

Perceptual load interacts with involuntary attention at early processing stages: Event-related potential studies

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ABSTRACT

Perceptual load is known to influence the locus of attentional selection in the brain but through an unknown underlying mechanism. We used event-related potentials (ERPs) to investigate how perceptual load interacts with cue-driven involuntary attention. Perceptual load was manipulated in a line orientation discrimination task in which target location was cued involuntarily by means of peripheral cues. Attentional modulation was observed for P1m (the posterior midline P1 component with peak latency between 108 and 140 ms) with invalid trials eliciting larger P1m than valid trials. This attentional effect on P1m increased as a function of perceptual load, suggesting an early temporal locus for the interaction of perceptual load and involuntary attention. Attentional modulation for the C1 component (peak latency at approximately 80 ms) was also observed, but only for high-load stimuli that were presented intermixed with low-load stimuli. Results suggest that (a) perceptual load affects attentional selection at early processing stages; (b) perceptual load interacts with *involuntary* attention earlier and with different brain mechanisms relative to *voluntary* attention; and (c) attentional modulation in the C1 time range is possible under optimal experimental conditions.

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Introduction

The question of how early in visual processing selective attention exerts its effects has long been debated in cognitive psychology (for a review, see Johnson and Dark, 1986). There is consistent support that early selection occurs in extrastriate cortex, based on work with the P1 component of the visual event-related potential (ERP) (Clark and Hillyard, 1996; Heinze et al., 1994; Mangun et al., 1998, 2001; Woldorff et al., 1997). Yet, other techniques provide evidence of even earlier selection: single-unit (Ito and Gilbert, 1999; McAdams and Reid, 2005; Motter, 1993; Roelfsema et al., 1998) and brain imaging studies (Gandhi et al., 1999; Hopf et al., 2004; Somers et al., 1999) have shown that attention can modulate activity in the striate cortex. However, the visual ERP C1 component – the first visual cortical component (peak latency at approximately 80 ms after stimulus onset) arising from visual information processing and reflecting the initial cortical volley (Clark et al., 1995; Clark and Hillyard, 1996) – is not consistently found to be modulated by attention. Several authors have argued that the attentional effects observed in the striate cortex reflect top-down processes from higher visual cortex back onto the striate cortex (Lamme and Spekreijse, 2000; Mehta et al., 2000a,b; Martinez et al.,

1999, 2001; Noesselt et al., 2002; Super et al., 2001; see also Juan and Walsh, 2003; and Pascual-Leone and Walsh, 2001, for confirmatory evidence obtained from transcranial magnetic stimulation studies). On the other hand, recent ERP and MEG studies have shown C1 modulation by perception and/or attention (Kelly et al., 2008; Khoe et al., 2005; Wu et al., 2005; see also Poghosyan et al., 2005 for MEG evidence).

However, the story is more complex than whether or not C1 is modulated by attention. Perceptual load also appears to influence the temporal locus of attentional selection in the brain. There is behavioral evidence that interference from task-irrelevant distractors with a target is reduced when the target is under high perceptual load (Lavie and Tsai, 1994; Lavie 1995). Early selection only occurs when the perceptual load is high. However, electrophysiological evidence is needed to determine how early in processing these influences are exerted. A direct translation of Lavie's behavioral conception of perceptual load into the ERP paradigm poses problems because simultaneously presented target and distractor stimuli produce overlapping ERP components. Nevertheless, by using operational definitions of perceptual load that vary somewhat from Lavie's, several researchers have explored the relationship between perceptual load and attention using ERPs (Fu et al., 2008; Handy and Mangun, 2000). Under voluntary attention conditions, different load by attention interactions have been observed for the visual P1 (Experiment 1 of Handy and Mangun, 2000) or N1 components (Fu et al., 2008; Experiment 2 of Handy and Mangun, 2000). The paradigms used in these

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studies differed in some respects, so the reasons for the different load by voluntary attention interactions for P1 or N1 are not clear.

Another important factor concerns how attention is deployed – voluntarily or involuntarily – as that affects the temporal locus of selection as well. It has been known for some time that involuntary attention affects stimulus processing in a manner distinguishable from voluntary attention. Cue validity effects have a different time course for the two types of attention shifts (Muller and Rabbitt, 1989; Yantis and Jonides, 1990). This is also seen in different characteristics of the amplitudes and latencies of ERP P1 and/or N1 components for involuntary relative to voluntary attention (Doallo et al., 2004; Fu et al., 2001; Hopfinger and Mangun, 1998; Hopfinger and West, 2006).

There are several reasons why an involuntary paradigm is advantageous for examining the locus of perceptual load effects. As attentional shifting is faster when attention is involuntarily captured by peripheral onset of cues (Eimer, 2000), involuntary attention can be expected to exert effects earlier in processing. Further, the timing of feedback modulation in V1 is different for voluntary and involuntary shifting of attention, as suggested by a recent study using the involuntary attention paradigm (Fu et al., 2005b). In that study, the initial C1 component (approximately 80 ms) was not modulated by attention; however, re-activation of V1 (approximately 110 ms) was evident in the P1 time range, suggesting a relatively early feedback mechanism for tasks involving involuntary attention (as compared with approximately 150 ms using voluntary attention). Despite substantial evidence that involuntary attention is fast and automatic (e.g., Mueller and Rabbitt, 1989), previous ERP studies using involuntary attention tasks have observed that the earliest attentional modulation occurs on the later P1 and not the earlier C1 component (Doallo et al., 2004; Fu et al., 2005a; Hopfinger and Mangun, 1998; Hopfinger and Maxwell, 2005; Van de Lubbe and Woestenburg, 1997). However, those studies did not manipulate perceptual load and most of the above-mentioned ERP studies on attention and the perceptual load–attention interaction (e.g., Fu et al., 2008; Handy and Mangun, 2000) have studied the locus of attention using voluntary attention paradigms with trial-by-trial cuing using central, symbolic cues. Therefore, to better understand the locus of attention, involuntary orienting should be assessed as perceptual load is manipulated.

Use of ERPs allows investigation into the temporal (and perhaps anatomic) locus of attentional selection and the interaction between perceptual load and attention. Previous work has shown that perceptual load interacts with voluntary attention within the P1 or N1 time range (Handy and Mangun, 2000) and the effect of this interaction on N1 has been localized to the temporal parieto-occipital region by using dipole modeling (Fu et al., 2008). The present study sought to extend our previous work to involuntary attention, investigating when the earliest attentional selection could occur and when perceptual load interacted with involuntary attention. We hypothesized that attentional selection might be evident earlier under conditions of high perceptual load and involuntary attention. We predicted earlier selection for high-load stimuli relative to low-load stimuli. We also expected that the interaction between perceptual load and attention would occur earlier under involuntary relative to the voluntary attention conditions that have been the focus of previous studies.

Method

Participants

Sixteen healthy college students participated as paid volunteers. Data from one participant were excluded because of technical problems, and data from two participants were also excluded from further analyses because of excessive eye blinks. The remaining 13 participants (7 male) were between 18 and 23 years of age (mean age 20.8 years). All the participants were right-handed and had normal or

corrected-to-normal vision. They reported no history of neurological problems. Informed consent was obtained from all the participants.

Stimuli

A black fixation cross ($0.31^\circ \times 0.31^\circ$) was presented on a white background at the center of the monitor throughout the entire recording session. On each trial, each target array ($2.45^\circ \times 2.54^\circ$) appeared randomly on the left or right side, with its center 6.36° to the side and 2.05° above the fixation cross. The perceptual load of the target array was manipulated as low, medium, and high (Figs. 1a, b, and c, respectively). The target arrays classified as medium load were identical to those used in our previous study (Fu et al., 2005b) and consisted of two horizontal, one vertical, and one diagonal line, with one line in each of the four quadrants. For each of the medium-load target arrays, the length of all the element lines was 0.9° and all the lines could appear at any of the quadrant with equal probability, with a restriction that the two horizontal lines were always displayed in the diagonal quadrants. The low-load target arrays were created by cutting the 3 non-target lines of the medium arrays into 10 small dot-like pieces, and then scrambling these small pieces at their respective quadrant, so that the target element (the diagonal line) could “pop-out” from the dot-like background. The high-load target arrays were created by adding a background of nine “X”s (each subtending 0.37°) to the medium arrays, so that the target line element needed to be disentangled from confounding elements with same orientation in these background “X”s, before participants could perform the orientation judgment of the target diagonal line. For all the target arrays, the diagonal line could appear in any of the four quadrants with equal probability, and its orientation could be backward (“\”) or forward (“/”) with equal probability. Prior to the presentation of each target array, a peripheral Kanizsa box ($2.95^\circ \times 3.11^\circ$) served as a location cue, which flashed randomly in the left or right visual field. The center of the cue overlapped with the center of the target array in the left or right visual field. The cue was non-informative about the location of the target array; that is, the target array could equally appear at the same location as the cue or at the opposite side. All the three types of target arrays were mixed in every experiment block with equal probability, and the stimulus sequence was randomized for every subject. In all the experimental trials, 3/7 trials were valid (with 1/7 for low, medium and high load each), and 3/7 trials were invalid (with 1/7 for low, medium and high load each). In the remaining 1/7 of the trials, the peripheral cue was presented without a following target (the cue-only condition). The purpose of this cue-only condition was to remove the ERP overlap from the cues (because of short and fixed cue-to-target SOA), as in our previous study (Fu et al., 2005b). The durations of cue and target were 50 and 100 ms, respectively. The cue-to-target stimulus onset asynchrony (SOA) was fixed at 150 ms, and the inter-trial interval (ITI, offset to onset) ranged randomly between 1200 and 1600 ms. The purpose of using a fixed cue-to-target SOA was to have a relatively constant cue validity effect, so that if there was any small but relatively constant attentional effect on early ERP components (such as C1), it would be more likely recorded relative to that varying across trials.

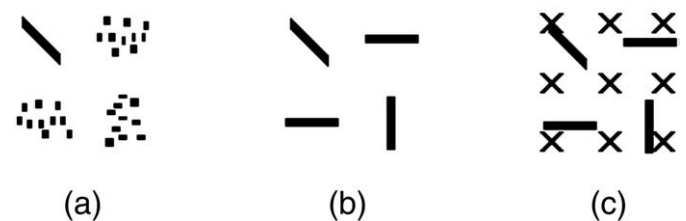


Fig. 1. Illustrations of the stimuli with low, medium and high perceptual load. Low-load stimuli (a) were developed by cutting the three non-target lines of the medium-load stimuli (b) into small parts and scrambling them in their respective quadrants. High-load stimuli (c) were developed by putting the medium-load stimulus on a background that consisted of “X”s.

Procedure

Participants were required to fixate the central cross and minimize eye blinks and body movements during all the experimental blocks. Their task was to discriminate the orientation of the diagonal line. They were instructed to respond to the backward diagonal (\) by pressing key 4 on a NeuroScan (NeuroScan, Texas, USA) Stimpad using their right thumb, and to respond to the forward diagonal (/) by pressing key 1 using their left thumb. To help participants memorize the stimulus-response mapping, they were told that their hand position matched the orientation of the stimuli, if they were to raise the Stimpad in front of them. Participants were instructed to respond as quickly as possible while maintaining higher than 90% of accuracy, and to withhold a response on the “cue-only” trials. Each participant was given 80 practice trials before the EEG recording; further practice was given if they did not reach 90% accuracy in target (line orientation) discrimination. During the EEG recording, short breaks were allowed after every 40 trials. To mitigate fatigue effects, all participants were required to take part in the EEG recording session twice within three days, with exactly the same task and procedure. There were 1344 trials in total for each EEG recording session, ensuring a theoretical sample size of 192 for each experimental condition across recording sessions.

Data acquisition

The STIM (NeuroScan, Texas, USA) software packages were used to present stimuli, and SCAN (NeuroScan, Texas, USA) software packages were used to record and analyze the EEG data. Sixty-four channels of EEG and EOG were recorded from the scalp with a NeuroScan quick-cap (AgCl electrodes). Standard 10–20 sites were FPZ, FP1, FP2, FZ, F3, F4, F7, F8, CZ, C3, C4, PZ, P3, P4, OZ, O1, O2, T3, T4, T5, and T6. Additional intermediate sites were AF3, AF4, AF7, AF8, F1, F2, F5, F6, FCZ, FC1, FC2, FC3, FC4, FC5, FC6, FT7, FT8, C1, C2, C5, C6, CPZ, CP1, CP2, CP3, CP4, CP5, CP6, TP7, TP8, P1, P2, P5, P6, PO3, PO4, POZ, PO5, PO6, PO7, and PO8. Physically linked left and right mastoid, rather than a commonly used mathematically linked mastoid (Picton et al., 2000), served as reference. Horizontal eye movements (HEOG) were monitored by placing two electrodes lateral to the left and right orbits. The impedances of all electrodes were kept below 5 k Ω throughout the recording session. Vertical eye movements (VEOG) and eye blinks were measured by placing two electrodes, with one 1.5 cm below and the other 1.5 cm above the left eye. The EEG from each electrode site was digitized at 500 Hz and was filtered with a band-pass of 0.1 to 40 Hz. The EEG for the 200 ms preceding target onset was used as baseline.

Data analysis

Prior to averaging the EEG, artifact rejection was performed to discard epochs contaminated by eye blinks, horizontal eye movements, body movements, and muscle activity. The rejection threshold was ± 75 μ V for eye blinks/muscle movements and was ± 40 μ V for horizontal eye movements. EEGs for the cue-plus-target conditions were averaged from the onset of the target stimulus (valid, invalid), and EEGs for the cue-only trials were averaged from the onset of the “blank” stimulus. All the data were collapsed over the two orientations of the diagonal line. An ERP subtraction procedure (Fu et al., 2005b) was applied to remove the ERPs of the cues. After ERP subtraction, the peak amplitudes and latencies were used for statistical analyses. For behavioral data analysis, RTs exceeding ± 3 standard deviations were excluded from data analysis (less than 2% data excluded). Behavioral data were analyzed by means of repeated measures analysis of variances (ANOVAs) with three factors: load (low, medium, or high), validity (valid or invalid), and visual field (left or right). For electrophysiological data analysis, data were analyzed from electrode exhibiting the largest amplitude waveform of each component of interest. The hemisphere factor (left or right) was included when

analyzing data from symmetrical electrodes (e.g., non-midline electrodes). The time window for obtaining peak latency and amplitude data was 50–110 ms for the C1 component, 70–160 ms for the P1 component, and 150–220 ms for the N1 component. The relatively wide ranges for searching for C1 and P1 peaks were set to accommodate individual differences in the C1 and P1 components; however, the overlap between these search ranges should not cause any confusion on the sequence of these components because of their polarities. For example, the peak latency of P1 for one participant (e.g., 80 ms) might be earlier than the peak latency of C1 for another participant (e.g., 110 ms), but for each participant, C1 should always be earlier than P1. Peak-baseline differences were calculated for peak amplitudes of each component. For statistical significance, Greenhouse–Geisser correction for non-sphericity was applied where appropriate. To be conservative in making statistic inference after multiple comparisons, the most stringent Bonferroni correction ($p = 0.05/3 = 0.017$, for comparisons under 3 load levels), was used to evaluate the critical comparisons between different load levels for each electrode of interest.

Results

Behavioral measures

Fig. 2 shows mean reaction times (RTs) and error rates to targets averaged across 13 participants. Participants responded faster on valid relative to invalid trials [$F(1, 12) = 38.792, p < 0.0005$; see Fig. 2a]. The

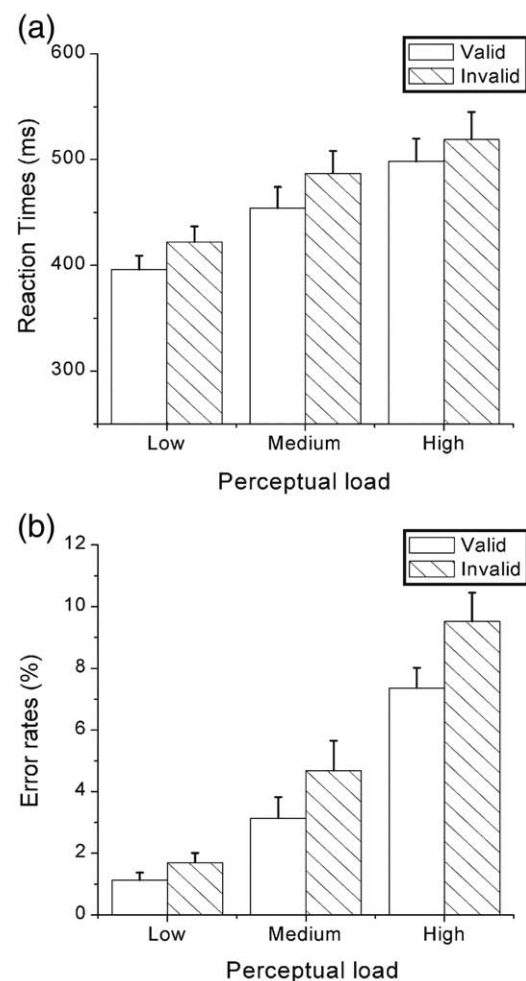


Fig. 2. Reaction times (RTs) and error rates as a function of perceptual load and cue validity.

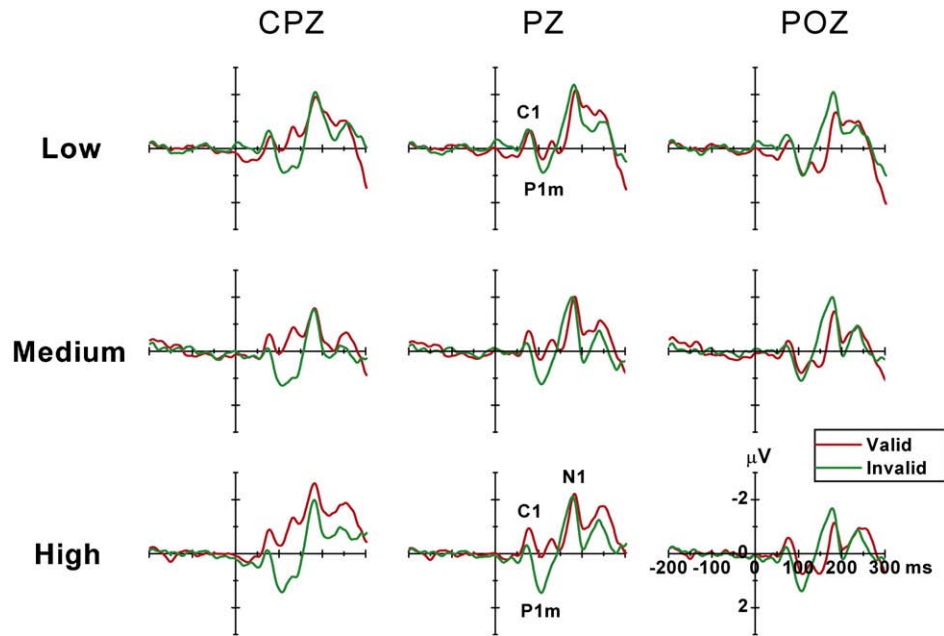


Fig. 3. The grand averaged ERPs across all participants for the valid and invalid trials under low-, medium- and high-load conditions for three midline electrodes (CPZ, PZ, and POZ). Data were averaged across visual fields. The attentional effect on P1m (the midline P1 component) increased as a function of perceptual load. The amplitude of C1 was larger for valid relative to invalid trials under the high-load condition.

main effect of load was significant [$F(2, 24) = 77.539, p < 0.0005, \epsilon = 0.835$]. Separate analyses showed that the participants responded fastest to low-load stimuli, slower to medium-load stimuli, and slowest to high-load stimuli (all $p < 0.0005$). The validity effect on RTs (invalid minus valid) was smallest for the high-load stimuli relative to both the low- and medium-load stimuli (both $p < 0.005$). Participants responded more accurately to valid relative to invalid trials [$F(1, 12) = 17.598, p < 0.001$; see Fig. 2b]. The main effect of load was significant [$F(2, 24) = 48.743, p < 0.0005, \epsilon = 0.971$]. Separate analyses showed that the participants had the fewest errors for low-load stimuli, more errors for the medium-load stimuli, and the highest

errors for the high-load stimuli (all $p < 0.005$). The validity effect on error rates was larger for high-load relative to low-load stimuli [$F(1, 12) = 7.59, p < 0.017$], which explains the smaller validity effect on RTs for high-load relative to low- and medium-load stimuli—participants made more errors to invalid trials with high load to achieve faster responses.

ERP measures

In order to isolate the ERPs to the target from the ERPs to the cue-plus-target, ERPs from the cue-only condition were subtracted from

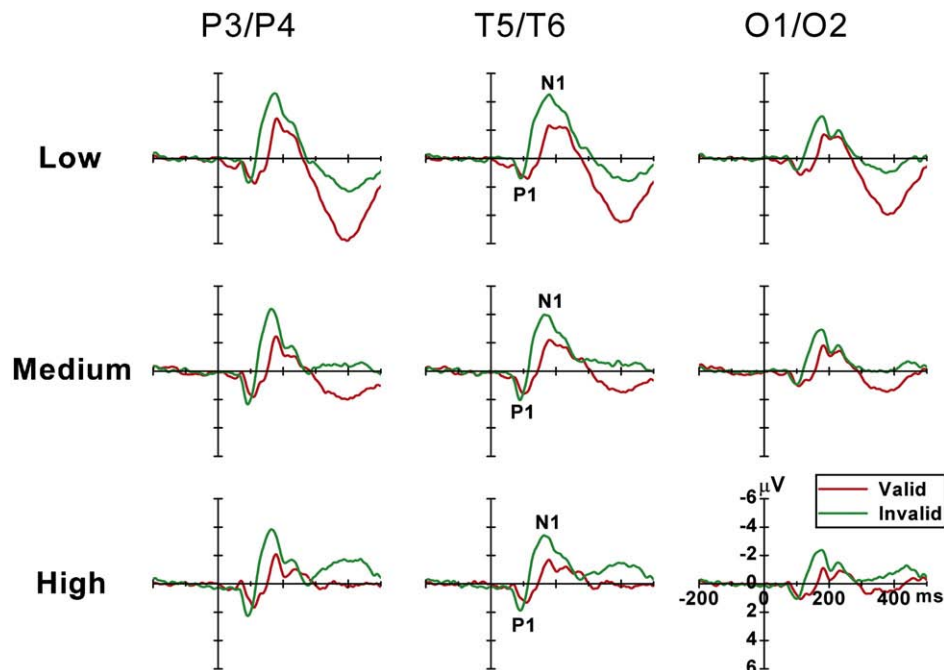


Fig. 4. The grand averaged ERPs across all participants for the valid and invalid trials under low-, medium- and high-load conditions at the parietal (P3/P4), temporal (T5/T6) and occipital (O1/O2) regions contralateral to the target location. Data were averaged across visual field and hemisphere.

ERPs from the cue-plus-target condition, a method used in our previous study (Fu et al., 2005b). By doing so, the target elicited ERPs can be compared between valid and invalid conditions. Figs. 3 and 4 show the target ERPs from valid and invalid trials for low-, medium-, and high-load stimuli after ERP subtraction. There was a clear negative C1 component over the parietal area about 80 ms after target onset, and a midline P1 component (P1m, Fig. 3); the lateral P1 and N1 components in posterior areas were also distinguishable (Fig. 4). There were effects of cue validity and perceptual load on these early ERP components.

C1

The C1 component was seen over parietal cortex with its largest amplitude at the PZ site (Fig. 3). The load \times validity interaction was significant [PZ: $F(2, 24) = 8.452, p < 0.003, \epsilon = 0.833$]. Separate analysis showed that valid trials elicited larger C1 for high-load stimuli [$F(1, 12) = 8.63, p < 0.012$]. This validity effect only approached significance for medium-load stimuli [$F(1, 12) = 2.297, p < 0.155$], and was not significant for low-load stimuli [$F(1, 12) = 0.165, p < 0.692$]. Figs. 5a and b show the scalp voltage maps of the difference waves obtained by subtracting ERPs on invalid trials from those on valid trials. At 80 ms after the onset of the target array, there were no attentional effects on the C1 component under the low-load condition, but a C1 attentional effect was evident over parietal areas under the high-load condition (Fig. 5a). For the C1 peak latency, no significant main effects or interactions were observed.

Midline P1 (P1m)

The amplitudes of the midline P1 component (P1m) were larger for invalid relative to valid trials at the central parietal area [CPZ: $F(1, 12) = 9.607, p < 0.009$], and this attentional effect increased with perceptual load, as suggested by a significant load \times validity interaction [$F(2, 24) = 6.551, p < 0.009, \epsilon = 0.830$] (Figs. 3; 5a and b, 100–140 ms). For the latency of P1m, invalid trials elicited an earlier P1m relative to valid trials [$F(1, 12) = 15.781, p < 0.002$].

Lateral P1 (P1l)

For the amplitude of the lateral P1 (P1l), the load \times validity interaction was significant [P3/P4: $F(2, 24) = 4.329, p < 0.031, \epsilon = 0.872$], suggesting that the validity effect on lateral P1 amplitude was more pronounced with increased load (Fig. 4). No other main effects or interactions related to load or validity were significant. Separate analyses showed no significant validity main effect or related interactions for all stimuli (all $p > 0.15$). For the latency of P1l, invalid trials elicited an earlier lateral P1 [$F(1, 12) = 7.043, p < 0.021$] relative to valid trials.

Lateral N1 (N1l)

For the amplitude of the lateral posterior N1 (N1l), the validity \times visual field \times hemisphere interaction was significant [P3/P4: $F(1, 12) = 18.924, p < 0.001$], suggesting that invalid trials elicited a larger contralateral N1 relative to the valid trials. The main effect of load approached significance [$F(2, 24) = 3.411, p < 0.057, \epsilon = 0.888$], and the load \times visual field \times hemisphere interaction was significant [$F(2, 24) = 11.416, p < 0.0005, \epsilon = 0.945$], suggesting that the effects of the perceptual load were more pronounced at sites contralateral to the stimulus visual field (Fig. 4). The scalp voltage distributions of ERPs at the P1 and N1 time range are shown in Fig. 5a (100–200 ms) and Fig. 5b (100–180 ms). For the latency of N1l, invalid trials elicited an earlier posterior N1 relative to valid trials [$F(1, 12) = 8.508, p < 0.013$].

Discussion

One challenge in attention research is to design a task that can reveal the full power of selectivity in attention (Desimone and Duncan, 1995). Such a task must be sufficiently sensitive to detect the earliest selective neural processing associated with attentional

modulation of task-relevant visual stimuli under demanding conditions with irrelevant distractors (Maunsell, 1995). We approached this challenge by using peripheral cueing to elicit involuntary attention (Yantis and Jonides, 1990) and by manipulating the perceptual load of the stimuli by varying distractors (Lavie, 1995). In the present study we hypothesized that observing the earliest cortical sign of attentional selection requires certain optimal experimental conditions, which include at a minimum, high perceptual load and involuntarily driven attention. Consistent with this hypothesis, the P1m (the posterior midline P1 component) was reliably modulated by involuntary attention in the main study and as well as in two follow-up studies.^{1,2} Moreover, the earliest visual C1 component (approximately 80 ms) was also modulated by attention under these optimal experimental conditions. Whether these conditions are sufficient to modulate C1 will require further investigation. Importantly, our novel finding of a P1m interaction between perceptual load and involuntary attention suggests that attention

¹ A C1 that is generated in striate cortex should show polarity inversion for upper vs. lower visual field stimuli (e.g., Di Russo et al., 2003). To test this, 15 healthy participants were asked to maintain central fixation while the cues and targets were presented in the upper and lower visual fields. Only high-load stimuli were used (Fig. 1c). The cue-to-target SOA was jittered between 100 and 250 ms. The cues predicted the location of the subsequent target on 50% of the trials. The participants were required to respond to the orientation of the diagonal line. The ADJAR algorithm (Talsma and Woldorff, 2005; Woldorff, 1993) was applied to remove the ERP overlap between the cues and the targets. The attentional effect on C1 was not found, although the reversed polarity of C1 for stimuli in LoVf vs. UVF fits well with the cruciform model of the striate cortex (Jeffreys and Axford, 1972; Mangun, 1995). Notably, the jittered cue-to-target SOA in this follow-up study could have smeared a potentially small C1 attentional effect. Perhaps more importantly, arousal might have played a role in eliciting C1 attentional effects differentially between these two studies. Previous studies have shown an arousal-like effect on a component in the C1 latency range (80–90 ms after stimulus onset) from emotional expressions (Eger et al., 2003; Pourtois et al., 2004) and threatening stimuli (Stolarova et al., 2006). Based on this, the mixed load levels in the main study might have increased the arousal level for the high-load stimuli and thus contributed to the C1 effect for high-load stimuli. Consistent with this arousal hypothesis, participants responded faster to the high-load stimuli when they were intermixed with low and medium load stimuli (main study) relative to when they were present alone (follow-up study). However, some researchers have argued that it is impossible—or only possible to a very limited extent—to observe visual ERPs derived from sub-cortical structures such as the thalamus (Proverbio and Zani, 2003), where manifestations of arousal might be generated. Thus, the role of arousal for the C1 effects remains unclear.

² One limitation of our main study is that the cue–target sensory interactions might have co-varied with the stimulus load, thereby contributing to the present attentional effects on C1 and P1m. That is, the sensory interactions under the high-load condition could have differed from those under medium- and low-load conditions as there were physical differences (such as orientation, luminance, and spatial frequency, etc.) among the stimulus arrays associated with different load levels. We addressed this issue by using a new set of stimuli that better controlled for the difference between stimulus physical properties and cue–target interaction between load levels. Nineteen healthy participants (2 participants' data were excluded because of a data collection issue, 5 male, mean age 20.3 years) were tested. The location of the cues was valid, invalid, or neutral (appeared simultaneously in both the left and right visual field) with equal probability. The durations of the cue and the target array were 50 ms and 100 ms, respectively. The SOAs between the cue and the target array was randomized between 100 and 300 ms, and the ITI (inter-trial interval) between the offset of the target array and the next cue was ranged between 1100 and 1600 ms. The participants' task was to discriminate the orientation of the bar in the center of the target array. The perceptual load of the stimuli was high or low with equal probability. In the high load condition, distractors sharing characteristic features surrounded the central bar — a central horizontal or vertical bar surrounded by crosses, or a central forward or backward bar surrounded by Xs. In the low load condition, the central bar did not share any features with the surrounding distractor — a central horizontal or vertical bar surrounded by Xs, or a central forward or backward bar surrounded by crosses. Note that the location of the four distractors was designed to avoid collinearity between the central bar and the distractors. The sequence of trials was randomized for each participant. In total 1920 trials were presented. The ADJAR algorithm (Talsma and Woldorff, 2005) was used to remove ERP overlap due to short SOAs (100–300 ms) between the cues and the targets. The attentional effect on P1m was found and the perceptual load by attention interaction was replicated for P1m but not for C1. The C1 attentional effect was observed, but with a more parietal distribution. Thus, this study basically replicated the major findings on C1 and P1m of our main study, but did so in the absence of target stimulus confounds and cue–target sensory interactions.

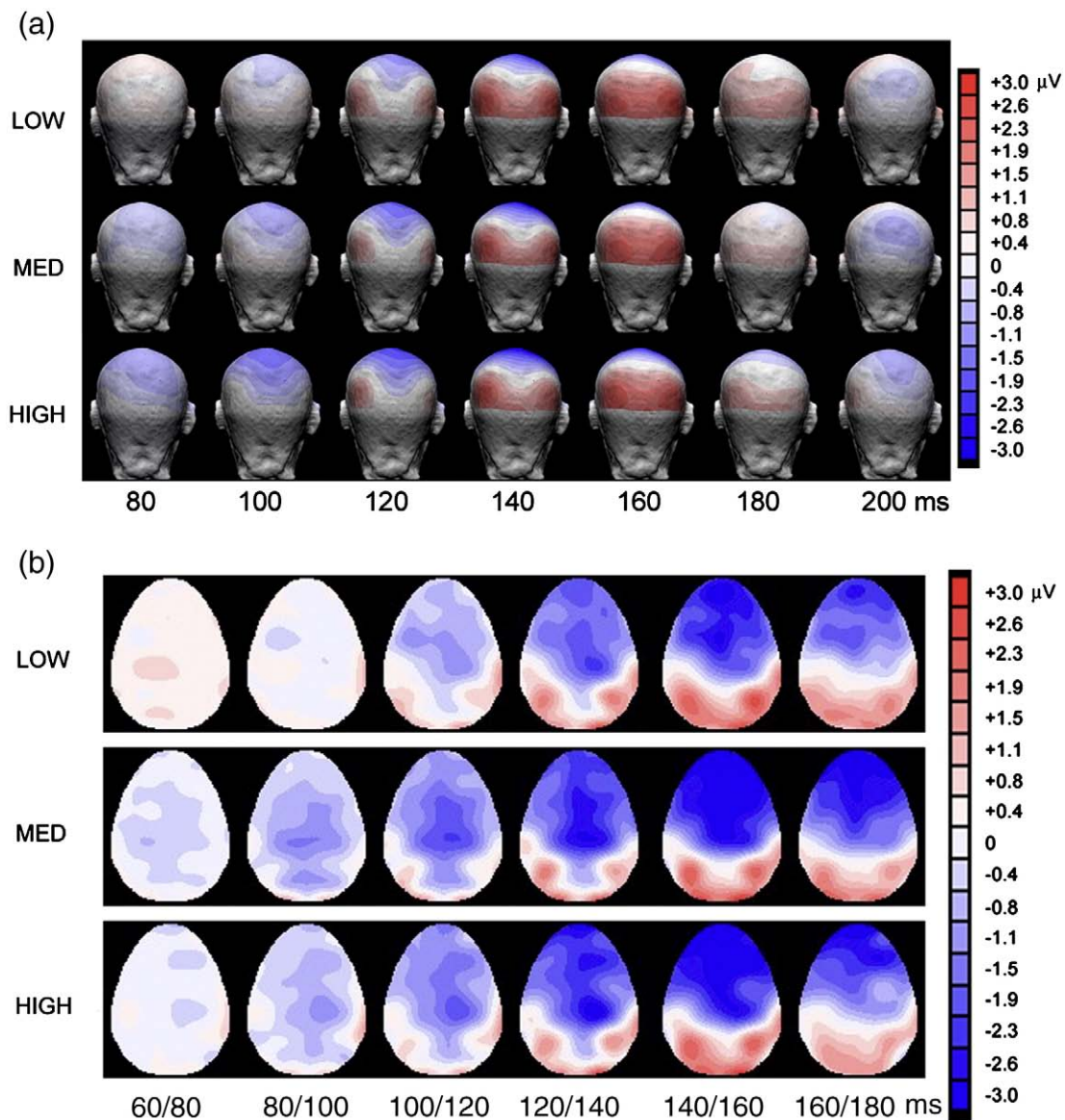


Fig. 5. (a) The 3D back view of the scalp voltage distributions of the attentional effects between 80 and 200 ms (every 20 ms) after target array onset. (b) The 2D top view of the mean scalp voltage distributions of the attentional effects between 60 and 180 ms (every 20 ms) after target array onset. ERP data were obtained from subtracting the averaged ERPs of the invalid trials from that of the valid trials. Data were collapsed across stimulus visual field. The attentional effects on the C1 (80 ms) and P1m (100–140 ms, midline area) increased with the increase of the perceptual load (a). The attentional effects at the P1 and N1 time range (120–180 ms) showed strong activities on the occipito-temporal area (a and b). Note that the bilateral occipito-temporal activities at the 120–180 ms time range was the results of averaging across left and right visual fields; these attentional effects were actually more pronounced on the hemisphere contralateral to the stimulus location. Moreover, the attentional effect on P1m over its latency range (100–140 ms) started on the parietal area, and then spread to the central and frontal areas, regardless of perceptual load (b).

type (involuntary vs. voluntary attention, via indirect comparison) involves different brain mechanisms.

P1m, attentional modulation, and the early perceptual load by attention interaction

The major finding of the present study was that for P1m perceptual load reliably interacted with involuntary attention. This was evident in our main study, whose findings were replicated in a follow-up study under conditions with better control over cue–target sensory interactions.² In our previous study using a voluntary (sustained) attention task, perceptual load interacted with voluntary attention during the lateral N1 time range (peak latency 190 ms) but not for P1m (Fu et al., 2008). Indirect comparisons between these two studies which used similar stimuli suggest that attention type affects the locus of interaction and possibly involves different underlying brain

mechanisms. This claim is based on the earlier onset and more medially distributed scalp locus of interaction we observed under involuntary relative to voluntary attention conditions.

To our knowledge, these are the first observations of perceptual load by attention interactions for P1m. These novel observations are important in light of previous findings of lateralized attentional effects on P1 and N1, i.e., P11 and N11 (e.g., Fu et al., 2008; Handy and Mangun, 2000). The load by *involuntary* attention interaction on P1m (approximately 140 ms for invalid trials) in the present study occurred earlier and the effects were distributed more medially compared to the load by *voluntary* attention interaction on posterior N1 (approximately 190 ms) in a previous sustained attention study (Fu et al., 2008) which used similar stimuli. The generators of the P1m are not known; presumably they are a part of the dorsal parieto-frontal network (e.g., superior parietal lobule and frontal eye field) that is involved in involuntary attention (Corbetta and Shulman, 2002).

Moreover, the scalp distribution maps (Figs. 5a and b, 100–140 ms) showed that the attentional effect on P1m started at posterior and then spread to more central and frontal areas over its latency range, regardless of perceptual load. This suggests that it is likely to be a feed-forward process from early visual cortex to parietal and frontal areas (Lamme, 2003). Therefore, both the underlying attentional processes involved and the scalp distribution suggested different generators between the P1m and the conventional lateral P1 component.

Why does perceptual load interact with involuntary attention at an early processing stage as we saw with P1m (and C1, under optimal experimental conditions)? One explanation is that attentional selection involves a competitive process between the target and the distractors in the stimulus display, akin to the competitive neural interactions in visual areas with large receptive field (Desimone and Duncan, 1995). Perceptual load may influence the timing of different competitive processes. That is, if there is little or no competition between the target line and the distractors, as in the low-load condition, the target line “wins” without the need for resolving the competition. In contrast, in the high-load condition, more attentional resources are required to resolve the competition so that the target line can “win out”. It is possible that the obligatory (or automatic) nature of involuntary attention may have involved early brain areas as shown on P1m, and perceptual load may have caused the flexible timing of attentional selection as shown on P1m and C1.

The attentional effect on P1m was robust. It was observed in our main study and two follow-up studies^{1,2}, with valid trials eliciting smaller P1m than invalid trials. In fact, this P1m attentional effect under involuntary attentional orienting has been clearly illustrated – although without statistical confirmation – in a previous study (Hopfinger and West, 2006, Fig. 3b, electrode Pz). Interestingly, the direction of the P1m attentional effect was reversed (i.e., P1m was larger for valid relative to invalid trials) in a recent study using voluntary attention task (Fu et al., 2008). There appears to be no simple explanation for this difference. Perhaps similar to the reversal of P1 attentional effect that have been observed in previous studies (e.g., Hopfinger and Mangun, 1998; McDonald et al., 1999), this P1m attentional effect may be affected by stimulus and task parameters. Furthermore, as we discussed previously, the neural sources of the P1m may be different from that of the extrastriate cortex-generated P1l. Specifically, we speculated that the generators of the P1m are a part of the dorsal parieto-frontal network (e.g., superior parietal lobule and frontal eye field) that is involved in involuntary attention (Corbetta and Shulman, 2002).

Attentional modulation and the C1 component

The combination of involuntary attention, a cluttered display, and line orientation targets in the present study may have contributed to the earliest C1 modulation of attention by involving predominantly neural activity in striate cortex, as we previously discussed (Fu et al., 2005b). The line orientation discrimination task is consistent with the neural specificity hypothesis of visual selective attention (Harter and Aine, 1984) that attentional selection is based on “neural channels,” aggregations of neurons with identical receptive field properties which are responsible for encoding a given feature (orientation in the present study) of a stimulus. The reflexive and fast nature of involuntary attention may have facilitated this attentional selection and the perceptual load by attention interaction, thereby modulating C1. This is also consistent with a model which proposes that the bottom-up saliency map is located in the primary visual cortex (Zhaoping, 2002) and that attentional capture could occur at the V1 level even without awareness (Zhaoping, 2008).

Nevertheless, the C1 component was not consistently modulated by attention. In our main study an interaction between perceptual load and attention on C1 was observed, but the attentional effect was seen only under the high-load conditions. However, when only high-

load stimuli were presented and cue-to-target SOAs were jittered in a follow-up study¹, this C1 attentional effect was absent. In another follow-up study² with better control of cue–target sensory interaction and again a jittered SOA, the C1 attentional effect for the high-load stimuli was not significant at the site where C1 was largest but was significant at more parieto-centrally distributed sites. Thus, consistent with the literature that attention-related C1 effects have not been consistently observed across studies (e.g., Clark and Hillyard, 1996; Martinez et al., 1999; Noesselt et al., 2002; and Khoe et al., 2005; Kelly and Foxe, 2008), the optimal conditions for eliciting such effects remain uncertain. The contributory factors may include perceptual load, arousal, cue–target sensory interaction, and cue-to-target SOA. The present study suggests that high perceptual load may be necessary for eliciting a C1 attentional effect, as seen in both the main study and the second follow-up study². Moreover, arousal might also have played a role in the present study, as suggested by our first follow-up study¹, which showed no C1 attentional effect for the high-load stimuli in the absence of lower load stimuli (see note 1 for more discussion). Consistently, previous studies have shown an arousal-like effect at the C1 time range with emotional facial expression (Eger et al., 2003; Pourtois et al., 2004) and threatening/arousing stimuli (such as attack scenes, mutilated bodies) (Stolarova et al., 2006). Nevertheless, an explanation based on a possible confound of cue–target sensory interaction in the main study is less likely. This is because our follow-up study² greatly reduced the difference on such cue–target interactions between the low- and high-load conditions yet still found a C1 attentional effect. In addition, individual differences in striate cortical structure might have also played a role in the present study, as suggested by a recent study (Kelly and Foxe, 2008). Kelly and Foxe pre-tested two stimulus locations and selected one location where C1 was largest to elicit C1 components from each participant. By doing so, individual differences in V1 architecture between participants was to some extent mitigated and thus not only the statistical power but also the chance to find a tiny C1 attentional effect was improved. Therefore, while the present approach of using high-load stimuli and involuntary attention is a promising one for eliciting the C1 attentional effect, the question of whether attention typically modulates the amplitude of C1 is still unanswered.

Although the relationship between the P1m and C1 attentional effects is unclear, one possibility is that the attention effect in striate cortex (indexed by C1) is “amplified” along the visual processing streams to higher cortex (indexed by P1m), similar to the progressively enhanced fMRI signal strength of the attentional effect from V1 to V4 (O'Connor et al., 2002). Alternatively, it is possible that the C1 attentional effect may be affected by the P1m attentional effect because of ERP overlap between these two components (see Fu et al., 2008 for similar overlap and possible account). This latter explanation seems less likely because the C1 attentional effect was not associated with a latency change for the high-load stimuli as it would be if it were contaminated with P1m.

Attentional modulation and the contralateral P1 and N1 components (i.e., P1l and N1l)

The attentional effects we observed on the contralateral P1l and N1l components essentially replicated our previous findings in a peripheral cueing paradigm (Fu et al., 2001, 2005a,b). Compared to invalid trials, valid trials elicited a later P1l, a later N1l, and a smaller N1l. Compared to the enhanced N1l for attended stimuli observed in previous voluntary attention tasks, this reversed N1l effect under involuntary conditions indicates that there may be different mechanisms underlying involuntary and voluntary attention. Moreover, a simple sensory gain control mechanism (for a review, see Hillyard et al. 1998) which proposes that attention amplifies processing of the attended stimuli at an early sensory processing stage without

changing the timing of the processing, cannot account for the presently observed attentional modulation of P11 and N11 latencies.

It should be noted that while previous studies (e.g., Fu et al., 2005b; Hopfinger and Mangun, 1998) observed P11 enhancement by attention under peripheral cueing conditions, the present study found no main effect of attention on contralateral P11 but a significant interaction between attention and stimulus load, such that the higher the load, the larger the P11 for invalid relative to valid trials (see also our follow-up studies^{1,2}). This lack of P11 attentional effect differs from our previous studies showing a smaller (and earlier) P11 for invalid relative to valid trials (Fu et al., 2001; Fu et al., 2005a, 2005b). This is noteworthy but not very surprising, because results from other research groups have also shown different patterns of attentional effects on P11 with peripheral cueing (e.g., Doallo et al., 2004; Hopfinger and Mangun, 1998; McDonald et al., 1999; Prime and Ward, 2004, Prime, 2006). The P11 attentional effect elicited by peripheral cueing has been reported as positive (i.e., larger P11 for valid relative to invalid trials, Hopfinger and Mangun, 1998, under short cue-to-target SOA condition; Hopfinger and Mangun, 2001), or negative (i.e., larger P11 for invalid relative to valid trials, McDonald et al., 1999; Prime and Ward, 2004, Prime, 2006), depending on stimulus properties and cue-to-target SOA. Similarly, the attentional effect on N11 has been shown to be positive (i.e., larger N11 for valid relative to invalid trials, see Hopfinger and Mangun, 1998, long SOA condition, but without statistical analysis on this component), negative (i.e., larger N11 for invalid relative to valid trials, Fu et al., 2001, 2005a,b; Hopfinger and Mangun, 2001, short SOA condition), or null (Hopfinger and Mangun, 1998, short SOA condition; Hopfinger and Mangun, 2001, long SOA condition) under involuntary attention tasks. Given that almost all the visual areas and also feedback mechanisms have been activated approximately 100 ms after stimulus onset (Lamme, 2003), it is not surprising that the P11 (approximately 70–150 ms) and N11 (approximately 160–200 ms) components vary across different stimuli and tasks. That is, the attentional effect on P11 and N11 may have overlapped with other processes occurring at the same time range in the present study.

Summary

The present work shows that perceptual load affects the locus of attentional selection at early processing stages as manifested in effects on P1m (the posterior midline P1 component). Additionally, perceptual load interacts with involuntary attention at the P1m time range (peak latency varied between 108 to 140 ms), with invalid trials eliciting a larger attentional effect which increased with perceptual load. The scalp distribution of P1m suggests that the attentional effects on it differ from conventional attentional effects on the lateral P1 and N1 components. Considered in the context of previous studies, these results suggest that the interaction between perceptual load and involuntary attention involves neural mechanisms that differ from those involved in the interaction between perceptual load and voluntary attention. Results also suggest that attentional modulation of the C1 component (presumably originating in striate cortex) may only be observed under optimal experimental conditions, and, further, that high and/or varying perceptual load may be required to elicit attentional effects on C1. If that is correct, it would suggest that under high load, the filter is set earlier, thereby modulating early components.

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