eliminate epochs contaminated above 75 µV, and epochs with incorrect responses were also excluded.

Analyses were conducted separately for ERPs in response to standards and targets. For standards, ERPs at occipital-temporal sites (PO7, PO8) were quantified by mean amplitudes with latency windows of 100-140 ms (post-stimulus) for P1, 140-180 ms and 180-220 ms for early and late N1s, and 230-280 ms for N2. The measurements were subjected to repeated-measures ANOVA: the factors considered were stimulus (separated, occluded, connected), laterality of the electrode sites relative to the attended visual field (ipsilateral, contralateral), and the attended visual field (left, right). If the interaction between stimulus and laterality was statistically significant, to clarify the attention effects, subtraction ERPs (contralateral vs. ipsilateral) were applied to further analyses.

Although the experimental paradigm focused on ERPs in response to standard stimuli, the present study analyzed ERPs in response to attended and unattended targets to examine target/feature selection processes (Anllo-Vento & Hillyard, 1996; Kasai & Kondo, 2007). ERPs at occipital-temporal sites (PO7, PO8) were quantified by mean amplitudes with the same latency windows as those for standards, and at 280-320 ms that involved the peak latency of target N2 (late target N2). The factors of repeated-measure ANOVA were type (attended targets, unattended targets) and those for standards.

For all ANOVAs, the Greenhouse-Geisser correction was used to reduce the positive bias resulting from repeated factors with more than two levels. In post-hoc tests, to clarify the effects of the stimulus (three levels), multiple comparisons were conducted for all combinations between stimulus pairs by t-tests with the Bonferroni correction.

3. Results

3.1 Behavioral Data

Table 1 summarizes the behavioral data. RTs for the right-attend condition were faster than those for the left-attend condition, which was reflected by a main effect of attended field [$F(1, 13)=7.3$, $p=0.018$]. There was also a main effect of stimulus [$F(2, 26)=5.9$, $p=0.0008$], which indicated that RTs for the separated condition were faster than those for the connected condition [t (13)=3.2, $p=0.019$]. Similarly, hit rates for the right-attend condition were higher than those for the left-attend condition, which was reflected by a main effect of attended field [$F(1, 13)=10.3$, $p=0.007$]. There was also a main effect of stimulus [$F(2, 26)=11.9$, $p=0.0002$], which indicated that there were more hits for the separated condition than for the occluded and connected conditions [*t* (13)=3.0, *p*=0.030; *t* (13)=4.6, *p*=0.001].

There was only a main effect of stimulus for FA rates (*F*(2, 26)=5.6, *p*=0.016), which reflected that FAs for the separated condition were greater than those for the occluded condition [*t* (13)=3.9, *p*=0.008].

--------------------- Table 1 about here ---------------------

3.2 Electrophysiological Data

In grand-averaged ERPs in response to standard stimuli, several spatial attention effects were revealed by comparing the differences between ERPs recorded at electrode sites ipsilateral and contralateral to task-relevant visual fields, which were most prominent at the occipital temporal brain area (Figures 2 and 3). Feature attention effects were revealed by comparing the differences between ERPs for attended and unattended targets, which were also most prominent at contralateral occipital temporal sites (Figure 4). Table 2 summarizes the *p* values of omnibus ANOVAs for the standard and target ERPs.

--------------------- Figures 2 and 3 about here ---------------------

--------------------- Table 2 about here ---------------------

In ERPs in response to standard stimuli (Figure 2), P1 (100-140 ms) had a greater amplitude at contralateral than at ipsilateral sites for all grouping conditions equally, which was reflected by the main effect of laterality [*F*(1,13)=13.2, *p*=0.003]. The amplitudes of early and late N1 differed across stimulus conditions (Figure 2a), as reflected by the main effects of stimulus [*F*(1,13)=5.2, *p*=0.0015; *F*(1,9)=6.9, *p*=0.011], and this may involve the physical differences among the stimulus conditions. Importantly, the attention effects in the early N1 (140-180 ms) latency were different across the stimulus conditions (Figure 2b), as reflected by the significant interaction of stimulus and laterality [*F*(1,13)=10.2, *p*=0.002]. To simplify further analyses, multiple comparisons were conducted for the contralateral minus ipsilateral subtraction ERPs (Figure 2c). The difference ERPs in the early N1 range for the occluded condition were significantly more positive than those for the separated condition and the connected condition [*t*(13)=3.6, *p*=0.010; *t*(13)=2.8, *p*=0.044]. In the scalp distributions for the occluded condition, the positive attention effect in the early N1 latency was very similar to that in the P1 latency (Figure 3).

Attention effects in the late N1 (180-220 ms) latency were also different across the stimulus conditions (Figure 2b), as reflected by the significant interaction of stimulus and laterality [*F*(1,9)=9.5, *p*=0.001]. The contralateral minus ipsilateral subtraction ERPs indicated that the late N1 attention effects for the occluded and connected conditions were more positive than that for the separated condition [*t*(13)=3.7, *p*=0.008; *t*(13)=4.2, *p*=0.003]. The ERPs in the N2 (230-280 ms) latency range also had a significant interaction of stimulus and laterality [*F*(2,18)=6.7, *p*=0.010], the attention effect of which shifted toward a more positive direction for the separated condition than for the occluded [but marginally, *t*(13)=2.7, *p*=0.053] and connected conditions [*t*(13)=4.0, *p*=0.005].

In ERPs in response to targets (Figure 4a), P1 had a greater amplitude at contralateral sites than at ipsilateral sites, as reflected by the main effect of laterality [*F*(1,13)=25.7, *p*=0.0002]. In contrast, there were no statistically significant results in the N1 latency ranges, except for a main effect of stimulus in the late N1 latency [*F*(1,13)=5.0, *p*=0.027], probably because the signal-to-noise ratio was smaller for target stimuli. However, attended targets elicited distinctive negative enhancements with a peak at around 300 ms, compared to unattended targets, more prominently at contralateral sites. The negativities were labeled as target N2 and were reflected by interactions of type and laterality in the early (230-280 ms) and late (280-320 ms) latencies [*F*(1,13)=22.2, *p*=0.0004; *F*(1,13)=28.7, *p*=0.0001].

The early latency of target N2 (230-280 ms) had an interaction of type, stimulus, and laterality [*F*(2,26)=5.7, *p*=0.012]. Post-hoc tests indicated that there was a type x laterality interaction only for the separated condition [*F*(1,13)=27.3, *p*=0.0002]. Further post-hoc tests of this effect showed that there was a significant type effect only at contralateral sites [*F*(1,13)=36.9, *p*=0.00004], which indicated that the target N2 enlarged at contralateral sites for the separated condition (Figure 4b). In addition, the laterality effect was significant only for unattended targets [*F*(1,13)=21.6, *p*=0.0005], reflecting that the early phase at ipsilateral sites was more negative than at contralateral sites for unattended targets. In contrast, later phase of target N2 effects (280-320 ms) were clearly observed for all stimulus conditions, as reflected by significant type x laterality interactions for the separated, occluded, and connected conditions [*F*(1,13)=12.7, *p*=0.003; *F*(1,13)=29.5, *p*=0.0001; *F*(1,13)=8.5, *p*=0.012]. The late target N2 was greater for the attend-right condition, as reflected by an interaction of attended visual field, type, and laterality [*F*(1,13)=4.7, *p*=0.048].

--------------------- Figure 4 about here ---------------------

4. Discussion

The present study aimed to examine attentional selection processes in the visual cortex for physically discontinuous, but perceptually unitary objects with amodal completion, compared with those for both physically and perceptually separated or connected objects. The lateralization effect of P1 at the occipital-temporal electrode sites according to spatial attention indicates that the participants successfully directed their attention to the task-relevant visual field for all stimulus conditions. However, the lateralized N1 attention effect was clearly observed only for the separated condition: it was more positive for the occluded condition in the early latency (140-180 ms), and equally around zero for the occluded and connected conditions in the late latency (180-220 ms). A prominent target N2 was also found only for the separated condition in the early latency (230-280 ms).

4.1 Connected vs. separated objects

Since connectedness is a fundamental grouping factor that robustly affects selective attention (e.g., Palmer, 2003; Watson & Kramer, 1999), it may be important to clarify differences between ERPs for the separated and connected conditions to identify a basic pattern of object-based selection processes. The present results showed that lateralized ERP spatial attention effects in the late N1 (180-220 ms) and early N2 (230-280 ms) latency ranges were clearly decreased in the connected condition, compared with those in the separated condition, which suggests that spatial attention spread over the whole region of the connected object in these time ranges. However, these results somewhat differed from those of two experiments in a previous study (Kasai, 2010), which used the same stimulus conditions except for the presence of an occluder or the occluded condition. In Kasai (2010), the object-based N1 attention effect started as early as 150 ms, and the positive attention effect in the early N2 latency for the separated condition was statistically insignificant. In addition, the object-based effect in the later latency (around 300-400 ms) in the previous study was indistinct in the present study. The continuous visual structure (i.e., occluder) in the display may have been a stimulus context that reduced the uncertainty of locations to be attended or may have had some effect on the processing of subsequent stimuli. These considerations lead to the notion that the time-course of object-based spatial selection can vary to some extent, depending on the stimulus and/or task context, although this should be tested in future studies.

The spatial attention effect with a positive polarity in the early N2 latency indicates that ERPs were more negative at sites ipsilateral, rather than contralateral, to the attended locations in the separated condition. Since lateralized negativity resembles N2pc (posterior-contralateral), which is a real-time measure of attentional direction in visual search tasks (e.g., Woodman & Luck, 1999), the present result reflects the notion that attention was guided to the side opposite the attended space in the latency. In previous studies that used focal attention tasks with bilateral-stimulus arrays, an N2 spatial attention effect in response to standards was either unreported (Heinze et al., 1990, 1994) or more negative at contralateral sites (Woldorff et al., 2002). We also previously found a more negative N2 attention effect for the dissimilar (i.e., perceptually more separated) condition than for the similar condition (Kasai et al., 2011). One plausible explanation for these inconsistencies is that, when the processing requirement for discriminating targets from standards is low, excess resources may be directed to the opposite side of standard stimuli. In fact, the behavioral task in the present study appeared to be less demanding than those in these previous studies, according to the type or number of stimuli and behavioral performance.

However, it is critical to determine whether the spread of N1 and N2 spatial attention effects for the connected condition was object-based or feature-based. Irrelevant features of an attended object can also facilitate processing of the same features of distractors in a visual search task (Boehler, Schoenfeld, Heinze, & Hopf, 2011), and the connecting bar in the present study may have increased feature (color or shape) similarity across the left and right stimuli. However, since the attention-spreading based on irrelevant feature was reflected within 80 ms after N2pc onset (Boehler et al., 2011), the connectedness-based modulation of early sensory processing (i.e., N1) may be due to preattentive operations of perceptual organization. On the other hand, the early N2 (230-280 ms) for unattended targets was more negative at ipsilateral sites that involved in target feature at unattended locations, which seems to reflect feature-based attention-spreading.

4.2 Spatial selection processes for occluded objects

The earliest effect that was specific to the occluded condition was found in the early N1 latency (140-180 ms), which was most positive in the occluded condition. However, this attention effect had a scalp distribution that was quite similar to that in the P1 latency, so that this may be a prolongation of the P1 attention effect (Figure 3). On the other hand, the scalp distributions showed that the N1 attention effect started in the early N1 latency in the separated condition and there were no distinctive attention effects in this latency in the connected condition. One possible interpretation is that the P1 selection mechanism operated more efficiently for occluded objects than for connected objects, in the absence of an early N1 operation. Such a P1 effect may be because the occluded objects had discontinuities that facilitate segregation. Thus, it is conceivable that attentional selection occurred based on an early level of object processing of perceptual grouping/segregation by connectedness. Although this point is still just speculation, the present results suggest that the early selection process was associated with processing for partly-occluded objects.

In the later latency (180-220 ms), the N1 attention effect decreased equally for the occluded and connected conditions relative to the separated condition. This is in contrast to the fact that the N1 attention effect was smaller for the unified-connected condition than for the ununified-connected condition (Kasai, 2010). Since the occluded objects had physical discontinuities across them, the present results suggest that the N1 spatial attention effect does not depend solely on physical discontinuities but is also associated with amodal completion or a unitary percept for the occluded objects. Generally, amodal completion requires depth organization: the bilateral stimuli should be perceived to be located behind the occluder. Therefore, the present results are consistent with the fact that the N1 component is sensitive to attention in depth or overlapped surfaces (Kasai, Morotomi, Katayama, & Kumada, 2003; Khoe, Mitchell, Reynolds, & Hillyard, 2005; Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998), and suggest that the N1 spatial attention effect is associated with the percept of invisible surfaces behind an occluder, in addition to visible surfaces according to modal completion (Martínez et al., 2007a, b).

According to the above interpretations, the present ERP results in the early and late N1 latencies suggest that fragmented representations were followed by completed object representations. This is consistent with the notion that a “mosaic stage” precedes a completion stage of processing, which has been suggested in behavioral studies with a masking procedure (Rauschenberger & Yantis, 2001; Sekuler & Palmer, 1992), although mosaic and completion stages may also be parallel (Bruno, Bertamini, & Domini, 1997; Plomp, Liu, Leeuwen, & Ioannides, 2006). On the other hand, evoked responses associated with amodal completion were identified as N1 and N2 components, both of which were considered to originate from the lateral occipital cortex (Murray, Foxe, Javitt, & Foxe, 2004). Although evoked responses and spatial attention effects may reflect similar long-range spatial integration processes in the visual cortex (Martínez et al., 2007a, b), the present study did not find a clear N2 spatial attention effect associated with amodal completion, and this may be due to the nature of the task.

4.3 Feature selection processes and behavioral outputs

The target N2 may involve, at least partly, feature selection processes at attended spatial location, since ERP differences between the conditions with and without target feature were more prominent at contralateral side to the attended visual field. In the present results, the target N2 was diminished for the occluded condition as well as the connected condition in the early latency (230-280 ms), yet there were no critical differences across the stimulus conditions in the later latency (280-320 ms). The pattern of early target N2 was similar to that of the late N1 spatial attention effect (180-220 ms). These suggest that object-based modulation of feature selection is time-limited and that local-feature selection becomes less efficient because spatial attention spreads over perceptually unitary objects.

The fact that feature selection depended on spatial attention resembles selection negativity (SN), which reflects a matching process between the task-relevant attentional trace of features and stimuli (Anllo-Vento & Hillyard, 1996; Hillyard & Anllo-Vento, 1998; Hillyard & Münte, 1984). Previous studies have found object-based feature selection effects for SNs (Kasai & Morotomi, 2001; Schoenfeld et al., 2003) and for target N2 (Kasai & Kondo, 2007). However, feature-based attention can influence feedforward sensory activity, as reflected by P1 (Zhang & Luck, 2009), and feature and spatial selective attention operates in an additive manner (Anderson et al., 2010; Anderson, Müller, & Hillyard, 2009), when stimuli are overlapping colored dots and simultaneous competition is increased. The late feature selection effects that depended on spatial attention may be due to the extent of competition or relatively low discriminability of task-relevant features in the present study. In sum, the present results suggest that spatial selection processes can transiently modulate following feature selection processes in a particular condition.

The early feature selection process may be more directly associated with behavioral outputs in the present study. In the present behavioral indices, worse performance (hits, RTs) may reflect a decrease in attentional resources to discriminate a feature (shape) at the attended location according to attention-spreading (e.g., Baylis & Driver, 1992; Driver & Baylis, 1989; Kramer & Jacobson, 1991; Richard, Lee, & Vecera, 2008), and the present results indicate that attention spread for perceptually-connected objects by amodal completion as well as physically-connected objects. This is consistent with a notion that has been suggested in extensive behavioral studies, i.e., attention selects a perceptually unitary object after amodal completion, in cueing paradigms (Moore & Fulton, 2005; Moore, Yantis, & Vaughan, 1998; Pratt & Sekuler, 2001; but see Haimson & Behrmann, 2001), visual search tasks (He & Nakayama, 1992; Rensink & Enns, 1998), divided-attention tasks (Behrmann, Zemel, & Mozer, 1998; Zemel, Behrmann, Mozer, & Bavelier, 2002), the inhibition of return (Yi, Kim, & Chun, 2003), and for chimpanzees (Ushitani, Imura, & Tomonaga, 2010).

Although FA is not a typical behavioral object-based attention effect, the present FA rates in the separated condition were greater than those in the occluded condition. In the previous study on connectedness (Kasai, 2010), FAs in the unconnected condition were greater than those in the connected condition, which was interpreted within the framework of the biased competition model (Desimone & Duncan, 1995). A segregated object that appeared within the attended location (i.e., unconnected condition) may become more salient by top-down biasing, compared with part of an object where attention is guided more to the opposite side of the object (connected condition). Since FAs in the focal attention tasks with bilateral-stimulus arrays reflect the extent of saliency, this predicts that the occluded objects were the least salient and the connected objects were relatively salient. This may be consistent with the fact that the bilateral squares appeared to be located behind for the occluder for the occluded condition and in front for the connected condition.

4.4 Conclusions

The present study showed that the N1 spatial attention effect can be decreased by long-range spatial integration with amodal completion, which is associated with the awareness of object presence rather than direct perception in object perception. The attention effect can also modulate to decrease the selection of local features, as reflected by an early phase of target N2 and behavioral performance. The visual system can resolve ambiguities in the three-dimensional world in an early stage of processing and transiently bias toward the recognition or identification of whole objects.

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Figure Captions

Figure 1. a) Schematic illustration of the attention-spreading paradigm of ERPs. Posterior lateralized activation according to spatial attention should decrease if bilateral stimuli are perceptually grouped and attention spreads. b, c) Stimuli and the stimulus sequence used in the present study. A central occluder remained visible and brief bilateral squares were presented with or without lines, which were behind or in front of the occluder.

Figure 2. Grand-average ERPs in response to standards at occipito-temporal electrodes (PO7, PO8). a) ERPs at hemisphere sites contralateral and ipsilateral to an attended visual field overlap, so that the left and right sites are collapsed. b) Difference waves for the spatial attention effect, i.e., ERPs at ipsilateral sites were subtracted from those at contralateral sites. c) Mean amplitudes of the contralateral minus ipsilateral attention effect in the N1 and early N2 latencies. Error bars indicate standard errors of the mean.

Figure 3. Scalp distributions of spatial attention effects in response to standards for each stimulus condition: ERPs in the attend-right condition were subtracted from those in the attend-left condition. White-line circles indicate the occipital temporal electrode sites (PO7, PO8).

Figure 4. a) Grand-average ERPs at the occipito-temporal electrodes (PO7, PO8) for the attended target and unattended target. ERPs at hemisphere sites contralateral and ipsilateral to an attended visual field overlap. b) Mean amplitudes of the feature attention effect in the N2 latency ranges (Target N2), i.e., ERPs for attended target

were subtracted from those for unattended target, at contralateral and ipsilateral sites, respectively. Error bars indicate standard errors of the mean.

Table 1
Summary of Behavioral Data

		Separated		Occluded		Connected	
		M	*SE*	*M*	*SE*	*M*	*SE*
Reaction time (ms)	Attend left	491	10	498	11	506	7
	Attend right	472	9	489	9	494	6
Hit rate (%)	Attend left	74.5	3.5	69.6	3.9	65.4	4.4
	Attend right	83.4	3.0	78.2	3.6	76.4	3.8
False-alarm rate (%)	Attend left						
	Standard	1.0	0.3	0.6	0.1	0.8	0.3
	Unattended target	1.3	0.3	0.3	0.2	0.9	0.3
	Attend right						
	Standard	1.4	0.3	0.5	0.1	0.7	0.2
	Unattended target	1.3	0.4	0.6	0.3	1.0	0.5

Table 2

Summary of Statistical Results for ERPs

	P1 100-140 ms	Early N1 140-180 ms	Late N1 180-220 ms	N2/Early target N2 230-280 ms	Late target N2 280-320 ms
Standards					
Attended visual field (*)					---
Stimulus		0.015	0.001		---
Laterality	0.003			0.025	---
Stimulus × Laterality		0.002	0.001	0.010	---
Targets					
Attended visual field (*)					
Type				0.002	0.0002
Stimulus			0.027	0.022	
Laterality	0.0002				0.039*
Type × Laterality				0.0004	0.0001 0.048*
Stimulus × Laterality				0.041	0.011
Type × Stimulus × Laterality				0.012	

Note: All significant *p* values for omnibus ANOVAs are shown. * indicates interaction with Attended visual field.

Figure 1

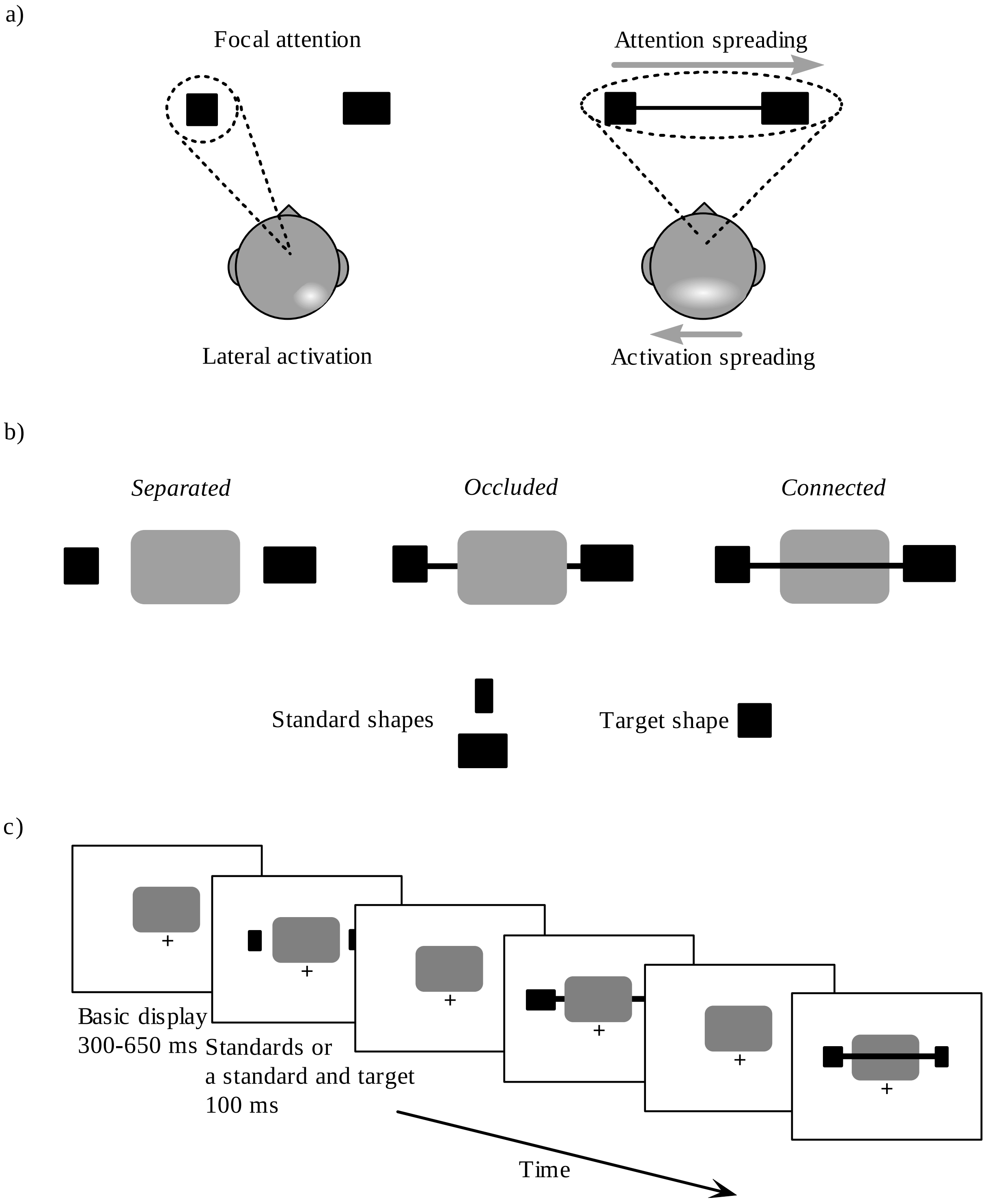

a)
Focal attention
Attention spreading
Lateral activation
Activation spreading
b)
Separated
Occluded
Connected
Standard shapes
Target shape
c)
Basic display
300-650 ms
Standards or
a standard and target
100 ms
Time

Figure 2

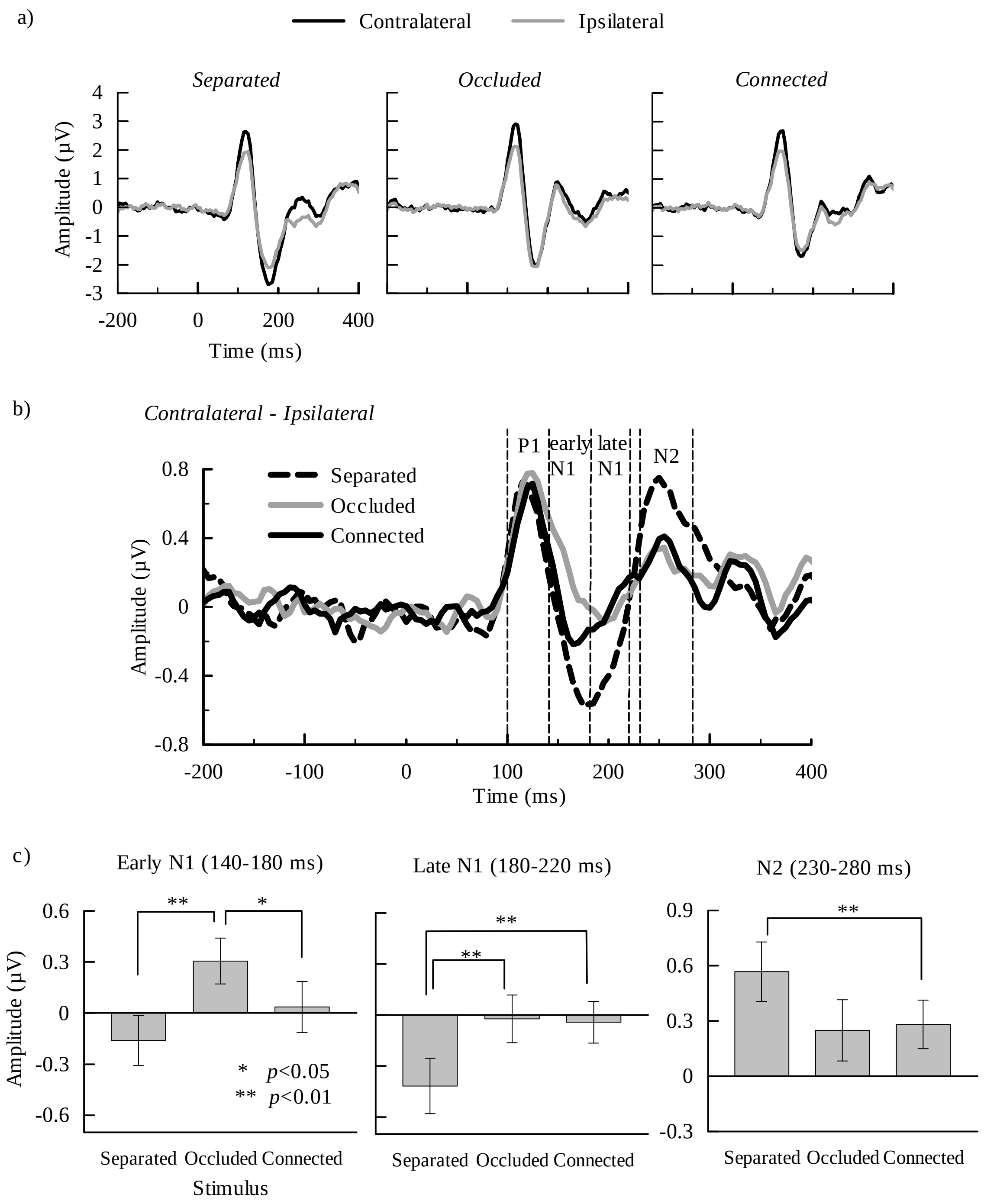

a)
Contralateral
Ipsilateral
Separated
Occluded
Connected
Amplitude (μV)
4
3
2
1
0
-1
-2
-3
-200
0
200
400
Time (ms)
b)
Contralateral - Ipsilateral
P1
early N1
late N1
N2
Separated
Occluded
Connected
0.8
0.4
0
-0.4
-0.8
Amplitude (μV)
-200
-100
0
100
200
300
400
Time (ms)
c)
Early N1 (140-180 ms)
Late N1 (180-220 ms)
N2 (230-280 ms)
Amplitude (μV)
0.6
0.3
0
-0.3
-0.6
**
*
* p<0.05
** p<0.01
0.9
0.6
0.3
0
-0.3
Separated Occluded Connected
Stimulus

Figure 3

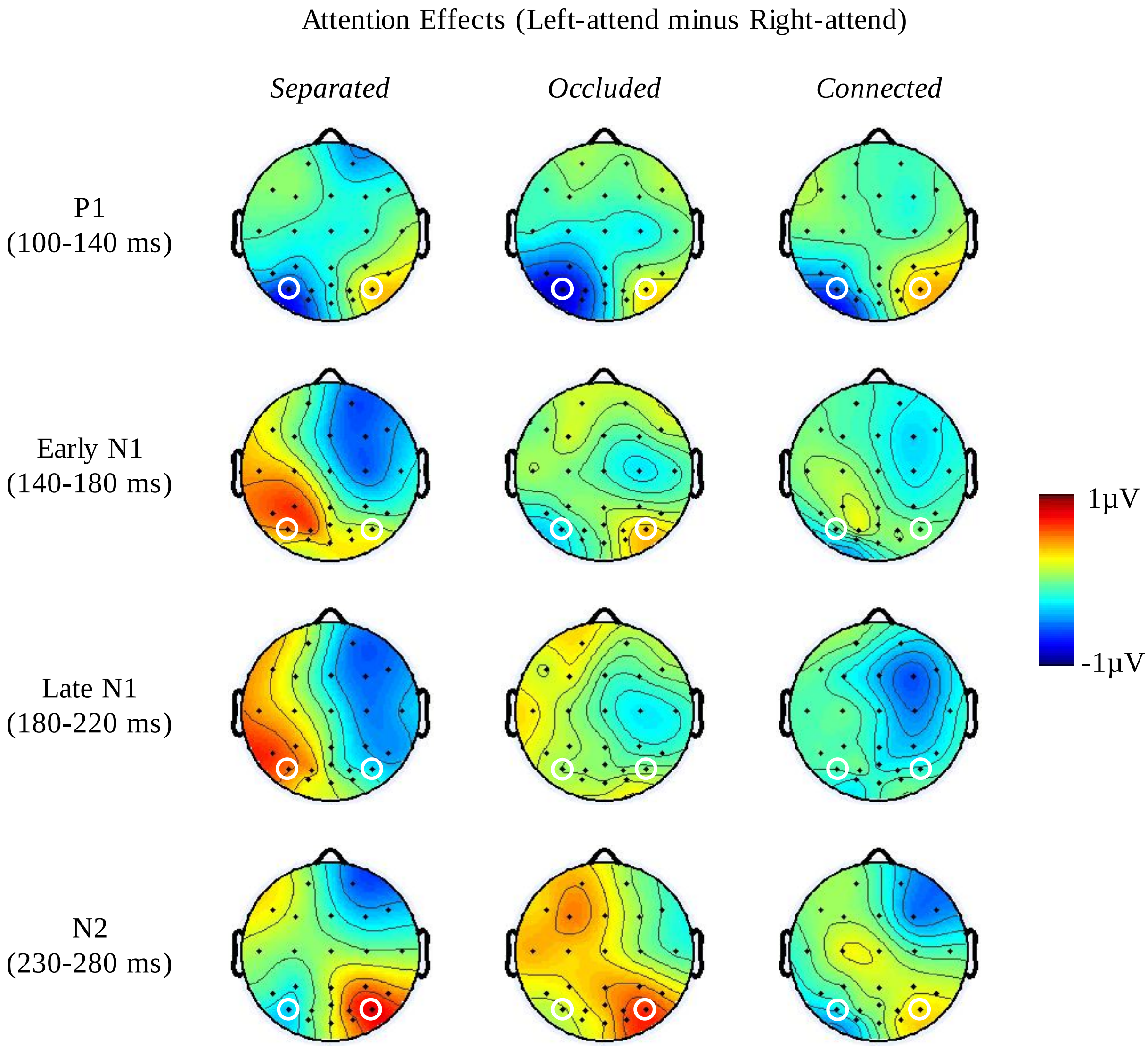
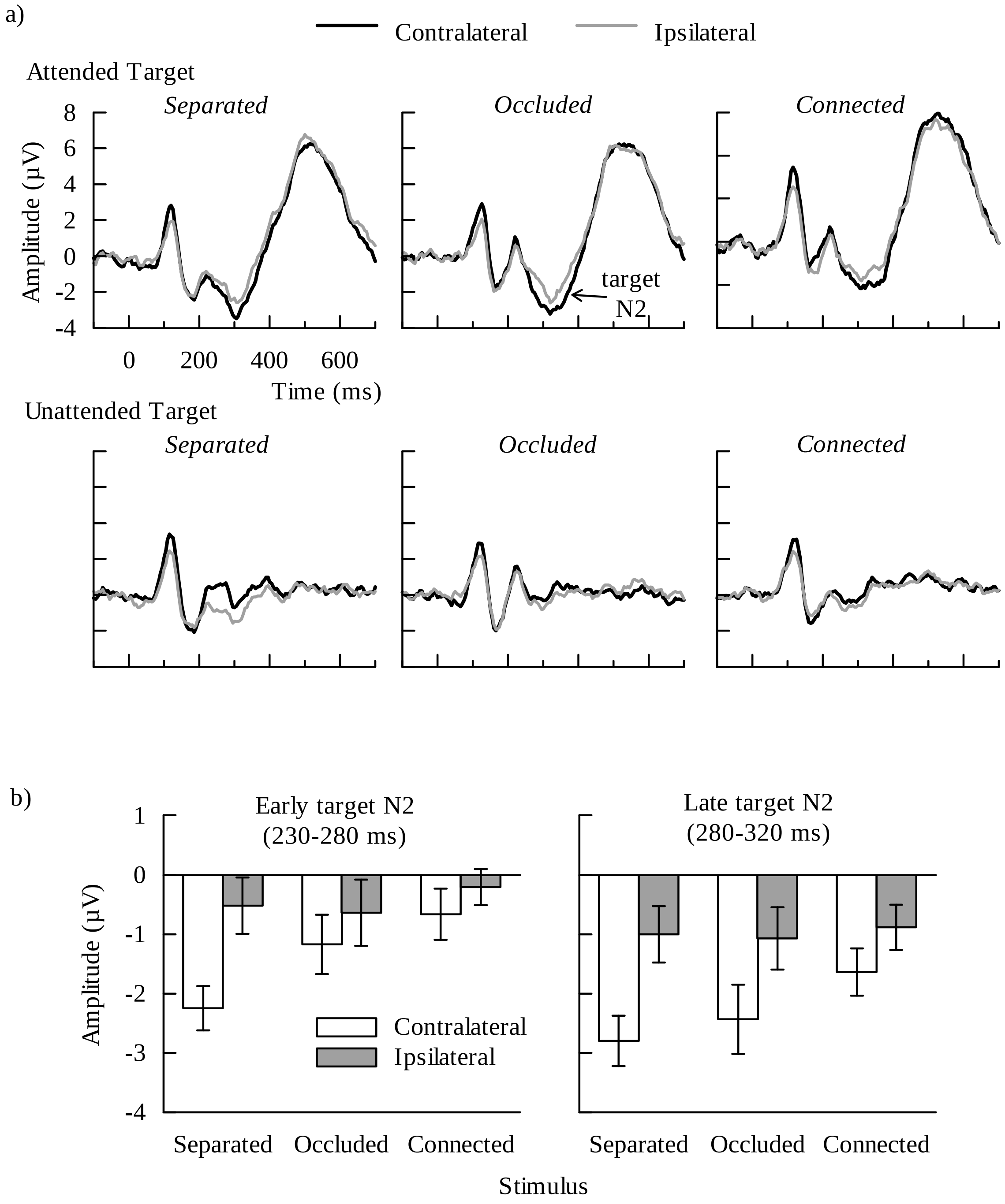

Attention Effects (Left-attend minus Right-attend)
Separated
Occluded
Connected
P1
(100-140 ms)
Early N1
(140-180 ms)
Late N1
(180-220 ms)
N2
(230-280 ms)
1μV
-1μV

Figure 4


a)
Contralateral
Ipsilateral
Attended Target
Separated
Occluded
Connected
8
6
4
2
0
-2
-4
Amplitude (µV)
target N2
0
200
400
600
Time (ms)
Unattended Target
Separated
Occluded
Connected
b)
Early target N2 (230-280 ms)
Late target N2 (280-320 ms)
1
0
-1
-2
-3
-4
Amplitude (µV)
Contralateral
Ipsilateral
Separated
Occluded
Connected
Separated
Occluded
Connected
Stimulus