

SENSORY GAIN CONTROL AT FIXATION

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by

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TABLE OF CONTENTS

| | Page |
|---|------|
| ACKNOWLEDGEMENTS | iii |
| LIST OF TABLES | vi |
| LIST OF FIGURES | vii |
| LIST OF SYMBOLS AND ABBREVIATIONS | viii |
| SUMMARY | ix |
| <u>CHAPTER</u> | |
| 1 Introduction | 1 |
| 1.1 Sensory Gain | 1 |
| 1.1.1 ERP Evidence | 3 |
| 1.2 Neural Bases of Sensory Gain | 4 |
| 1.2.1 Imaging Studies | 4 |
| 1.2.2 Animal Physiology | 6 |
| 1.2.3 N1 ERP Component | 6 |
| 1.3 Study Overview | 8 |
| 1.3.1 Perceptual Load | 8 |
| 1.3.2 Sensory Gain in the Periphery and at Fixation | 9 |
| 1.3.3 Current Study | 10 |
| 2 Method | 12 |
| 2.1 Participants | 12 |
| 2.2 Stimuli | 12 |
| 2.3 Procedure | 14 |
| 2.4 Electrophysiological Recording | 16 |

| | |
|---|----|
| 2.5 Statistical Analysis | 17 |
| 3 Results & Discussion: Behavior | 18 |
| 3.1 Results | 18 |
| 3.2 Discussion | 19 |
| 4 Results & Discussion: P1 | 20 |
| 4.1 P1 Results | 20 |
| 4.2 P1 Discussion | 23 |
| 4.2.1 Foveal Stimuli | 23 |
| 4.2.2 Extrafoveal Stimuli | 24 |
| 5 Results & Discussion: N1 | 27 |
| 5.1 N1 Results | 27 |
| 5.2 N1 Discussion | 28 |
| 5.2.1 Perceptual Load Validation | 28 |
| 5.2.2 Discrimination | 28 |
| 5.2.3 Early Visual Processing | 28 |
| 6 General Discussion | 31 |
| 6.1 Main Findings and Future Directions | 31 |
| 6.1.1 Foveal Stimuli | 31 |
| 6.1.2 Extrafoveal Stimuli | 31 |
| 6.2 Conclusion | 32 |
| REFERENCES | 34 |

LIST OF TABLES

| | | |
|---------|--|----|
| Table 1 | Accuracy and reaction time data by condition | 18 |
| Table 2 | Paired sample t-test values for changes in P1 amplitude between the high-load and low-load conditions. | 20 |
| Table 3 | Paired sample t-test values for changes in N1 amplitude between the high-load and low-load conditions. | 27 |

LIST OF FIGURES

| | | |
|----------|---|----|
| Figure 1 | This study used a stimulus set consisting of four maximum contrast gabor patches, oriented at four different angles. They were oriented at 1° to the left or right of the vertical axis, and 1° above or below the horizontal axis. These stimuli were paired and divided into 4 block types: the high-load blocks used pairs of stimuli that are separated by 2°, which would be the two near-vertical gabors or the two near-horizontal gabors. The low-load blocks used pairs of 1 near-vertical and 1 near-horizontal stimuli that are separated by 90°. Data analysis was collapsed across load type, meaning that both high-load blocks were averaged together and both low-load blocks were averaged together. This assures that low-level stimulus effects on P1 amplitude remain constant across load manipulation conditions. | 13 |
| Figure 2 | Experimental procedure for a typical trial. Subjects viewed a fixation point for a random intertrial interval of 800-1200 seconds, after which a target stimulus was presented at fixation. The stimulus in the figure has been enlarged for visibility; in the experiment it was presented at 1° (foveal) or 2° (extrafoveal) of visual angle. Following stimulus presentation, the subject made a response by pressing the left or right control key, according to the instructions. | 15 |
| Figure 3 | Grand-average waveforms elicited by foveal stimuli are shown for all seven electrodes of interest. P1 and N1 component peaks are labeled on the PO3 waveform. | 21 |
| Figure 4 | Grand-average waveforms elicited by extrafoveal stimuli are shown for all seven electrodes of interest. P1 and N1 component peaks are labeled on the PO3 waveform. | 22 |

LIST OF SYMBOLS AND ABBREVIATIONS

| | |
|------|---------------------------------------|
| cm | Centimeter |
| CMS | Common Mode Sense |
| DRL | Driven Right Leg |
| EEG | Electroencephalography |
| EOG | Electrooculogram |
| ERP | Event Related Potential |
| fMRI | Functional Magnetic Resonance Imaging |
| ITI | Intertrial Interval |
| LGN | Lateral Geniculate Nucleus |
| ms | Millisecond |
| RT | Reaction Time |
| VEP | Visual Evoked Potential |

SUMMARY

One mechanism by which spatial attention affects visual perception is through the alteration of the signal-to-noise ratio for a particular stimulus. This is known as sensory gain control. Sensory gain effects can be measured electrophysiologically through changes in the amplitude of the P1 event related potential (ERP) component. Manipulating perceptual load by increasing or decreasing task difficulty can influence spatial attention and can therefore modulate the P1 component. Sensory gain effects are well characterized with peripheral attention, but have rarely been studied at fixation. The few studies that have been conducted that look at sensory gain for foveal stimuli have yielded conflicting results, and sensory gain with centrally presented extrafoveal stimuli has only been found in emotion studies. The present study manipulated attention allocation towards foveal and extrafoveal stimuli at fixation, using two levels of perceptual load for each stimulus size. ERPs were recorded in response to stimulus onset, and tested for differences in P1 and N1 amplitude across perceptual load conditions. Sensory gain effects, as indexed by an increase in P1 amplitude with an increase in perceptual load, were predicted for extrafoveal but not foveal stimuli. Changes in P1 amplitude were not found for either type of stimuli, suggesting that sensory gain effects either may not be present at fixation or are not susceptible to manipulation by perceptual load. The N1 component was expected to increase in amplitude for high-load stimuli, due to the N1 attention effect. However, the opposite result was found, suggesting that there is an additional effect of perceptual load on early visual processing, distinct from sensory gain control.

CHAPTER 1

INTRODUCTION

Attending to a stimulus is known to facilitate performance on visual tasks by speeding reaction time to targets at the cued location and slowing reaction time at uncued locations (Posner, Nissen, & Ogden, 1978; Posner, Snyder, & Davidson, 1980). Attention improves an observer's ability to detect stimuli presented near their perceptual threshold (Bashinski & Bacharach, 1980; Hawkins, Hillyard, Luck, Mouloua, Downing, & Woodward, 1990) and to better discriminate differences in specific stimulus features or properties (Downing, 1988). This effect of attention is typically interpreted as support for the theory that visual attention acts as a "spotlight" or "zoom lens" that can be directed at a location in the visual field, where it then enhances processing of a stimulus at that location (Eriksen & St. James, 1986; Posner, 1980). Enhancement of performance for stimuli at the attended location has been attributed to a variety of factors, ranging from facilitation of high-level executive control (Shaw, 1978; Müller & Findlay, 1987; Shiu & Pashler, 1994; Prinzmetal, Nwachuku, Bodanski, Blumenfeld, & Shimizu, 1997) to low-level perceptual enhancement (Bashinski & Bacharach, 1980; Downing, 1988; Lu & Doshier, 1998; Treue, 2001).

1.1 Sensory Gain

Constraints imposed by attentional resource limitations suggest that the benefits of spatial attention are more dynamic, and may not be purely facilitatory as the spotlight analogy may suggest. Instead, the degree of processing for a particular stimulus or region of the visual field increases or decreases along with the amount of attentional resources

allocated to that area (Mangun & Hillyard, 1990). This can happen one of two ways; either visual cortex neurons respond more strongly when attention is directed towards their receptive fields, or the orientation-tuning curve of these neurons is altered. Both forms have similar effects but act on different qualities of the stimulus, and therefore should be considered complimentary and not mutually exclusive. The first effect works by improving the signal-to-noise ratio for a particular stimulus or region of the visual field, and is known as sensory gain control (Hillyard, Vogel, & Luck, 1998). With sensory gain control, the effect of attention on neural response patterns is essentially the same as the effect of directly altering visual properties of the stimulus (Carrasco, Ling, & Read, 2004). The latter effect works by making the neurons more selective, causing more precise coding of the attended stimulus (Haenny & Schiller, 1988; Spitzer, Desimone, & Moran, 1988). This is the effect typically found when looking at orientation tuning curves, which display a cortical cell's average response to a range of orientations. This can in a way be considered a form of sensory gain control as well, specialized for metathetic dimensions such as orientation tuning, which has no absolute maximum or minimum. For the purposes of the present study, however, sensory gain control will refer to the general enhancement of visual stimuli along prothetic dimensions, particularly contrast.

Sensory gain control effects have been found consistently and across a wide variety of attentional and perceptual manipulations. Although attention-dependent sensory gain effects are present in a variety of visual dimensions, such as color saturation (Fuller & Carrasco, 2006), rate of flicker (Montagna & Carrasco, 2006), and acuity (Gobell & Carrasco, 2005), it is most often studied in terms of contrast (McAdams &

Maunsell, 1999; Reynolds, Pasternak, & Desimone, 2000; Di Russo, Spinelli, & Morrone, 2001; Lu, Lesmes, & Doshier, 2002; Martinez-Trujillo & Treue, 2002; Cameron, Tai, & Carrasco, 2002; Carrasco, Ling, & Read, 2004). Evidence for sensory gain control is well established for peripheral attention, but relatively few studies have looked at sensory gain control for stimuli presented at fixation (Zani & Proverbio, 1995) or more specifically at the fovea (Handy & Khoe, 2005; Miniussi, Rao, & Nobre, 2002). Potential variation in sensory control gain effects across the visual field will be discussed in more detail below.

1.1.1 ERP Evidence

Visual sensory gain effects are frequently studied behaviorally in humans, but can also be observed and measured using electroencephalography (EEG) methods. One mechanism for measuring sensory gain control utilizes an early positive component of the event-related potential (ERP), known as the P1 component. The P1 component is generally interpreted as the product of early visual processing and most likely originates from the extrastriate visual cortex, which is thought to be the earliest stage in visual processing stream at which attention can exert a direct effect (Clark & Hillyard, 1996; Luck, Heinze, Mangun, & Hillyard, 1990; Mangun, Hopfinger, Kussmaul, Fletcher, & Heinze, 1997; Heinze et al., 1994). Some striate cortex attention effects have been identified in imaging studies, discussed below, but these are likely due to feedback projections and therefore cannot be observed in the P1 component. P1 has been shown to increase in amplitude as perceptual load increases, and to decrease when attention is directed elsewhere (Eason, Harter, & White, 1969; Handy & Mangun, 2000). This attention-dependent P1 modulation effect has been attributed to sensory gain control due

to its rapid onset and point of origin (Handy & Khoe, 2005; for review, see Luck, Woodman, & Vogel, 2000). The present study explored the nature of sensory gain at fixation using both foveal and extrafoveal stimuli, utilizing amplitude modulations of the P1 ERP component as the measure of attention-dependent sensory gain.

1.2 Neural Bases of Sensory Gain

The most likely neural mechanism underlying visual sensory gain is direct attention-dependent modulation of visual cortical activity. Evidence for attentional effects on visual processing areas, specifically the extrastriate and striate cortex, has been found with brain imaging and ERP studies in humans and with single-cell recording studies in monkeys.

1.2.1 Imaging Studies

In a functional magnetic resonance imaging (fMRI) study, Brefczynski & DeYoe (1999) measured changes in visual cortex activation in areas V1, V2, V3, VP, and V4v as subjects attended to cued segments of a complex visual stimulus. The authors were able to retinotopically map all of these areas based solely on the shifts of attention, with no changes in the visual stimulus. Attention-dependent V1 modulation was also found in another fMRI study (Gandhi, Heeger, & Boynton, 1999). Here, attention increased activation in V1 contralateral to the stimulus. Similar findings were obtained in a single-cell recording study of attentional effects on V1 of the macaque monkey (Roelfsema, Lamme, & Spekreijse, 1998). Neuroimaging studies have even found attention-dependent activation in the lateral geniculate nucleus (LGN) of the thalamus (O'Connor, Fukui, Pinsk, & Kastner, 2002; for review, see Kastner, Schneider, & Wunderlich, 2006). However, immediate sensory gain effects may actually be limited to the extrastriate

visual areas, as V1 and LGN may be too early in the processing stream to be directly modulated by attention (He, Cavanagh, & Intriligator, 1996). These changes in V1 and LGN activation may instead be due to later feedback projections (Ito & Gilbert, 1999; for review, see Posner & Gilbert, 1999).

Martinez et al. (1999) combined the use of ERP and fMRI methodology in a single study, taking advantage of ERP's superior temporal resolution and fMRI's ability to localize areas of cortical activation. They found that the C1 component, which is the earliest visual ERP response that can be recorded from the scalp and is thought to originate in area V1 (Clark & Hillyard, 1996), showed no modulation by attention despite finding an attention-dependent modulation of V1 with fMRI. However, they did find changes in activation in the extrastriate visual cortex that correlated with changes in amplitude of the P1 ERP component. These data support similar results found in an earlier study that combined positron emission tomography and EEG (Heinze et al., 1994). A more recent fMRI study replicates this finding of attentional influence on extrastriate visual areas but not on the striate cortex (Liu, Pestilli, & Carrasco, 2005). These studies are consistent with ERP studies of visual attention, which typically find effects in the P1 and later components, but not in the earlier C1 component (Mangun, 1995; Luck, Woodman, & Vogel, 2000).

Together, these studies support the idea that the extrastriate visual cortex is the first region in which attention directly modifies perception by modifying the response in feed-forward projections from the thalamus. The lack of a C1 effect suggests that changes in V1 or LGN activation found with fMRI are instead due to later feedback from top-down projections.

1.2.2 Animal Physiology

The ERP and fMRI research reviewed above is consistent with single-cell recording data from the macaque monkey visual cortex as well (Moran & Desimone, 1985; Luck, Chelazzi, Hillyard, & Desimone, 1997). Attention has even been shown to cause increases in spontaneous firing of the associated visual cortex neurons in the absence of visual stimulation (Reynolds, Pasternak, & Desimone, 2000), and attentional selection capabilities seem to severely diminish following a lesions of the extrastriate visual cortex (De Weerd, Peralta, Desimone, & Ungerlieder, 1999). Importantly, there is significant evidence demonstrating that attention modifies single-cell firing in the extrastriate visual cortex, specifically areas V4 and MT, in a way consistent with the sensory gain model.

1.2.3 N1 ERP Component

The P1 component of the visual evoked potential (VEP) is often immediately followed by a negative posterior ERP component known as the N1, also thought to originate from the extrastriate visual cortex. Like the P1, the N1 has been found to increase for attended versus unattended visual stimuli (Luck, Woodman, & Vogel, 2000). Early sensory gain studies grouped the two components together, suggesting that they both indexed changes in visual processing due to sensory gain control (Van Voorhis & Hillyard, 1977; Eason, Harter, & White, 1969). However, this view has been rejected by more recent attention studies (Handy & Khoe, 2005). Luck et al. (1990) found that when a stimulus appears again in the same location to which attention was directed in the previous trial, P1 continues to show the typical effect but N1 is actually decreased in amplitude. Based on this evidence, they suggest that N1 plays a role in directing attention

to a specific region of the visual field, while P1 indexes sensory gain as previously hypothesized.

A study that compared differences in the N1 attention effect between a simple reaction time (RT) task and a discrimination task showed a much greater effect in the discrimination condition (Mangun & Hillyard, 1991). An earlier study also demonstrated evidence of a greater N1 during discrimination versus simple RT tasks, referring to the N1 as a pattern recognition mechanism (Ritter, Simson, & Vaughan, 1983). Vogel & Luck (2000) took this a step further, claiming that the N1 component reflects a discrimination process within the focus of attention. They tested both color and form discrimination versus a simple reaction time task and found discrimination-specific increases in N1 amplitude. These effects were robust to a variety of filtering and analysis methods that were aimed at eliminating potential confounds. This study also tested discrimination tasks with varying degrees of difficulty, in order to pull apart whether the N1 effect was due to discrimination itself or simply due to discrimination being a more difficult task than a simple reaction time task. They found no effect of task difficulty, although the discrimination effect remained (Vogel & Luck, 2000).

This is in contrast to two other studies that demonstrated paradoxical N1 attention effects. One study found that N1 peaks elicited by parafoveal stimuli were greater for the less difficult condition, which was assumed to require more attentional resources than the more difficult condition (Handy, Soltani, Mangun, 2001). This effect was replicated with a cueing paradigm, where greater N1 peaks were found for unattended versus attended stimuli with foveal as well as peripheral stimuli (Handy & Khoe, 2005). However, this effect has not yet been explained and its cause remains an open question.

1.3 Study Overview

1.3.1 Perceptual Load

The present study used a simple task difficulty manipulation to affect how participants attended to centrally presented stimuli. VEPs were then used to examine the neural responses to those stimuli as a function of task difficulty. Attention was manipulated by varying the level of perceptual load. Perceptual load can be varied by varying the number of items that are to be perceptually processed, or by varying the difficulty of processing the same number of items; both of these processes are thought to alter attentional demands (Lavie, 1995; Rees, Frith, & Lavie, 1997; Lavie & de Fockert, 2003; for review, see Lavie, 2005). Perceptual load can be dissociated from other forms of task-difficulty manipulation, particularly working memory load which may depend on a separate underlying control mechanism (Lavie, Hirst, de Fockert, & Viding, 2004). Perceptual load can also be considered different from other low-level perceptual manipulations, based on evidence that altering task difficulty by increasing perceptual load versus degrading the target stimuli has differential effects on the processing of irrelevant distractor stimuli. Specifically, increases in perceptual load make distractors less salient whereas target degradation makes distractors more salient. (Lavie & de Fockert, 2003). This is supported by imaging evidence demonstrating that perceptual load effects on visual cortex activity can be dissociated from the effects of interhemispheric stimulus competition, another low-level task difficulty manipulation (Schwartz, Vuilleumier, Hutton, Maravita, Dolan, & Driver, 2004).

Based on this prior work, the task difficulty manipulation in the present study will be more specifically referred to as perceptual load, as the manipulation is inconsistent

with stimulus degradation, stimulus competition, or working memory load, all of which are alternative task difficulty manipulations that are not believed to influence perceptual load.

1.3.2 Sensory Gain in the Periphery and at Fixation

The overwhelming evidence for sensory gain effects from covert attention presented above suggests that similar effects may be found at fixation, thereby predicting an increase in P1 amplitude with an increase in perceptual load. However, it may not be possible to manipulate sensory gain control for foveal stimuli; if this is the case, then there should be no attention-dependent changes in P1 amplitude for stimuli that are confined entirely within the foveal region of the visual field. This may be for physiological reasons, such as the high mapping ratio of foveal photoreceptors to ganglion cells (Wässle, Grünert, Röhrenbeck, & Boycott, 1990), that suggest that the contrast response may already be at maximum sensitivity for foveal stimuli and that there may be little to no room for attention-based improvement.

Handy & Khoe (2005) presented evidence that sensory gain may be limited to peripheral regions. In their experiment they used an endogenous cue to manipulate attention allocation to a foveal or peripheral stimulus. They found sensory gain effects, as indexed by an increase in P1 amplitude, only for the peripheral stimulus. An earlier study had managed to manipulate P1 amplitude with attention for foveal stimuli (Miniussi, Rao, & Nobre, 2002); however, Handy & Khoe attributed this to a confounding effect of divided versus focused attention. Sensory gain control effects have been shown to be bidirectional, in that diverting attention from a stimulus reduced sensory gain for that stimulus (Pestilli & Carrasco, 2005; Handy, Soltani, & Mangun, 2001), which may

explain the P1 effect found in the Miniussi et al. study. Studies of attentional effects on P1 for extrafoveal stimuli presented at fixation seem to be lacking. Extrafoveal stimuli here are defined as stimuli that are presented at fixation but are too large to be represented entirely within the fovea, and are therefore simultaneously represented by the fovea as well as surrounding regions of the retina. However, a number of emotion studies have managed to manipulate P1 in response to an extrafoveal probe presented at fixation following emotional images (Smith, Cacioppo, Larsen, & Chartrand, 2003) and faces (Corballis, Mienaltowski, Parks, & Blanchard-Fields, 2006).

1.3.3 Current Study

The present study manipulated attention towards foveal and centrally presented extrafoveal stimuli in order to uncover possible sensory gain control effects at fixation. Fixation is defined as the point in the visual field towards which the eyes are focused, regardless of stimulus size. Foveal stimuli are defined as stimuli at fixation that can be entirely represented within the fovea, being less than 1° of visual angle in size and centrally presented. Extrafoveal stimuli are defined as centrally presented stimuli that extend beyond this border; in this experiment, we used stimuli that were identical to the foveal stimuli except that they were 2° of visual angle in size.

Previous studies of sensory gain control have manipulated covert attention in response to peripheral stimuli; this will be among the first to look at these effects for sustained attention towards stimuli presented at fixation. It is reasonable to predict that sensory gain effects may vary between these two forms of spatial attention, as they have been dissociated both anatomically (Juan, Shorter-Jacobi, & Schall, 2004) and behaviorally (Shepherd, Findlay, & Hockey, 1986).

Perceptual load was manipulated by varying the level of task difficulty, using a methodology similar to that used in previous ERP work (Vogel & Luck, 2000). It has previously been demonstrated that P1 amplitude varies with perceptual load (Mangun et al., 1997), and that this reflects sensory gain effects in the extrastriate visual cortex (Handy & Mangun, 2000; Handy & Khoe, 2005). Variations in amplitude of the P1 component were therefore used in the present study as the measure of sensory gain variation.

CHAPTER 2

METHOD

2.1 Participants

Eighteen right-handed volunteers (8 women, 10 men; age 18-23 years; 4 left-handed) with normal or corrected-to-normal vision participated in the study. Two subjects were excluded due to data recording problems. The results presented are for the remaining 16 subjects (6 females; age 18-23 years; 3 left-handed). All subjects were recruited from the GA Tech subject pool and received extra credit in their psychology course for their participation. Informed consent was obtained from all participants and all procedures and protocols were approved by the Georgia Tech Institutional Review Board.

2.2 Stimuli

The test stimulus in this experiment was a gabor patch (sinusoidal contrast grating filtered through a Gaussian envelope; 6 cycles per degree, 100% contrast). Each gabor patch was tilted in one of 4 ways: 1° clockwise from vertical, 1° counterclockwise from vertical, 1° clockwise from horizontal, or 1° counterclockwise from horizontal. The stimuli were presented in two different sizes (foveal: 1 degree of visual angle; extrafoveal: 2 degrees of visual angle; size was varied by changing the kernel of the Gaussian window) between blocks, with 8 blocks using foveal stimuli and 8 blocks using extrafoveal stimuli. In the high-perceptual load condition, subjects were asked to discriminate between gabor patches that varied in orientation by 2 degrees. In the low perceptual load condition, subjects were asked to discriminate between gabor patches that varied in orientation by 90 degrees. Pilot testing was conducted to ensure that this

manipulation would yield accuracy effects typical of prior perceptual load studies (Lavie, 2005), validating the difference in task conditions as a manipulation of task difficulty.

See figure 1 below for examples of the discrimination conditions and a more detailed task explanation.

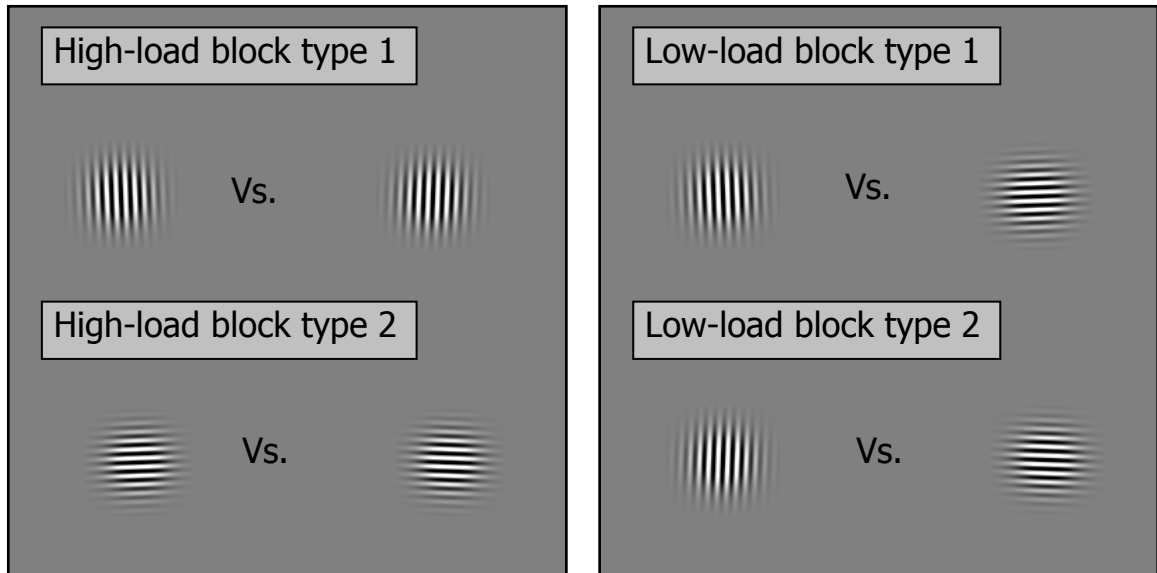


Figure 1: This study used a stimulus set consisting of four maximum contrast gabor patches, oriented at four different angles. They were oriented at 1° to the left or right of the vertical axis, and 1° above or below the horizontal axis. These stimuli were paired and divided into 4 block types: the high-load blocks used pairs of stimuli that are separated by 2° , which would be the two near-vertical gabors or the two near-horizontal gabors. The low-load blocks used pairs of 1 near-vertical and 1 near-horizontal stimuli that are separated by 90° . Data analysis was collapsed across load type, meaning that both high-load blocks were averaged together and both low-load blocks were averaged together. This assures that low-level stimulus effects on P1 amplitude remain constant across load manipulation conditions.

A small black dot surrounded by a black square outline served as the fixation point. The outline square varied in size to match the stimuli for the appropriate block. The fixation point appeared in gray following stimulus presentation until a response was made, at which time the fixation returned to white. All stimuli for the study were displayed using Presentation software running on a Pentium 4 computer.

2.3 Procedure

The experiment consisted of 1600 test trials (2 task types x 2 stimulus sizes x 400 repetitions) divided into 16 blocks of 100 trials each. Breaks were provided between each block until the subject was ready to proceed. The experiment also included 4 brief practice blocks, one for each condition, consisting of 10 trials each and presented prior to the first experimental block. Practice blocks were included to familiarize the subject with the task and were excluded from subsequent analysis. Feedback was provided on screen for each response in the practice block, but not in the actual experiment itself. There was a brief eye-movement calibration session prior to the first experimental block, to be used during analysis to identify eye movements that occurred during the experiment.

The participant was seated in front of a computer monitor at a distance of 57 cm with his or her head resting in a chin rest. There were four task-conditions; low-load foveal, high-load foveal, low-load extrafoveal, and high-load extrafoveal. Each condition was divided into two block types, to ensure that all four stimulus types were used in each condition. There was therefore a total of 8 block types, with block order counterbalanced across the 16 subjects used in the analysis. The foveal and extrafoveal conditions were identical except for the size of the stimuli; the low-load and high-load conditions were identical except for the degrees of separation between the two stimuli between which the subject was discriminating. A typical trial is depicted in figure 2.

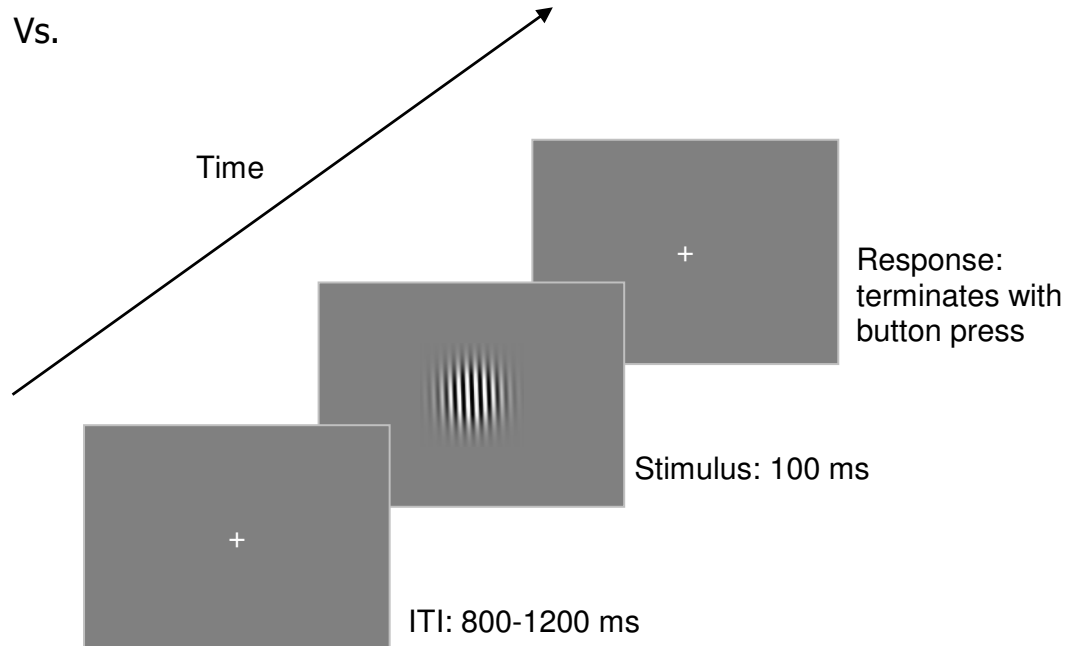


Figure 2: Experimental procedure for a typical trial. Subjects viewed a fixation point for a random intertrial interval of 800-1200 seconds, after which a target stimulus was presented at fixation. The stimulus in the figure has been enlarged for visibility; in the experiment it was presented at 1° (foveal) or 2° (extrafoveal) of visual angle. Following stimulus presentation, the subject made a response by pressing the left or right control key, according to the instructions.

Both the high-load and low-load conditions shared a common stimulus presentation procedure. The fixation point remained on the screen for a random intertrial interval (ITI) of 800-1200 ms, at which point the stimulus appeared for 100 ms. The ITI began again once the participant had made a response. In both conditions, the subject was asked to make a discrimination based on the tilt of the stimulus. In the high-load conditions, the tilt varied by only 2° (359° versus 1° in one block type, 89° versus 91° in the other block type); in the low-load conditions it varied by 90° (359° versus 89° in one block type, 1° versus 91° in the other block type). Once collapsed across blocks, both the high-load and low-load conditions used stimuli with the same four degrees of tilt.

In the foveal blocks, both conditions were presented at 1 degree of visual angle. In the extrafoveal blocks, both conditions were presented at 2 degrees of visual angle. The

intention of the two discrimination conditions was to manipulate attention at fixation without redistributing it across the visual field or altering the properties of the stimulus between conditions. This study attempted to measure sensory gain at two distinct levels of attention allocation using identical stimuli.

2.4 Electrophysiological Recording

Electroencephalography (EEG) activity was recorded at 34 electrode sites (FP1, FP2, F7, F3, Fz, F4, F8, C3, Cz, C4, P7, P3, Pz, P4, P8, T7, T8, O1, Oz, O2, AF3, AF4, FC1, FC2, CP1, CP2, PO3, PO4, FC5, FC6, CP5, CP6, A1, and A2) using Ag/AgCl electrodes mounted in an elastic cap, referenced online to the common mode sense (CMS) electrode with the driven right leg (DRL) electrode serving as the ground. After recording the EEG data, all scalp electrodes were re-referenced offline to the average across all electrodes. Additional electrodes were placed above and below the left eye and on the left and right canthi to record electrooculogram (EOG) for detecting blinks and eye movements. Data was recorded at a sampling rate of 1024 Hz and digitally band-pass filtered offline from .1 to 30 Hz. Trials were rejected if blinks and eye movements exceeded a predetermined threshold. These thresholds were established based on an EOG calibration session prior to the start of the experiment. Additional ocular correction was conducted using an automated regression method (Gratton, Coles, & Donchin, 1983). Baseline correction was performed on the segments by setting the average of the 200ms pre-stimulus interval equal to zero. Average waveforms were computed for each condition for each subject. Separate grand average ERP waveforms were then computed across all participants. Trials in which the subject made an error were excluded prior to averaging, leaving only correct-response trials.

2.5 Statistical Analysis

The data were first segmented by perceptual load condition, and then split between foveal and extrafoveal stimulus sizes. The time course of the P1 and N1 components was identified for each subject based on the grand average waveforms. A computer algorithm then identified the peak P1 and N1 amplitudes for each subject and condition at occipital and parieto-occipital electrode sites selected a priori, specifically Oz, O1, O2, PO3, PO4, P7, & P8. The P1 and N1 amplitudes were calculated as the mean of 10 data points centered around the point of maximum voltage. They were then split by stimulus type into foveal and extrafoveal groups. Paired samples t-tests were used to compare load conditions at electrodes Oz, O1, O2, PO3, PO4, P7, & P8. Comparisons were conducted separately for foveal and extrafoveal conditions. Error rates and reaction time were also tested using paired-samples t-tests within each stimulus size condition, in order to ensure that the perceptual load manipulation yielded appropriate behavioral effects. Specifically, a proper perceptual load manipulation should yield an increase in reaction time or a decrease in accuracy for the high-load relative to the low-load condition.

CHAPTER 3

RESULTS & DISCUSSION: BEHAVIOR

3.1 Results

Reaction time (RT) and accuracy data are reported in Table 1 below, as a function of stimulus size and perceptual load condition. Accuracy was significantly lower for the high perceptual load condition compared to the low perceptual load condition, for both foveal, $t(15) = 5.90, p < .05$, and extrafoveal stimuli, $t(15) = 4.47, p < .05$, showing that the perceptual load manipulation was effective. The effect of perceptual load on RT for extrafoveal stimuli was significant as well, $t(15) = -2.81, p < .05$, with subjects responding more quickly in the low-load relative to the high-load condition. The effect on RT was not statistically reliable for foveal stimuli, $t(15) = -1.20, p = .252$, but the trend was in the proper direction with quicker responses in the low-load condition.

Table 1. Accuracy and reaction time data by condition.

| | Accuracy | Accuracy (sd) | Reaction Time | RT (sd) |
|------------|----------|---------------|---------------|---------|
| Fovea Low | 0.939 | 0.069 | 433.898 | 154.743 |
| Fovea High | 0.734 | 0.158 | 488.911 | 144.944 |
| Extra Low | 0.942 | 0.049 | 444.028 | 126.914 |
| Extra High | 0.768 | 0.168 | 509.368 | 147.374 |
| Total | .846 | 0.153 | 469.051 | 143.365 |

Note: There was a significant difference in accuracy between the conditions, with lower accuracy for the high-load conditions, as predicted. There was a significant difference in RT for extrafoveal stimuli, with longer RTs for the high-load condition. No significant effect was found for RT for foveal stimuli, although the trend was in the same direction as the extrafoveal stimuli effect.

3.2 Discussion

The information provided by the behavioral data is relatively limited compared to the ERP data. However, the demonstration of an effect of perceptual load on accuracy is essential in validating the perceptual load manipulation. Although the RT effect was only significant for extrafoveal stimuli and not for foveal stimuli, it is in the correct direction for both stimuli types. This further supports the validity of the perceptual load manipulation, and eliminates the speed-accuracy trade-off as an alternative explanation for the accuracy effect. The RT difference for foveal stimuli may not have been significant in part due to the shorter overall RT for the foveal conditions. These accuracy and RT effects are consistent with effects found in prior perceptual load studies (Lavie & DeFockert, 2003).

CHAPTER 4

RESULTS & DISCUSSION: P1

4.1 P1 Results

The grand-average ERP waveforms for foveal stimuli are shown in Figure 3. Posterior electrode sites P7, PO3, O1, Oz, O2, PO4, & P8 were selected a priori as electrodes of interest for statistical testing, based on previous studies using the P1 component (for a review, see Luck, Woodman, & Vogel, 2000). Consistent with the results of prior research (Handy & Khoe, 2005) there was no effect of perceptual load on P1 amplitude for foveal stimuli at the posterior electrode sites. Similarly, there was also no change in P1 amplitude at posterior electrode sites for extrafoveal stimuli, as seen in the grand-average ERP waveforms in figure 4. Results of the paired-samples t-tests between load conditions at all electrode sites of interest are provided in Table 2. Paired samples t-tests of posterior electrodes revealed that only a single electrode for foveal stimuli, P7, and no electrodes for extrafoveal stimuli approached statistical significance.

Table 2: Paired sample t-test values for changes in P1 amplitude between the high-load and low-load conditions.

| | t-value (foveal) | p-value (foveal) | t-value (extrafoveal) | p-value (extrafoveal) |
|-----|---------------------|---------------------|--------------------------|--------------------------|
| P7 | 2.01 | 0.063 | -0.14 | 0.894 |
| PO3 | -0.17 | 0.864 | -0.09 | 0.931 |
| O1 | 1.49 | 0.157 | -0.26 | 0.799 |
| Oz | -0.16 | 0.878 | 1.02 | 0.325 |
| O2 | 0.46 | 0.655 | 0.99 | 0.338 |
| PO4 | 0.11 | 0.914 | 0.48 | 0.639 |
| P8 | 1.56 | 0.141 | 0.68 | 0.509 |

Note: Paired sample t-test values for changes in P1 amplitude between the high-load and low-load conditions. No significant

differences were found for foveal or extrafoveal stimuli. A marginally significant difference was found at only a single electrode, P7, for foveal stimuli.

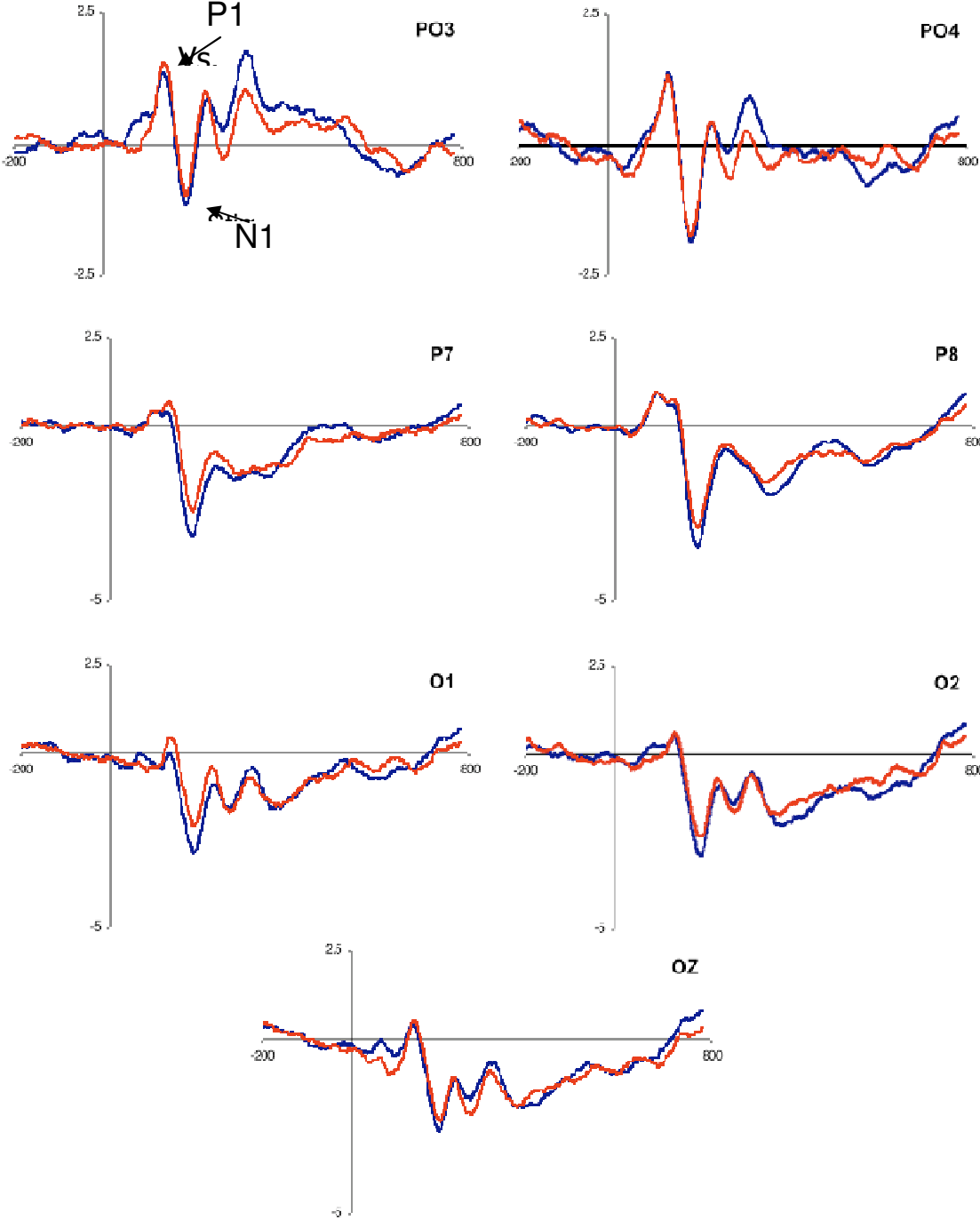


Figure 3: Grand-average waveforms elicited by foveal stimuli are shown for all seven electrodes of interest. P1 and N1 component peaks are labeled on the PO3

waveform. Only trials in which the subject made the correct response are included.

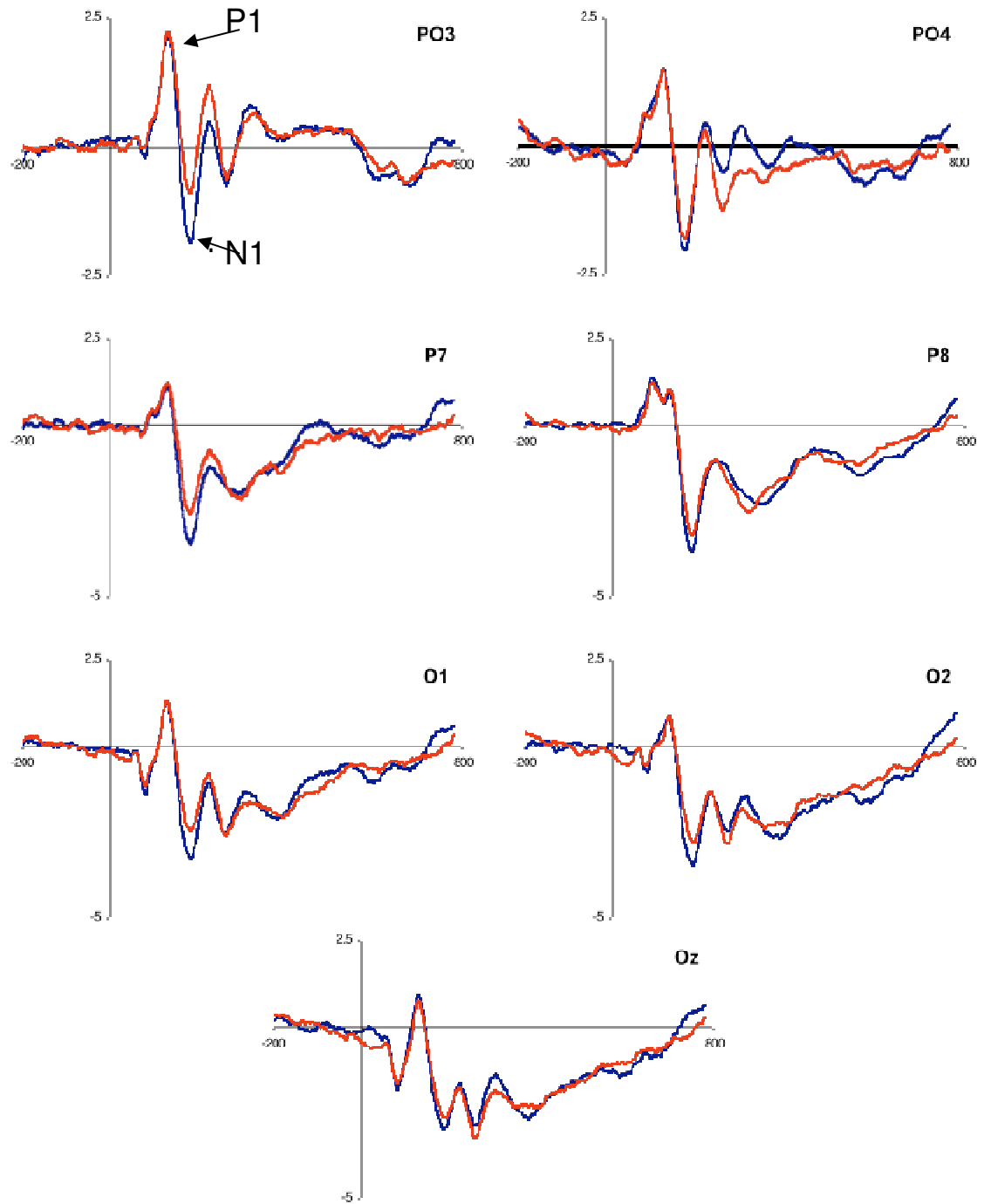


Figure 4: Grand-average waveforms elicited by extrafoveal stimuli are shown for all seven electrodes of interest. P1 and N1 component peaks are labeled on the PO3 waveform. Only trials in which the subject made the correct response are included.

4.2 P1 Discussion

4.2.1 Foveal Stimuli

The lack of any P1 effect is evidence against the presence of a task difficulty dependent sensory gain effect at fixation, for either foveal or extrafoveal stimuli. The lack of a P1 effect at the fovea replicates an earlier sensory gain study (Handy & Khoe, 2005). Within the entire visual field, the fovea seems to be the region that is least likely to be susceptible to sensory gain control effects. The proliferation of cones in this region as well as the high mapping ratio of photoreceptors to ganglion cells which is unique to this area suggest that the fovea may be essentially pre-wired for maximum acuity (Wässle, Grünert, Röhrenbeck, & Boycott, 1990). Therefore, it may not be as susceptible to sensory gain effects as other regions of the visual field. This is not to say that attention cannot affect performance or processing related to foveal stimuli. Attentional blink studies, for example, have demonstrated that perception of stimuli at fixation can be impaired by the appearance of peripheral distractors (Folk, Leber, & Egeth, 2002). Even more convincing is ERP evidence that the visual stimuli missed during the attentional blink period are actually processed in the visual cortex, but not consciously perceived because the subject was still attending to the prior target (Luck, Vogel, & Shapiro, 1996; Vogel, Luck, & Shapiro, 1998). It is therefore more likely that attention exerts effects at a variety of levels within the visual system, ranging from sensory gain to executive facilitation, and that it is simply the lowest level influences that are not present for foveal attention.

An alternative possibility is that it is only possible to decrease rather than increase gain control at the fovea; if this region is already at a maximum level of perceptual

sensitivity then gain would only be adjustable in one direction. Some evidence for this comes from a P1 study in which P1 was reduced for divided versus focused attention (Miniussi, Rao, & Nobre, 2002), suggesting that attending to a wider range of the visual field including the fovea would reduce gain relative to attended solely to the foveal region. This possibility was not explicitly tested in the present study. Comparing foveal to extrafoveal conditions would have provided a similar manipulation, but the differences in the stimuli themselves would have confounded any potential P1 effect.

4.2.2 Extrafoveal Stimuli

No previous research was found that directly tested sensory gain at fixation for extrafoveal stimuli. Nonetheless, the null result was unexpected as it seemed likely that extrafoveal stimuli would show similar effects as peripheral stimuli have in the past (Handy & Khoe, 2005), due to the fact that the outer portion of an extrafoveal stimulus extends into what is essentially the periphery. This may be due to methodological difference between the present study and prior peripheral spatial attention studies, which will be discussed below. However, the present null result did replicate our earlier findings from unpublished pilot data. The pilot study used a relatively weak manipulation of task difficulty, making it less likely to find an effect. The present study used a more legitimate manipulation, as evidenced by the increased error rate and reaction time in the high load versus low load condition. Furthermore, N1 varied with task difficulty (see discussion below) in a way consistent with prior perceptual load studies (Handy & Khoe, 2005; Handy, Soltani, & Mangun, 2001), adding further validity to the load manipulation.

It is possible that the reasons for the lack of an extrafoveal P1 effect are quite similar to those for the lack of a foveal P1 effect. Although the extrafoveal stimulus, at 2

degrees of visual angle, did extend beyond the boundaries of the fovea, it was still confined within the parafoveal region of the macula. The parafoveal region is an area of optimal or near optimal visual acuity, and may also be at a ceiling level of perceptual sensitivity that cannot be enhanced by sensory gain control mechanisms. The peripheral stimuli used by Handy & Khoe (2005), for which they did find a significant sensory gain effect, were presented 2.2° away from central fixation and were likely within the parafoveal region as well. This to some extent contradicts the claim that the parafoveal region may be exempt from sensory gain control effects; however, it is possible that their stimuli were too far from fixation to be considered analogous to the extrafoveal stimuli used in the present study. It would be interesting to test the effects of attention on increasingly large centrally-presented stimuli, as they expand into the perifovea region and finally into the true peripheral area. This may clarify the point at which sensory gain control is able to exert an influence.

Another possible explanation for the lack of an effect with the extrafoveal stimuli is that subjects may have been able to complete the task using only the central portion of the stimulus. That is, they could have relied on foveal information, despite the stimuli being larger in size. However, it seems unlikely that subjects would have intentionally employed this strategy as there is no intuitive benefit and it would have required additional effort to selectively ignore a portion of the stimulus. Furthermore, the outer region of the stimulus would still influence P1 amplitude even if it was not being used to complete the task. When attention is drawn away from a particular area by increasing perceptual load at a different area, the P1 to the unattended area is reduced in amplitude (Handy, Soltani, & Mangun, 2001). This would suggest that, if the subjects were relying

solely on the fovea to complete the task, a P1 component elicited by an extrafoveal stimulus should actually decrease as perceptual load at the fovea increases. This was not found to be the case.

It is difficult to draw any conclusions about the P1 effect in this experiment, as the null was not rejected for either condition. The results are consistent with previous work, and suggest that Handy & Khoe's (2005) claim that sensory gain control mechanisms do not act on foveal stimuli may be extended to parafoveal stimuli as well. However, this claim cannot be made with certainty without further evidence.

CHAPTER 5

RESULTS & DISCUSSION: N1

5.1 N1 Results

The grand-average ERP waveforms for foveal stimuli are shown in Figure 3 (see chapter 4). The posterior electrode sites selected for P1 testing (P7, PO3, O1, Oz, O2, PO4, & P8) were selected a priori as electrodes of interest for statistical testing of N1, based on previous N1 studies (for a review, see Luck, Woodman, & Vogel, 2000). There was a significant effect of perceptual load on N1 amplitude for foveal stimuli at posterior electrode sites. Similarly, there was also a significant change in N1 amplitude at posterior electrode sites for extrafoveal stimuli, as can be seen in the grand-average ERP waveforms shown in Figure 4 (see chapter 4). Specifically, N1 amplitude was greater (more negative) in the low perceptual load relative to the high perceptual load condition. Results of the paired-samples t-tests between load conditions at all electrode sites of interest are provided in Table 3.

Table 3: Paired sample t-test values for N1 changes between the high-load and low-load conditions.

| | t-value (foveal) | p-value (foveal) | t-value (extrafoveal) | p-value (extrafoveal) |
|-----|---------------------|---------------------|--------------------------|--------------------------|
| P7 | 5.03 | <.01 ** | 3.40 | <.01 ** |
| PO3 | 1.33 | 0.204 | 3.38 | <.01 ** |
| O1 | 3.95 | <.01 ** | 4.03 | <.01 ** |
| Oz | 2.14 | <.05 * | 1.93 | 0.073 |
| O2 | 2.46 | <.05 * | 4.95 | <.01 ** |
| PO4 | 0.95 | 0.360 | 1.48 | 0.159 |
| P8 | 2.56 | <.05 * | 3.54 | <.01 ** |

Note: Significant differences were found in N1 amplitudes for both foveal and extrafoveal stimuli at five of the seven posterior electrode

sites tested. Significant differences at the $p < .05$ level are marked by an asterisk, significant differences at the $p < .01$ level are marked by dual asterisks.

5.2 N1 Discussion

5.2.1 Perceptual Load Validation

A significant N1 effect similar to that found in the present study has been previously found in sensory gain studies using perceptual load (Handy, Soltani, & Mangun, 2001) and cueing manipulations (Handy & Khoe, 2005). This consistency with prior perceptual load ERP studies, in conjunction with the behavioral data presented above, validates the perceptual load manipulation used in the present study. Although the specific role of the N1 component in this study is unclear, it seems that N1 may be a more sensitive measure of attention manipulations than P1.

5.2.2 Discrimination

The N1 component is widely believed to index discrimination processes within the focus of visual attention (Vogel & Luck, 2000). However, the N1 discrimination effect generally does not vary with the difficulty of the discrimination task, responding instead in a more on/off manner related to the presence or absence of a visual discrimination. It is therefore unlikely that the N1 changes in the present experiment are due to the N1 discrimination effect, as participants performed a discrimination task in all experimental conditions.

5.2.3 Early Visual Processing

Early evidence suggesting that N1, like P1, is also a measure of sensory gain control (Van Voorhis & Hillyard, 1977; Eason, Harter, & White, 1969) is no longer

widely accepted due to more recent work dissociating the two components (Vogel & Luck, 2000; Luck et al., 1990). However, the N1 is generally believed to be generated at least in part by the extrastriate visual cortex and is known to be modulated by attention (for review, see Luck, Woodman, & Vogel, 2000). This therefore leads to the conclusion that the N1 is indexing some effect on early visual processing that is dependent on task difficulty, but is separable from the N1 attention effect, the N1 discrimination effect, and sensory gain, which is indexed by the P1 component.

Task difficulty is therefore modulating early visual processing, but the mechanisms behind this effect are not clear. One possible explanation can be drawn from the theory proposed by Luck et al. (1990) that N1 reflects orienting of attention towards a particular stimulus. Mangun & Hillyard (1990) demonstrated that the degree of processing for a region of the visual field is dependent on the attentional resources available for processing at that region. It is possible that in the high-load condition, each trial reduces the amount of attentional resources available for the subsequent trial, therefore reducing the amount of processing. Specifically, an increase in resources used on a particular trial would reduce the resources available for preparing to attend to the next stimulus, thereby reducing N1 amplitudes in trials that follow high load trials versus trials that follow low load trials. As this experiment used a block design, all high load trials followed other high load trials, and all low load trials followed other low load trials. In order to fully test this hypothesis it would be necessary to have a mixed block of high and low load trials together, and to then look at the N1 based on the prior trial type. If this truly is the mechanism underlying the N1 effect, then trials that follow high-load trials should show a reduced N1, even in a mixed-block design. Unfortunately such data is not

available in the current set, so this hypothesis is only speculative, pending a follow-up study.

Based on the inconsistencies between the results of this study and most prior N1 studies, it seems that the effect found here is not the typical N1 attention effect (Luck et al., 1990) or the N1 discrimination effect (Vogel & Luck, 2000). The use of N1 as a measure of sensory gain has long since been dismissed as well (Luck et al., 1990). N1 in the present study therefore must index some other form of perceptual load effects on early visual processing, in a way consistent with a limited resources model. However, further evidence is required to conclusively uncover the root of the N1 effect in the present study.

CHAPTER 6

GENERAL DISCUSSION

6.1 Main Findings and Future Directions

The primary goal of this study was to provide evidence that sensory gain control does or does not exist for foveal and extrafoveal stimuli presented at fixation. No changes in P1 amplitude were found for either condition suggesting that these regions may be exempt from sensory gain control effects, possibly due to maximal performance levels at baseline for the fovea and immediately surrounding areas. The secondary goal of this study was to attempt to explain an unexpected N1 effect. The data show a significant but paradoxical modulation of N1, with reduced N1 amplitude for high perceptual load stimuli and greater N1 amplitude for low perceptual load stimuli. This goes against predictions of either no effect or a simple N1 attention effect of greater N1 amplitude as perceptual load increases. The effect found here does, however, replicate a previous finding (Handy & Khoe, 2005; Handy, Soltani, & Mangun, 2001) that was largely ignored in previous papers.

Three main findings were presented in this study; 1) lack of a sensory gain effect for foveal stimuli was replicated; 2) no evidence was found for sensory gain effects with extrafoveal stimuli presented at fixation; and 3) there is some effect of task difficulty on early visual processing, possibly related to the expenditure of limited attentional resources.

6.1.1 Foveal Stimuli

The lack of any sensory gain control effect for foveal stimuli was predicted, and is consistent with prior research (Handy & Khoe, 2005). However, both studies have only demonstrated a failure to reject the null, suggesting that the lack of an effect may be due power issues. The P1 component may not be the ideal measure for finding sensory gain control effects with foveal stimuli. Establishing psychophysical detection and discrimination functions using behavioral methods may yield more informative data in regards to the effects of attention on foveal processing.

6.1.2 Extrafoveal Stimuli

The lack of any sensory gain control effect for extrafoveal stimuli was somewhat unexpected, and the reason for the null result is less clear. It is possible that sensory gain is limited to certain regions of the visual field, with the regions represented by the fovea, parafovea, and perhaps the entire macula exempt from sensory gain effects. Another possibility is that sensory gain control effects increase with stimulus eccentricity, with areas that are typically less responsive being more susceptible to attentional benefits as they have more room for improvement. Testing for sensory gain with either progressively larger stimuli presented at fixation or peripheral stimuli presented at progressively greater eccentricities would allow a greater understanding of sensory gain effects across the visual field.

6.2 Conclusion

The strong N1 effect found consistently for both foveal and extrafoveal stimuli in this experiments suggests that the perceptual load manipulation had an effect on early visual processing. However, the lack of any effect on the P1 component and the fact that the change in N1 amplitude is in the opposite direction of the typical N1 attention effect

suggests that the effect of the perceptual load manipulation in the present study must be explained by some mechanism other than sensory gain control. The reduction in N1 for high-load versus low-load stimuli suggests that N1 may reflect a limitation in attentional resources, but this cannot be said with certainty until further research has been conducted.

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