Attention and Sensory Gain Control: A Peripheral Visual Process?

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Abstract

■ Attention-related sensory gain control in human extrastriate cortex is believed to improve the acuity of visual perception. Yet given wide variance in the spatial resolution of vision across the retina, it remains unclear whether sensory gain operates homogenously between foveal and nonfoveal retinotopic locations. To address this issue, we used event-related potentials (ERPs) in a variant of the canonical spatial attention task. Participants were cued to expect targets at either fixation (foveal targets) or at a location several degrees above fixation (parafoveal targets). At both target locations, manual reaction times were shorter for cued relative to uncued targets, indicating that attention was consistently oriented to the cued location. Nevertheless, attention-related increases in sensory-evoked cortical activity were only observed at the parafoveal target location, as measured by the amplitude of the lateral occipital P1 ERP component. A second experiment replicated this data pattern using targets with lower stimulus contrast, indicating that the absence of a P1 effect for foveal targets could not be attributed to a saturated P1 response under higher-contrast stimulus conditions. When considered in light of retinogeniculate projections to cortex showing systematic changes in their physiological organization beginning within a degree of visual angle of the fovea, our findings support the proposal that the strategic functions of visual attention may vary with the retinotopic location involved. ■

INTRODUCTION

In humans, attention is used to sculpt our moment-to-moment perceptions of the visual world. Integral to this process is the ability to volitionally modulate the intensity of sensory-evoked activity in the extrastriate visual cortex (e.g., Woldorff et al., 1997; Heinze et al., 1994). In particular, when spatial attention is oriented to a nonfoveated location in the visual field, event-related potentials (ERPs) have shown that it amplifies the sensory-evoked response to stimuli presented in that location (e.g., Martinez et al., 1999; Mangun & Hillyard, 1991; Van Voorhis & Hillyard, 1977). This effect of attention—measured as an increase in the amplitude of the lateral occipital P1 ERP component—is referred to as sensory gain control (e.g., Hillyard, Vogel, & Luck, 1999; Mangun & Hillyard, 1995; Eimer, 1993, 1994), and is assumed to improve the acuity of visual perception within the attended location of space (e.g., Mangun, 1995; Luck et al., 1994; Eimer, 1993, 1994). A central unanswered question, however, is whether sensory gain control extends to our most effective system for achieving high-resolution visual perception—foveal processing—or whether it may be uniquely associated with the functions of lower-resolution parafoveal vision.

Several prior ERP studies have considered the differences in attention between foveal and nonfoveal visual processing, but these investigations were not directly interested in the question of foveal gain per se. An early series of experiments comparing visual attention in normal and hearing-impaired participants reported that sustained attention to foveal stimuli increased the amplitude of the P1 over occipital scalp locations, relative to when sustained attention was focused away from the fovea (Neville & Lawson, 1987a, 1987b, 1987c). However, the ERP waveforms for foveal stimuli were only presented in one of the three studies (Neville & Lawson, 1987a), and at that, only the single-subject waveforms from three participants were provided. Not only does this make evaluation of the P1 effects difficult, the waveforms themselves show no clear evidence that a P1 deflection was even present over the occipital scalp sites recorded. In a more recent study of sustained visual attention, no attention effects in the lateral occipital P1 were reported when comparing the ERP responses to foveal stimuli as a function of whether sustained attention was focused on the fovea or to a discrete location in the visual periphery (Miniussi, Rao, & Nobre, 2002). Although P1 modulations were reported for foveal stimuli in this study, it was only when comparing foveal ERP responses between conditions of focused versus divided spatial attention. Thus, the data of both Miniussi et al. (2002) and Neville and Lawson

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(1987a, 1987b, 1987c) remain equivocal regarding whether the act of spatial orienting itself—already known to modulate gain *beyond* the fovea—can modulate gain *at* the fovea.

Towards directly testing this possibility, we examined the effect of focused spatial attention on foveal stimuli using a paradigm optimal for modulating visual sensory gain: trial-by-trial attentional orienting (e.g., Posner, 1980) under conditions of relatively high perceptual load (e.g., Handy, Soltani, & Mangun, 2001; Handy & Mangun, 2000; Mangun & Hillyard, 1990). On each trial, participants were cued as to the most likely location of an impending target (an ''A'' or an ''H'') that was either at fixation or at a parafoveal location several degrees above fixation (Figure 1). The task required discriminating the target letter, which was presented briefly and masked at offset. If attention-related sensory gain control operates homogenously across the retina, it predicted that an effect of attention should be observed in the amplitude of the P1 elicited by both parafoveal and foveal targets. Conversely, if sensory gain control is restricted to parafoveal visual processing, it predicted that only parafoveal targets should show attention-related modulations in P1 amplitude.

RESULTS

Two ERP experiments were performed using the same basic paradigm (Figure 1). In both, planned analyses centered on examining the amplitude of the lateral occipital P1 ERP component elicited by targets as a function of their location (foveal vs. parafoveal) and cueing condition (cued/attended vs. uncued/unattended). Our initial experiment revealed attention-related increases in sensory-evoked cortical activity only at the parafoveal target location, as measured by P1 amplitude. A control experiment then replicated this data pattern using targets with lower stimulus contrast, confirming that the absence of a P1 effect for foveal targets could not be attributed to a saturated P1 response under higher-contrast stimulus conditions. Notably, these analyses were based on quantifying peak P1 amplitude at scalp electrode sites OL and OR, where the P1 was maximal for targets in both locations in both experiments—a bilateral occipital focus that is normative for the P1 (e.g., Mangun & Hillyard, 1991). As discussed at the end of Experiment 2, a broader analysis of the data from the two experiments showed that the Attention × Location interaction in the P1 extended beyond OL/OR

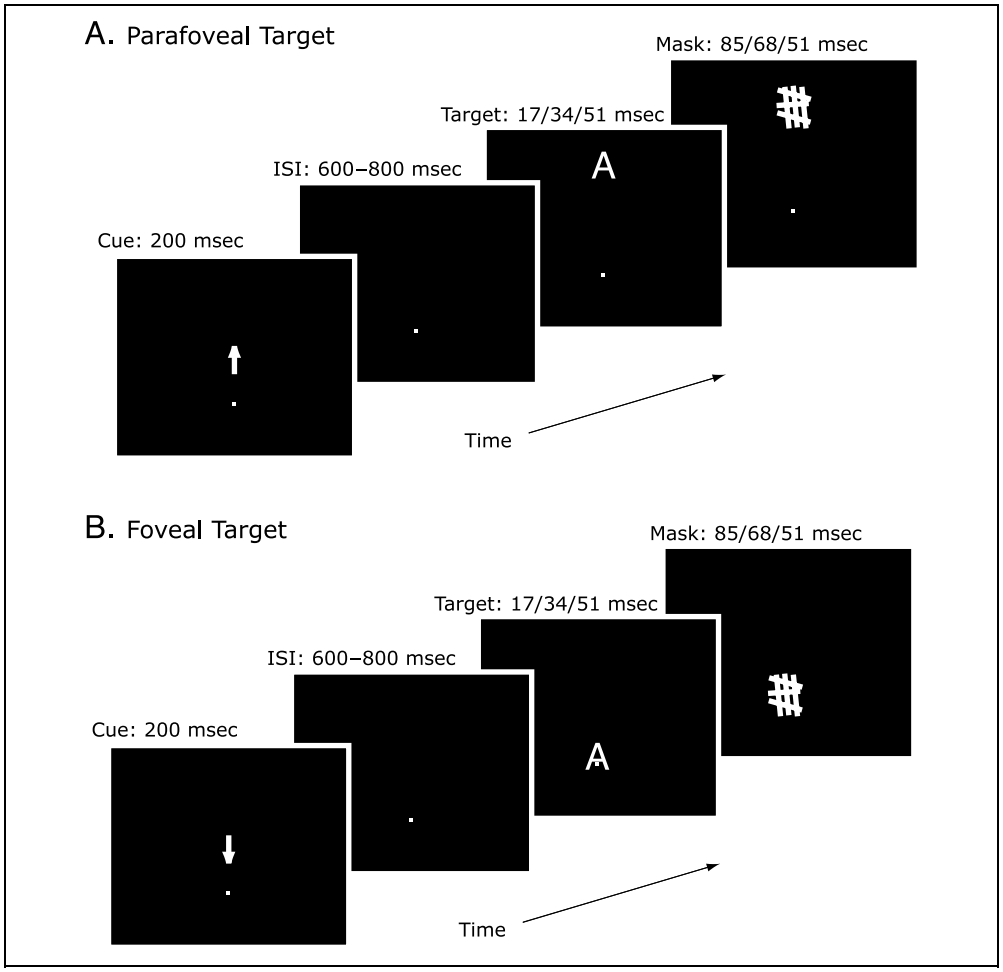

Figure 1. Basic trial conditions. Shown are cued (or attended) trials for targets in the (A) parafoveal and (B) foveal locations, respectively. The relative ratio of target and mask durations always summed to 102 msec, with the ratio varied within each subject on a run-to-run basis in order to avoid floor and/or ceiling effects in performance accuracy. For uncued (or unattended) targets in the parafoveal location, the foveal location was cued; conversely, for uncued targets in the foveal location, the parafoveal location was cued.

spatially, but did not extend to the N1 latency range temporally.

Experiment 1

Twenty-four right-handed, paid volunteers participated (12 women, 12 men; age 18–27 years). All gave their informed consent and all procedures and protocols were approved by the Dartmouth Committee for the Protection of Human Subjects. Out of the original 24 participants, the data from three were excluded from analyses due to large (>1°) systematic eye movements in response to the visual cues. The results reported below are for the remaining 21 participants.

Behavior

Reaction times (RTs) and discrimination accuracy (d') are reported in Table 1 (top) as a function of target location and attention condition; mean durations for foveal and parafoveal targets are reported in Table 2 (top). RTs were faster for cued (or attended) targets independent of whether they were presented at the foveal or parafoveal location. This was confirmed in a repeated-measures ANOVA which showed a main effect of attention [$F(1,20) = 83.50$, $p < .0001$], but no main effect of target location (foveal vs. parafoveal) or Attention × Location interaction (both Fs < 1.0). Similarly, responses were more accurate for cued than for uncued targets. However, unlike RTs, the magnitude of the accuracy effect was larger at the parafoveal location, as was overall accuracy. This was confirmed in a repeated-measures ANOVA which showed a main effect of attention [$F(1,20) = 23.77$, $p < .001$], a main effect of target location [$F(1,20) = 32.05$, $p < .001$], and an Attention × Target location interaction [$F(1,20) = 6.68$, $p < .05$]. Importantly, these behavioral results support the conclusion that participants successfully oriented their attention to the cued location independent of whether it was in the foveal or parafoveal region.

Table 1. Reaction Times (msec) and Accuracy (d') for Target Discrimination from Experiment 1 and Experiment 2, as a Function of Target Location and Attention Condition, Averaged across Participants

		Target Location	
Measure	*Attention*	*Fovea*	*Parafovea*
Experiment 1			
RTs	Cued	482 (27)	470 (22)
	Uncued	524 (28)	516 (25)
d'	Cued	2.49 (0.17)	3.57 (0.18)
	Uncued	2.23 (0.17)	3.06 (0.12)
Experiment 2			
RTs	Cued	586 (22)	541 (26)
	Uncued	633 (20)	576 (21)
d'	Cued	1.71 (0.21)	2.85 (0.27)
	Uncued	1.79 (0.14)	2.57 (0.20)

Standard errors are in parentheses.

Table 2. Mean Target Duration (msec), as a Function of Target Location, Averaged across Participants

	Target Location	
Experiment	*Fovea*	*Parafovea*
1	23.2	23.5
2	35.4	24.2

Event-related Potentials

The sensory-evoked ERP responses elicited by the targets over the posterior cortex are presented in Figure 2 as a function of target location and attention condition; the peak amplitudes of the P1 from electrode sites OL and OR are reported in Table 3 (left). For targets at the parafoveal location, the amplitude of the P1 was larger on cued relative to uncued trials. However, for targets at the foveal location, the amplitude of the P1 did not vary as a function of attention. This was confirmed in a repeated-measures ANOVA on the peak P1 amplitudes from OL and OR, which showed a significant interaction between the target location and attention condition [$F(1,20) = 9.36$, $p < .01$]. The effect of attention at the parafoveal location was sufficiently strong to drive an overall main effect of attention in the P1 [$F(1,20) = 8.50$, $p < .01$]. Additionally, the overall amplitude of the P1 was larger for targets at the parafoveal location [$F(1,20) = 17.09, p < .001$].[1] In sum, these data indicate that there was an effect of attention on the P1 elicited by parafoveal but not foveal targets.

Discussion

The results from Experiment 1 show a dissociation in how attention modulated the early sensory-evoked response to targets as a function of their retinotopic location. For targets presented in the parafovea, the amplitude of the P1 was larger for cued relative to uncued targets, the ERP signature of attention-related increases in visual sensory gain (e.g., Luck et al., 1994; Mangun & Hillyard, 1991; Van Voorhis & Hillyard, 1977). In contrast, the P1 elicited by foveal targets showed no evidence of increased sensory gain. This dissociation in the P1 effect occurred even though manual responses were quicker and more accurate when the target's location was cued relative to uncued,

Figure 2. P1 responses to targets in Experiment 1. The P1 and N1 components are highlighted in the lower right-hand plot in each figure, and all waveforms are displayed relative to a baseline of −200 to 0 msec prestimulus. Shown are the waveforms from posterior electrode sites for (A) parafoveal and (B) foveal targets. Statistical results for these data are summarized in Table 5.

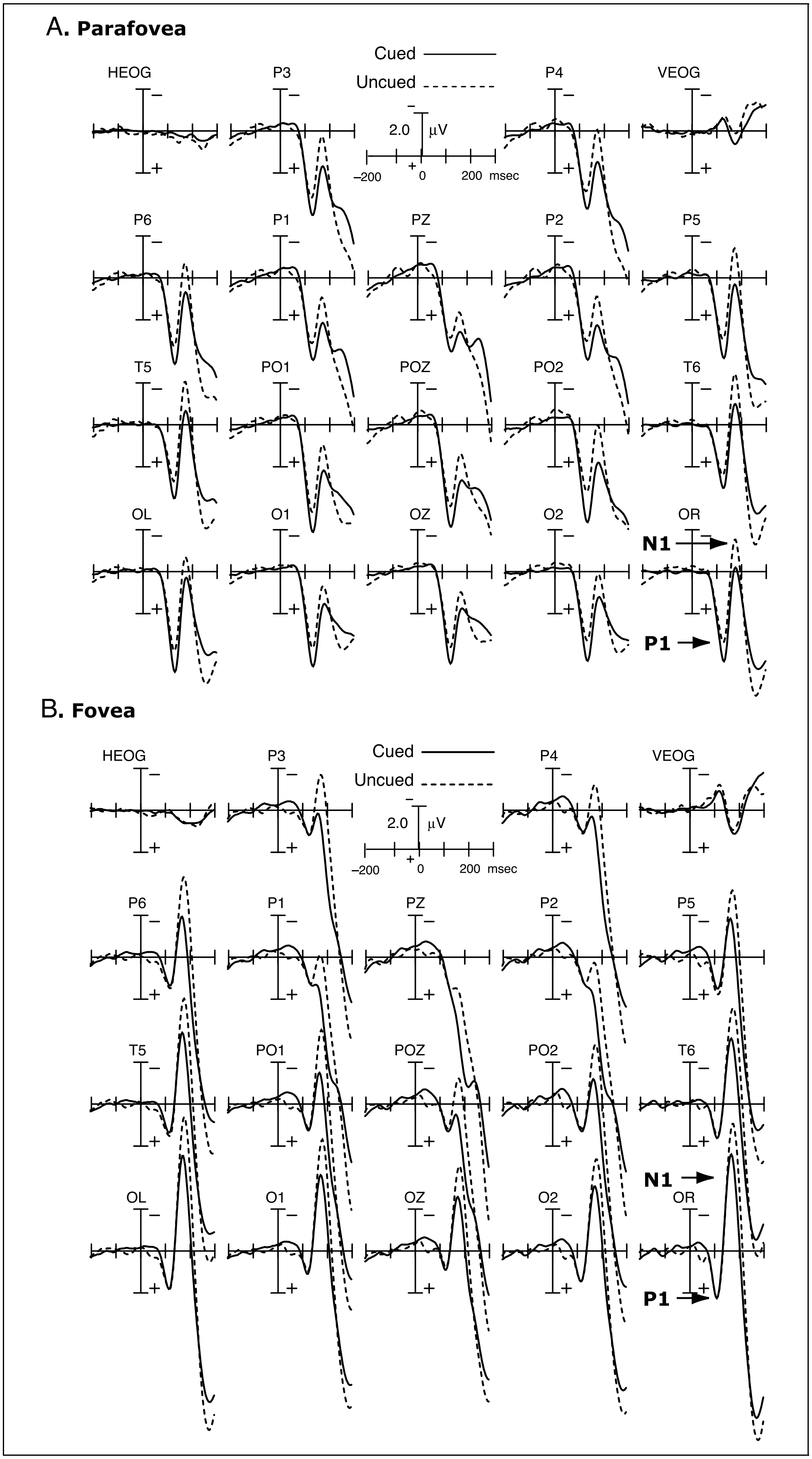

Table 3. Peak Amplitudes of the Lateral Occipital P1 Component (μV) for Experiments 1 and 2, as a Function of Target Location, Attention Condition, and Scalp Electrode Location, Averaged across Participants

		Experiment 1		*Experiment 2*	
Electrode	*Attention*	*Fovea*	*Parafovea*	*Fovea*	*Parafovea*
OL	Cued	1.86 (0.39)	4.86 (0.57)	1.74 (0.64)	4.47 (1.17)
	Uncued	1.95 (0.45)	3.92 (0.61)	2.26 (0.77)	3.82 (1.12)
OR	Cued	2.33 (0.43)	4.27 (0.52)	1.73 (0.83)	4.46 (1.17)
	Uncued	2.29 (0.45)	3.47 (0.51)	1.79 (0.67)	3.51 (1.03)

Standard errors are in parentheses.

a behavioral pattern suggesting that participants had indeed oriented their spatial attention to the cued location independent of whether it was foveal or parafoveal. This finding is thus consistent with the hypothesis that attention-related sensory gain control may in fact operate differentially between parafoveal and foveal visual processing.

However, an alternative explanation may be that, due to the use of white targets and masks presented against a black background, the lack of a P1 attention effect for foveal targets may have been related instead to high luminance contrast. In particular, single-unit recordings in area V4 of the monkey cortex has shown that covert visual attention produces greater increases in stimulus-evoked excitability under conditions of lower relative to higher stimulus contrast (Reynolds, Pasternak, & Desimone, 2000). Given that the P1 likely indexes sensory-evoked processing in the V4 region of the human cortex (e.g., Woldorff et al., 1997; Heinze et al., 1994), the absence of a P1 attention effect at the fovea in Experiment 1 may be attributable to the use of high-contrast stimuli rather than an inability of attention to modulate foveal sensory gain. In other words, the high luminance contrast may have maximally stimulated the P1-generating cortical tissue, and as a result, attention was unable to increase P1 amplitude due to response saturation. To examine this possibility, we thus conducted a second experiment that replicated the basic design of our initial experiment while reducing the relative contrast of the target stimuli.

Experiment 2

In our initial experiment, the target and the mask had a luminance value of approximately 59.50 cd/m^2. These stimuli were presented on a black background with a luminance value of approximately 0.02 cd/m^2, providing a contrast ratio of 2975. The goal of Experiment 2 was to determine whether the absence of attention-related modulations in the P1 amplitude elicited by foveal targets was due to these high-contrast stimuli. Accordingly, Experiment 2 replicated the same basic design of Experiment, but—to reduce contrast—the targets and masks were presented in dark gray, with a luminance value of approximately 0.28 cd/m^2 and a contrast ratio of 14. In question was whether foveal targets would now show an effect of attention on P1 amplitude using lower contrast stimuli.

Fifteen right-handed volunteers participated (7 women, 8 men, age 18–26 years). Out of these 15, the data from three were excluded from analyses due to large (>1°) systematic eye movements in response to the visual cues, and the data from two more participants were excluded after it was identified that they were contributing a disproportionately large amount of variance to the prestimulus ERP baselines. The results reported below are for the remaining 10 participants. All methods, procedures, and analyses were identical to Experiment 1, with two exceptions. First, all stimuli—including cues, targets, and masks—were presented at a reduced contrast level, as described above. Second, the spatial cue was changed to a bilateral pair of arrowheads (0.20° × 0.20°) presented approximately 0.5° on either side of fixation along the horizontal meridian (i.e., just distal to the foveal location of the target/mask complex); the foveal location was cued by having the arrowheads point inward, and the parafoveal location was cued by having the arrowheads point upwards. Although ERP data analyses were restricted to trials without eye movement artifacts, this change in cueing configuration was designed to minimize the number of trials inducing cue-related movements, relative to placing a single cue above fixation as in Experiment 1.

Behavior

RT and d' data are reported in Table 1 (bottom) as a function of target location and attention condition; mean durations for foveal and parafoveal targets are reported in Table 2 (bottom). Although overall RTs were faster for parafoveal relative to foveal targets [$F(1,9) = 18.30$, $p < .005$], there was again an overall main effect of cueing on RT [$F(1,9) = 27.48$, $p < .0005$] that did not

interact with target location [$F(1,9) = 0.39$]. For accuracy, overall d' values were significantly higher for parafoveal relative to foveal targets [$F(1,9) = 31.00$, $p < .0005$],[2] but although d' values were greater for cued relative to uncued targets only at the parafovea, the Cue × Location interaction did not reach statistical significance [$F(1,9) = 2.39$]; in addition, there was no main effect of cueing [$F(1,9) = 1.83$]. Although the RT data thus support the conclusion that participants were orienting their attention to the location of the spatial cue, the d' data indicate that there was no attention-related facilitation in discrimination accuracy under conditions of reduced stimulus contrast.

Event-related Potentials

The sensory-evoked ERP responses elicited by the targets over the posterior cortex are presented in Figure 3 as a function of target location and attention condition; the peak amplitudes of the P1 from electrode sites OL and OR are reported in Table 3 (right). As in Experiment 1, there was an interaction between the target location and the cue condition [$F(1,9) = 8.32, p < .05$]. For targets at the parafoveal location, the amplitude of the P1 was larger on cued relative to uncued trials, whereas for targets at the foveal location, the amplitude of the P1 did not appear to vary as a function of attention. There was also a main effect of target location on overall P1 amplitude [$F(1,9) = 10.58, p < .01$], with the amplitude larger for parafoveal versus foveal targets (see footnote 1). Supporting our assumption that contrast was in fact lowered, the latency of the P1 peak at OL and OR was later in all cue–target conditions in Experiment 2 relative to Experiment 1, as reported in Table 4—a shift in P1 latency that is characteristic of decreased stimulus luminance (e.g., Wijers, Lange, Mulder, & Mulder, 1997).

Discussion

Experiment 2 was predicated on reducing the luminance contrast of the target/mask stimuli, relative to the contrast values used in Experiment 1. Despite this change in target/mask luminance, the results from Experiment 2 again showed no attention-related facilitation in the amplitude of the P1 ERP component elicited by foveal targets. This suggested that the absence of a P1 attention effect for foveal targets in Experiment 1 was not simply an artifact of using high-contrast stimuli—stimuli which can saturate any attention-related changes in the stimulus-evoked excitability of extrastriate cortical responses (Reynolds et al., 2000). Instead, the ERP data were again consistent with the possibility that attention-related sensory gain control may operate differentially between foveal and parafoveal visual processing.

Towards strengthening the basis for this proposal, we wanted to address several additional control issues. First, given that the data pattern involved interpreting a null result in the foveal P1 data, we wanted to eliminate the possibility that perhaps the foveal ERPs in our paradigm remained insensitive to *any* effects of attentional orienting. Accordingly, we examined the midline parietal P300 ERP component elicited by foveal targets in both Experiments 1 and 2. Not only is this component sensitive to stimulus expectancies, such that the amplitude is larger for unexpected relative to expected stimuli (e.g., Coles & Rugg, 1995), an increased P300 for infrequent/unexpected targets at the fovea has previously been observed (Miniussi et al., 2002). As shown in Figure 4, the P300 amplitude was larger for uncued relative to cued targets in both Experiment 1 [$F(1,21) = 30.81, p < .0001$] and Experiment 2 [$F(1,9) = 9.46$, $p < .05$], based on a peak amplitude measure relative to a −200 to 0 msec prestimulus baseline. This analysis indicated that not only were location expectancies being generated by the cueing condition, but that we could not attribute the null P1 result for foveal targets to a general insensitivity of our foveal ERPs to transient attentional states.

Second, although artifact rejection was used to remove trials from the ERP averages that contained large eye movements, we wanted to examine the magnitude of any residual differences in eye position between foveal and parafoveal cueing conditions. At issue was whether the P1 attention effects for parafoveal stimuli might be explained by a tendency to shift gaze upward in response to the parafoveal, but not foveal, cues. Accordingly, we examined the EOGs time-locked to cue onset as a function of cue condition for both Experiment 1 (Figure 5A) and Experiment 2 (Figure 5B). These data revealed that any cue-related differences in vertical EOG (VEOG) amplitude in the cue–target interval in both experiments were at most 1 μV or less. Importantly, EOG channels will often include signal components having cortical origins, and thus, this small difference in the VEOG might not reflect a true shift in eye position. Nevertheless, we performed a control experiment (with four participants, including one of the authors) to determine the eye movement equivalent of 1 μV on our recording system, should the VEOG differences in the cue–target interval in fact be due to small shifts in eye position. In response to a target presented above the vertical midline (randomly varied between 1°, 2°, 3°, or 4° above), participants moved their eyes from the central fixation point to the target's location until target offset, when gaze was moved back to the fixation point. These data revealed that a 1° eye movement was associated with a VEOG amplitude of approximately 4 μV (Figure 5C), suggesting that any residual effects of cue type on eye position would be on the order of at most 0.25°——a difference not likely to explain the P1 data pattern reported here. Indeed, the small VEOG difference in Experiment 2 only began to emerge in the target window (800–1000 msec post-

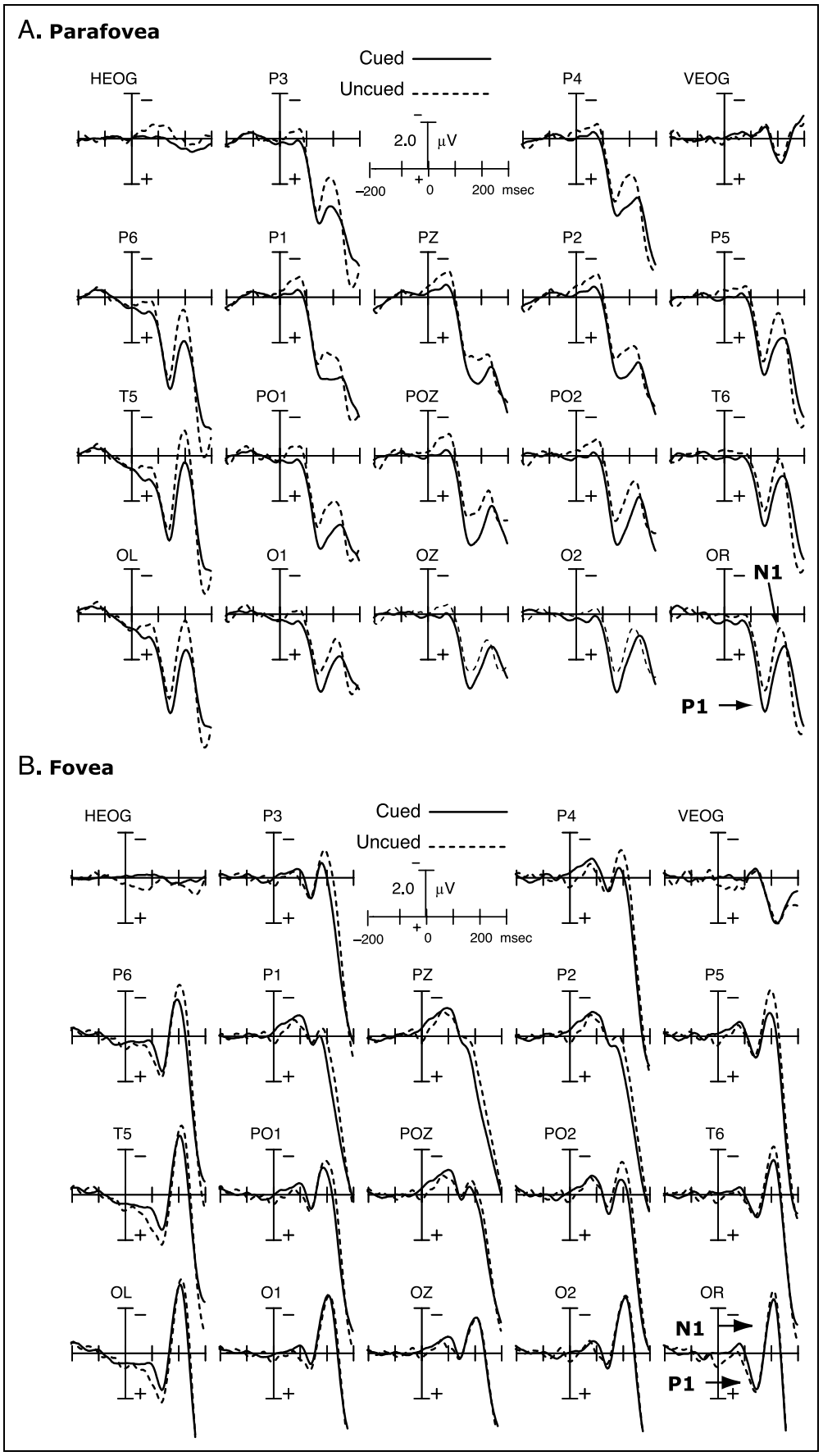

Figure 3. P1 responses to targets in Experiment 2. The P1 component is highlighted in the lower right-hand plot in each figure, and all waveforms are displayed relative to a baseline of −200 to 0 msec prestimulus. Shown are the waveforms from posterior electrode sites for (A) parafoveal and (B) foveal targets. Statistical results for these data are summarized in Table 5.

Table 4. Latencies of Peak Amplitudes of the Lateral Occipital P1 Component (msec) for Experiments 1 and 2, as a Function of Target Location, Attention Condition, and Scalp Electrode Location, Averaged across Participants

		Experiment 1		*Experiment 2*	
Electrode	*Attention*	*Fovea*	*Parafovea*	*Fovea*	*Parafovea*
OL	Cued	113	128	136	144
	Uncued	117	124	132	140
OR	Cued	109	128	144	152
	Uncued	109	124	140	152

cue), indicating that eye positions may not have even differed between cueing conditions at the time of target presentations.

Third, analysis of P1 amplitude was restricted a priori to lateral occipital scalp electrode sites OL and OR. However, given the interaction we found between target location and attention, we wanted to examine the broader sensory-evoked ERP responses in our data in order to determine whether this interaction extended beyond (1) these scalp sites and (2) the P1 latency range. For the data within each experiment, we thus performed additional ANOVAs on the peak N1 amplitudes at OL/OR and on both the P1 and N1 peak amplitudes at each neighboring bilaterally symmetric electrode pair (O1/O2, PO1/PO2, P5/P6, and T5/T6) that had factors of target location (fovea vs. parafovea) and attention condition (cued vs. uncued). The results of these statistical tests are reported in Table 5. For the P1, a significant Location × Attention interaction extended to all of the electrode pairs examined from Experiment 1, and to the more posterior electrode pairs in Experiment 2 (O1/O2 and PO1/PO2). This indicates that the spatial extent of the interaction was not limited to OL/OR, and further, discounts the possibility that the interaction was simply driven by random noise at those electrode sites. On the other hand, no significant interaction was observed in the N1 at any electrode pair in either experiment. Instead, the N1 showed a significantly larger peak amplitude in the unattended relative to attended condition in all comparisons. Interestingly, this pattern in the N1 mirrors previous ERP data also showing an increased N1 amplitude for midline parafoveal stimuli under conditions of focused attention at fixation (Handy, Soltani, et al., 2001), yet why the N1 for midline stimuli may paradoxically increase with less attention remains an open question.

Finally, although the P1 data were the central focus of our study, the pattern of behavioral results obtained in the two experiments warrants consideration as well. In particular, the reduction in stimulus contrast in Experiment 2 relative to Experiment 1 produced two notable

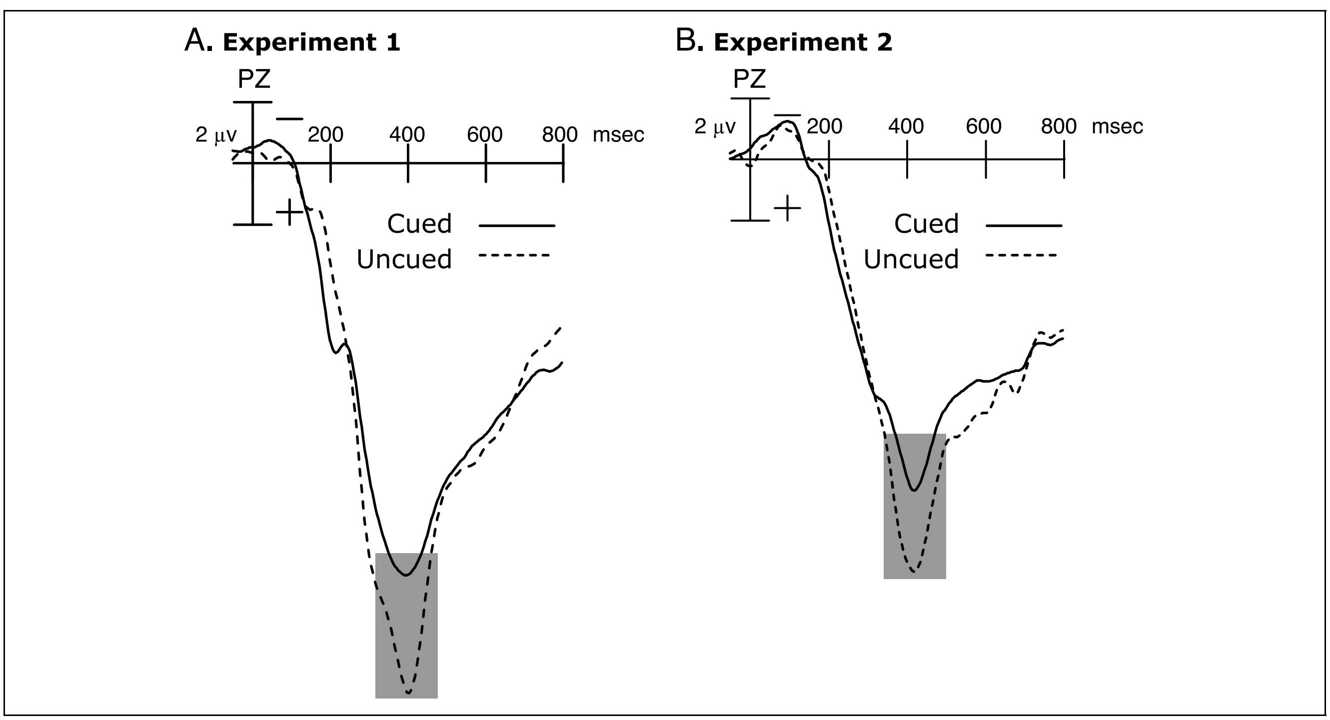

Figure 4. The midline parietal P300 component elicited by targets. The P300 is shown shaded in gray at midline parietal electrode site PZ, and all waveforms are displayed relative to a baseline of −200 to 0 msec prestimulus. These data demonstrate that despite null P1 attention effects for foveal targets, the P300 showed an increase in amplitude for uncued targets at the fovea in both Experiments 1 (left) and 2 (right). This indicates that the null P1 result for foveal targets was not simply due to an insensitivity of foveal ERPs to the attentional manipulation. Further, it confirms that participants were in fact generating expectancies about the pending target location.

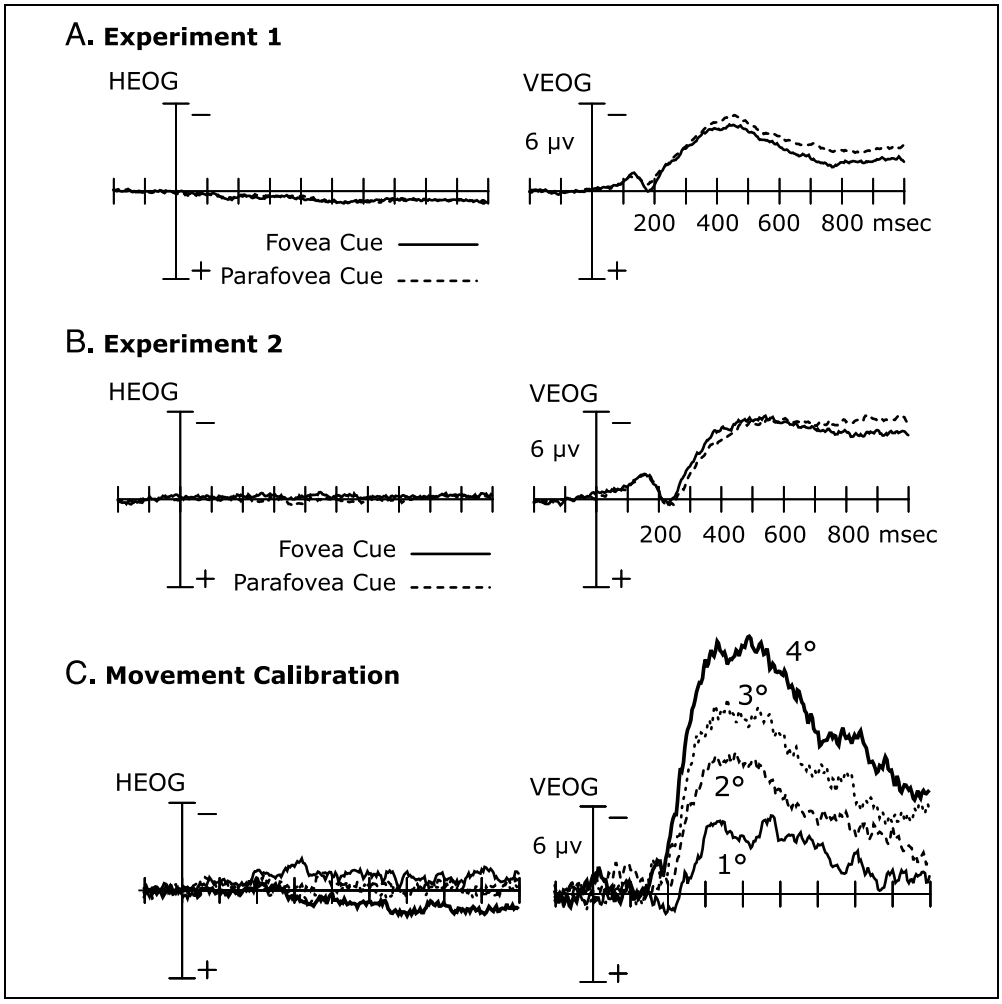

Figure 5. EOGs generated in response to the spatial cues. Data from both Experiment 1 (A) and Experiment 2 (B) show evidence consistent with a small (~1.0 μV) deviation in eye position for foveal versus parafoveal targets. Calibrations showing the translation of microvolts into degrees of eye movement (C) suggest that eye positions differed by no more than 0.25°, on average, between cueing conditions.

changes in behavioral performance. First, decreased stimulus contrast led to an overall RT advantage for parafoveal targets. This effect of target location on RTs—with RTs to parafoveal targets faster than RTs to foveal targets—parallels recent psychophysical data showing that processing speeds increase with the retinal eccentricity of the given stimulus (e.g., Carrasco, McElree, Denisova, & Giordano, 2003). If so, our data raise the possibility that the effect of retinotopic location on processing speeds may interact with stimulus contrast, such that eccentricity advantages may only emerge at lower luminance contrasts. Second, the reduction in contrast for targets and masks also eliminated attention-related facilitation in discrimination accuracy but not RT. Beyond demonstrating a potentially important dissociation in RT versus d' measures of foveal stimulus processing, the systematic accuracy advantage for parafoveal over foveal targets is consistent with the proposal that attention may impair foveal processing under stimulus conditions having high spatial resolution (e.g., Yeshrun & Carrasco, 1998). Again, however, our collective findings indicate that luminance contrast may play a critical role in determining the magnitude of these impairments.

GENERAL DISCUSSION

In two experiments we found that focused spatial attention to the parafoveal location of a visual target increased the amplitude of the lateral occipital P1 ERP component it elicited. In contrast, focused spatial attention appeared to have little, if any, effect on the amplitude of the P1 elicited by targets presented at fixation. That is, conditions sufficient for modulating sensory gain in the parafovea were insufficient for producing a similar effect at the fovea. This difference between retinotopic locations could not be attributed to a saturated ERP response at the fovea under high-contrast stimulus conditions, nor did it reflect a more generalized inability of attention to modulate the ERPs associated with foveated stimuli. Rather, our results support the hypothesis that sensory gain control may not operate homogenously across the visual field. Instead, it appears that the functional uses of gain

Table 5. Statistical Results for P1 and N1 at OL and OR and their Neighboring Bilateral Electrode Pairs

		Experiment 1			*Experiment 2*		
Peak	*Electrodes*	*Loc*	*Attn*	*L × A*	*Loc*	*Attn*	*L × A*
P1	OL/OR	.001	.01	.01	.01	–	.05
	O1/O2	.0001	.05	.01	.01	.05	.05
	P01/P02	.0001	.005	.05	.001	.05	.05
	T5/T6	.001	.05	.05	.05	–	–
	P5/P6	.0001	–	.01	.0005	–	–
N1	OL/OR	.005	.0005	–	.05	–	–
	O1/O2	.0001	.0005	–	.01	–	–
	P01/P02	.005	.0001	–	.005	–	–
	T5/T6	.0001	.0005	–	.05	.05	–
	P5/P6	.005	.0001	–	.005	.05	–

Reported are $p <$ values .05 and lower, with $F(1,20)$ for Experiment 1, and $F(1,9)$ for Experiment 2, based on peak amplitude measures.

Loc/L = target location; Attn/A = attention condition.

control—and the strategic conditions under which it may arise—will systematically vary with the retinotopic location involved. In the following sections, we consider this proposal in light of the neurophysiology underlying retinogeniculate projections to cortex, and how this neurophysiology may relate functionally to the data pattern reported here.

Retinocortical Neurophysiology

Previous comparisons of foveal and peripheral visual ERPs have discussed differences in the ERP responses as reflecting processing dominated by retinocortical and retinotectal pathways, respectively (e.g., Neville & Lawson, 1987a). However, the retinocortical pathway alone shows a clear differentiation in the neurophysiology associated with foveal versus parafoveal input (e.g., Schneider, Richter, & Kastner, 2004). Beginning with the spatial distribution of ganglion cells across the retina, the arrangement of retinogeniculate projections to the cortex suggests that the nature of visual representations will qualitatively vary with the retinotopic origins of the given input. Although Pβ ganglion cells in the retinae dominate at the fovea, there is a decrease in the ratio of Pβ to Pα ganglion cells with increasing retinal eccentricity (e.g., Azzopardi, Jones, & Cowey, 1999; Drasdo, 1989; Wässle, Grünert, Röhrenbeck, & Boycott, 1989). Because Pβ and Pα ganglion cells give rise to the parvocellular (P) and magnocellular (M) pathways, respectively, there is thus an asymmetry favoring greater P output from the fovea relative to the parafovea that is further magnified in geniculostriate projections (e.g., Azzopardi et al., 1999). As a consequence, not only is the fovea overrepresented in visuocortical processing, but it has a high degree of spatial resolution that is paired with neurons having relatively low contrast sensitivity and slow, sustained stimulus responses. In comparison, the parafovea has a lower degree of spatial resolution, but relatively high contrast sensitivity and fast, transient stimulus responses (see e.g., Shapley, 1995; Livingstone & Hubel, 1987). Thus, as a stimulus is presented with greater eccentricity on the retina, the neural representation of that stimulus will be increasingly shaped by the response properties of the M pathway, relative to the P pathway.

Given this systematic relationship between retinal eccentricity and P versus M pathway coding, the retinotopic location of a stimulus will also dictate where that stimulus representation is ultimately projected in cortex. In the cortico-cortical projections extending beyond the V2/V3/V4 complex, the output into posterior parietal and visuomotor cortex is dominated by information originating in the M pathway, whereas the output into inferior temporal (IT) cortex is dominated by information originating in the P pathway (e.g., Baizer, Ungerleider, & Desimone, 1991; Morel & Bullier, 1990). To be sure, significant cross-talk certainly exists between these projection streams (e.g., Milner & Goodale, 1995; Van Essen & DeYoe, 1995; Zeki, 1993). However, the relative biases towards M and P input into the posterior parietal and IT cortices, respectively, indicate that the retinal eccentricity of a stimulus directly shapes its visual representation in the retinocortical pathway in at least two ways: (1) the initial coding of that representation within the M relative to P pathway as discussed above, and (2) by the ultimate strength of projection of that representation to dorsal relative to ventral visuocortical areas.

Functional Consequences

Considering these differences in the neurophysiology underlying foveal versus parafoveal input into cortex, it is perhaps not surprising to find evidence suggesting that at least some aspects of visual attention may vary with retinal eccentricity. For example, if sensory gain control serves to improve the acuity of visual perception (e.g., Hillyard et al., 1999; Luck et al., 1994), increases in gain at the fovea would seem superfluous in the face of neurophysiology that already provides a relatively fine degree of spatial resolution and a bias towards projection to object perception areas in IT cortex. Conversely, with relatively coarse spatial resolution in the parafovea, increases in gain would help improve the acuity of percepts arising in these locations. At the same time, with a comparatively sparser density of projections to the IT cortex, increased gain for parafoveal stimuli may also facilitate the degree to which those representations are analyzed in IT cortex. Such a

possibility is not only consistent with the notion of ''sensory gating'' as a mechanism of attentional selection in visual cortex (e.g., Eimer, 1993; Mangun & Hillyard, 1991), but it would raise the possibility that gating may include a direct modulatory influence on the moment-to-moment degree of functional interactions between dorsal and ventral visual pathways (e.g., Milner & Goodale, 1995; Van Essen & DeYoe, 1995; Zeki, 1993).

Although gain control has long been linked to facilitatory effects on visual perception, perhaps the more important point to consider here is whether gain control may also have functional consequences in the visuomotor domain. In particular, covert visual attention has close ties with oculomotor programming, where the orienting of attention to a nonfoveated location occurs prior to an eye movement to that location (e.g., Rizzolatti, Riggio, & Sheliga, 1994; Rizzolatti, Riggio, Dascola, & Umiltá, 1987). Indeed, not only is a saccade, by definition, made to a parafoveal location, but researchers have recognized that the parafovea is overrepresented in the retinocollicular projections into parietal cortex that mediate visual orienting functions (e.g., Neville & Lawson, 1987a). However, the relationship between covert attention and motor processing appears to extend beyond the oculomotor domain. Not only has recent ERP evidence shown that visual sensory gain increases at the location of a parafoveal object implicitly recognized as graspable (Handy, Grafton, Shroff, Ketay, & Gazzaniga, 2003), but covertly attending to the location of a graspable object has a direct modulatory influence on the implicit visuomotor response generated by that object (Handy, Schaich Borg, et al., 2005). In challenging the canonical view of sensory gain as a purely perception-related mechanism, the notion here is that whereas visual perception is typically best served by foveating an object of interest rather than covertly attending to its location, reaching and grasping movements are frequently made to objects falling outside of central vision.

Conclusions

Importantly, the implications of our results extend beyond just questions of sensory gain per se. In particular, that objects in the visual world compete for our attention has emerged as a dominant theory of visuocortical processing over the last decade (e.g., Kastner & Ungerleider, 2001; Duncan, Humphreys, & Ward, 1997; Desimone & Duncan, 1995). According to this view, attention can be biased towards some objects relative to others on the basis of factors both bottom-up (or exogenous) and top-down (or endogenous) in nature. For example, multiple objects presented simultaneously to an observer will automatically inhibit each other's representations in the cortex, yet if attention is selectively oriented to one of the objects in view, it will serve to counteract any of these competitive, suppressive effects directed towards that object (Kastner, De Weerd, Desimone, & Ungerleider, 1998). Placed within this broader theoretical context, what our data suggest is that retinotopic location itself may be a critical factor influencing the competitive interactions between objects. Not only is this possibility consistent with the functional and neurophysiological differences in foveal versus parafoveal processing investigated here, but it also speaks to known visual field asymmetries in object–attention interactions. For instance, a tool—when presented in a bilateral display with a nontool object in the opposite lateral hemifield—can automatically draw attention to its location when in the right visual field location of the bilateral display, but not when in the left visual field location (Handy, Grafton, et al., 2003). The implication arising from such data is that we may need to consider retinotopic variance in visuocortical neurophysiology as an additional factor mediating the competitive interactions between objects—and a factor not necessarily encapsulated within the traditional dichotomy of bottom-up versus top-down effects in visual selective processing.

In closing, our findings do not come without several caveats to consider as well. First, although we have emphasized differences in attention effects between the fovea and the parafovea, there certainly may be aspects of attention that remain relatively homogenous across visual locations. For example, the consistent cueing effects in RT at both target locations suggest the possibility of a common attentional influence that was unaffected by differences in sensory gain. Second, it remains possible that changes in foveal gain may be induced under appropriate strategic conditions. For instance, although foveal neurophysiology suggests that there may be no need to increase gain at the fovea, perhaps gain can be *decreased* centrally if stimulus and task parameters so warrant. Finally, we recognize that under many classification schemes, our ''parafoveal'' location would still fall under the label of ''central'' rather than ''peripheral'' retina. Nevertheless, not only does the retinal mosaic—and Pβ cells in particular—show significant changes in density within several degrees of the fovea (e.g., Dacey, 1993; Drasdo, 1989), our data indicate that a distance of this magnitude is sufficient to produce considerable differences between foveal and ''parafoveal'' vision, in terms of their interactions with attention. Indeed, it may be of interest for future investigations to systematically correlate retinotopic changes in sensory gain across the foveal/parafoveal region with corresponding changes in known retinotopic neurophysiology. Given such possibilities, the data reported here highlight that it may no longer be valid to consider the strategic functions of visual attention independent of the retinotopic location involved.

METHODS

Stimuli and Procedures

All stimuli were presented on a VGA monitor controlled by a Pentium PC using the VAPP stimulus presentation system (http://nilab.psychiatry.ubc.ca/vapp/). The sequence and timing of each trial type (foveal or parafoveal target) is presented in Figure 1. The arrow used for the spatial cue was 0.5° in length and was presented 0.75° to center above fixation. The target letters were 0.85° in width and 1.0° in height; the mask had equivalent dimensions, and consisted of an array of randomly oriented lines. For foveal targets, the target and the mask were centered on the fixation point. For parafoveal targets, the target and the mask were presented 2.2° to center above fixation on the vertical meridian. All stimuli were in white (59.5 cd/m^2), presented on a black background (0.02 cd/m^2).

Each participant performed 10 blocks of 80 trials. Within each trial block, there were 32 validly cued targets in each of the two target locations (i.e., the cue predicted the correct target location), and 8 invalidly cued targets in each of the two target locations (i.e., the cue incorrectly predicted the target location). Within each of these conditions, there were equal numbers of the two target types (''A'' or ''H''), and the order of trials within each block was randomized. Participants were instructed to maintain fixation on each trial while orienting their attention to the location indicated by the spatial cue prior to the arrival of the target. In order to ensure response accuracy was above chance but below ceiling at each target location, response accuracy at each location was monitored on-line during each block. Between-blocks, the ratio of the target duration and the mask duration (i.e., the target signal-to-noise ratio) was varied as necessary between 51/51 msec, 34/68 msec, and 17/85 msec within each target location—or 3, 2, or 1 screen cycles showing the target, with rounding up—in order to maintain the participant's performance near 0.75% correct (see Handy & Mangun, 2000). In this manner, the duration of the target/mask complex always remained 102 msec, but depending on individual performance, the ratio could be different for foveal relative to parafoveal targets. For each experiment, the mean target durations across subjects reported in Table 2 were based on first computing the average target duration across runs within each subject for each of the two target locations.

At the beginning of the experiment, each participant was given one letter as the ''go'' target and one letter as the ''no-go'' target, with the order counterbalanced between participants. As such, participants made a button press (with a thumb, counterbalanced between participants) only when they discriminated their specific target letter. The hit rate for calculating d' was thus defined as the ratio of ''target present'' responses relative to the total number of ''go'' trials, and the false alarm rate was defined as the ratio of ''target present'' responses relative to the total number of ''no-go'' trials, averaged across all trial blocks for that participant (and after trials were removed for eye movement artifacts; see below). The reported RTs are for correct target responses only, whereas the reported ERPs are averaged across both ''go'' and ''no-go'' trials in each of the cue and target conditions (see below).

Electrophysiological Recording

Scalp potentials were recorded from 17 tin electrodes in posterior scalp locations mounted in a custom elastic cap: standard sites O1, O2, OZ, T5, T6, P1, P2, P3, P4, P5, P6, and PZ, along with PO1, PO2, and POZ (midway between O1/O2/OZ and P1/P2/PZ), OL and OR (midway between O1/O2 and T5/T6); an additional channel recorded potentials from the right mastoid. All electroencephalographic (EEG) activity was recorded relative to the left mastoid, amplified (Grass Instruments, Model 12 Neurodata Acquisition System) with a band pass of 0.1–30 Hz (1/2 amplitude cutoffs), and digitized on-line at a sampling rate of 256 samples-per-second. To ensure proper eye fixation, vertical and horizontal electrooculograms (EOGs) were also recorded, the vertical EOG from an electrode inferior to the right eye, and the horizontal EOG from an electrode on the right outer canthus. All electrode impedances were kept below 5 kΩ. Off-line, computerized artifact rejection was used to eliminate trials during which detectable eye movements (>1°), blinks, muscle potentials, or amplifier blocking occurred. For each subject, ERPs were averaged into 3000-msec epochs, beginning 1500 msec before stimulus onset. Subsequently, all ERPs were algebraically rereferenced to the average of the left and right mastoid signals, and filtered with a low-pass Gaussian filter (25.6 Hz half-amplitude cutoff) to eliminate high-frequency artifacts in the waveforms (for details on average number of trials rejected per condition, see below).

Because half of the target trials were from ''go'' trials (and thus included a manual response following the target) and the other half of the target trials were from ''no-go'' trials (and thus did not have a manual response following the target), we wanted to confirm that there was no apparent effect of trial type on the amplitude of the P1 prior to collapsing the ERP averages across trial types within each cue–target condition for the main statistical analyses. For each experiment, a separate ANOVA was performed within each cue–target condition (cued foveal target, uncued foveal target, cued parafoveal target, and uncued parafoveal target) and lateral occipito-temporal electrode pair (O1 and O2, OL and OR, T5 and T6, PO1 and PO2, and P5 and P6) that directly compared the effect of trial type (go vs. no-go target) on the P1 elicited by the target; no significant main effect of trial type or interaction between trial type

and electrode site (left vs. right hemisphere electrode) was found in any of the comparisons. For each experiment, the waveforms for ''go'' and ''no-go'' trials were thus collapsed for each subject within each cue–target condition, and the resulting ERPs were then used to derive the grand-averaged waveforms for main analysis and display. In Experiment 1, the average number of trials per subject in each collapsed cue–target condition were: 300.8 (out of 320 possible) for cued foveal targets, 75.8 (out of 80 possible) for uncued foveal targets, 297.9 for cued parafoveal targets, and 75.1 for uncued parafoveal targets. In Experiment 2, the average number of trials were: 307.2 for cued foveal targets, 75.9 for uncued foveal targets, 306.3 for cued parafoveal targets, and 75.6 for uncued parafoveal targets.

Statistical analysis of the ERP data was based on peak amplitude measures (relative to a −200 to 0 msec prestimulus baseline) taken at lateral occipital scalp sites OL and OR, the scalp locations where the P1 has previously been shown to be maximal (e.g., Mangun & Hillyard, 1991) and where the P1 was indeed maximal in both experiments. The latency of the peak of the P1 was first identified in the grand-averaged waveform for each electrode (OL and OR) and condition of interest. For the data points entered into the ANOVA, the amplitudes of the single-subject waveforms were then measured within each electrode and condition at the corresponding peak latency identified in the grand-averaged waveform (see Handy, 2005).

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Notes

1. Given that the fovea is overrepresented in the visual cortex, it may appear surprising that P1 amplitudes were larger for parafoveal relative to foveal stimuli—a main effect of target location that was replicated in Experiment 2. However, the amplitude of an ERP component recorded at the scalp surface does not simply depend on the volume or mass of tissue responding to that stimulus. Rather, the critical factors determining amplitude are (1) the extent to which the stimulated tissue generates a far-field potential that can be measured at a remote scalp location (e.g., Martin, 1991) and (2) the orientation of the generator of that far-field potential relative to the scalp site of recording (e.g., Clark, Fan, & Hillyard, 1995; Mangun et al., 1993). Given that both the neurophysiology of the tissue involved and the location of the ERP generator in the cortex varied between foveal and parafoveal locations in our experiments, either or both factors may be contributing to the retinotopic differences in P1 amplitude reported here. At the same time, Neville and Lawson (1987a) also present ERP data consistent with a reduced P1 amplitude for foveal relative to peripheral stimuli, suggesting that this P1 data pattern is not idiosyncratic to the current paradigm and stimuli.

2. Although we attempted to equate each participants' accuracy performance between foveal and parafoveal target locations, accuracy was nevertheless higher for parafoveal targets. This result was likely due to a number of participants still performing near-ceiling for parafoveal targets at the shortest target duration possible with our video display (17 msec). Importantly, however, central to our findings is that despite greater perceptual difficulty at the fovea, there was no corresponding increase in sensory gain to help aid performance.

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