Pre-Saccadic Modulation of the Visually Evoked Potential

Leslie Guadron
CUNY City College

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Pre-Saccadic Modulation of the Visually Evoked Potential

Thesis
Submitted in partial fulfillment of the requirement for the degree
Master of Science (Biomedical Engineering)
at
The City College of New York
of the
City University of New York
by
Leslie Guadron
May 2014
Approved:

Professor Simon Kelly, Thesis Advisor

Professor Mitchell B. Schaffler, Chairman
Department of Biomedical Engineering
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ABSTRACT

Saccades are rapid eye movements that allow us to focus the fovea on different parts of our visual environment. Many psychophysical studies have shown that subjects can discriminate stimuli presented at the saccadic target better than at any other location before an eye movement is made. It is believed that covert attention allotted to the intended destination of a saccade, called pre-saccadic attention, accounts for the improved discrimination of stimuli. Covert top-down attention, which consists of orienting your attention, and not your gaze, to an object in your visual periphery, is known to facilitate behavioral performance in a manner similar to that seen with eye movement planning. It is not known how the mechanisms governing these two processes differ. While covert top-down attention has been studied electrophysiologically, pre-saccadic attention has only been studied behaviorally in humans due to technical challenges. We overcame these challenges with an innovative paradigm to elucidate the neural correlates of pre-saccadic attention using electroencephalography (EEG). Event related potentials were compared for attended and unattended stimuli in three tasks: one involving saccades only, one involving saccades and a perceptual task, and one involving a perceptual task without eye movements. We found that it is unlikely that the primary visual cortex is the location at which visual processing is modulated by attention. More feasible candidates include the extrastriate and parietal cortex.

INTRODUCTION

Pre-saccadic facilitation is characterized by an increase in visual processing of stimuli at a location to which an eye movement is being planned. It is a widely held belief that this shift in spatial attention prior to a saccade is an integral part of the process of planning eye movements. Psychophysical studies have provided evidence in support of this belief by showing that subjects are better able to report on stimuli that appear at the saccadic target (Baldauf & Deubel, 2008; Deubel & Schneider, 1996; Gersch, Kowler, & Dosher, 2004; Godijn & Theeuwes, 2003). Generally, when the location of a stimulus matches that of the saccade goal, improvements in reaction time and accuracy of subjects’ perception of the stimulus are seen (Chelazzi, Biscaldi, & Corbetta, 1995). A classic pre-saccadic attention study by Deubel and Schneider (1996) found that not only are pre-saccadic attentional effects spatially selective, they are also necessarily tied
to eye movement planning. In other words, one allocates resources based on attention at the saccadic goal such that processing objects at other locations is not feasible (H Deubel & Schneider, 1996; Gersch et al., 2004). Further evidence for the coupling of attention and saccades is seen when comparing performance relative to saccade onset. Long before the saccade, a time span of a few hundred milliseconds, the attentional effects on behavior are not as pronounced as they are immediately prior to the saccade (Heiner Deubel, 2008). It has been suggested that the purpose of this attentional facilitation is to aid in maintaining a stable representation of the visual scene across eye movements as well as directing the movement of the eyes by creating a vector in space for the saccade to follow (Sommer & Wurtz, 2008).

All of these studies have shown that eye movement preparation has an influence on perception of objects at saccade targets; however, none have been able to determine the locus of these purported attentional shifts in the brain. There has been much speculation about the neural substrates that mediate the allocation of attention during saccade planning. There is a fronto-parietal circuit that is thought to be responsible for the parsing of resources for visual processing (Godijn & Theeuwes, 2003). This includes the areas that are known to be involved in eye movement planning, such as the lateral intraparietal area (LIP), the frontal eye fields (FEF), and the superior colliculus (Itti & Koch, 2001). It has been speculated that the LIP is the area that mediates object processing and saccade programming (Godijn & Theeuwes, 2003). Or that the FEF are responsible for providing attentional signals that facilitate perception (Berman, Joiner, Cavanaugh, & Wurtz, 2009; Gersch et al., 2004). However, these ideas have not been confirmed with electrophysiological studies involving saccades in humans.

Conversely, covert top-down attention has been studied extensively using electroencephalography. Covert top-down attention and pre-saccadic attention are often compared to one another because they appear, at least superficially, to be similar mechanisms. In both cases, there is a spatially specific facilitation of processing while the gaze is fixated and the eye is stationary. But pre-saccadic attention precedes a motor event while covert orienting of attention does not. Additionally, the types of attention that are employed differ in the two cases. In the covert case, attention is directed in a top-down manner. The subject chooses where and when to shift their attention while maintaining their gaze at a location different from that which
they are attending. In the case of pre-saccadic attention, it is believed that one does not necessarily have a choice about where attention is directed prior to a saccades and, in fact, we are incapable of consciously doing so (H Deubel & Schneider, 1996; Gersch et al., 2004). It has been shown in a psychophysical study that voluntary attention and saccade preparation can be dissociated (Belopolsky & Theeuwes, 2009). This would suggest that these two processes are not necessarily governed by the same neural mechanisms.

More compelling evidence for the dissociation between these two processes was presented in an experiment involving a patient with right posterior parietal lobe damage that resulted from a stroke (Blangero et al., 2010). This lesion made it impossible for the patient to covertly orient their attention but they retained the ability to make saccades and showed spatially specific pre-saccadic behavioral facilitation (Blangero et al., 2010). Additionally, a study involving a patient with a congenital defect that precluded her from making eye movements found that she still displayed covert facilitation but not spatially selective exogenous (involuntary) facilitation (Smith, Rorden, & Jackson, 2004). This reinforces the idea that covert and pre-saccadic attention are dissociable processes since they can occur independently of each other.

Ideally, the neural mechanisms that govern pre-saccadic attentional shifts would be studied using electroencephalography (EEG), which is a method of noninvasively recording the brain's electrical activity using electrodes on the scalp. One of advantages of this method, apart from its impressive temporal resolution, is that it is possible to average data that is time locked to a specific event, effectively revealing the brain’s response to that event (Luck, Woodman, & Vogel, 2000). This method of averaging time locked signals results in a characteristic wave known as the event related potential (ERP). When the stimulus that evokes this activity is visual, the resulting ERP is known as the visually evoked event related potential (VEP). This wave is composed of characteristic bumps known as components, as shown in Figure 1. The earliest ERP component is known as C1 and it is thought to reflect activity in the early visual cortex, also known as striate cortex or the primary visual cortex (Luck et al., 2000; Russo, Sereno, Pitzalis, & Hillyard, 2001). It typically peaks around 80ms after the presentation of the stimulus. The next component is the P1 which can occur between 100 and 150ms after the presentation of the stimulus. This component is thought to originate from the visual processing in the extrastriate
cortex (Luck et al., 2000; Russo et al., 2001). Finally, the last component of interest in this study is the P3, which peaks at around 300-400ms. This is one of the latest components and has so far been associated with the process of decision making (O’Connell, Dockree, & Kelly, 2012; Squires, Donchin, Squires, & Grossberg, 1977). Interestingly, it has been shown that these components, aside from demonstrating the time course of activity in response to a stimulus, also reflect the amount of attention allotted to certain stimuli (Hillyard & Anillo-Vento, 1998; Luck et al., 2000). The magnitude of a component is amplified when it is in response to an attended stimulus and attenuated when the same stimulus is presented but is unattended (Hillyard & Anillo-Vento, 1998; Luck et al., 2000).

Figure 1: (Left) Response to an attended stimulus flashed in the left visual field is shown with a solid line. The amplitude of the ERP components is greater than that of the response to the same stimulus when attention is directed elsewhere. Image from Luck, 2005. (Right) The location of the primary visual cortex, the generator of the earliest ERP component, C1 (not shown at left), and the calcarine fissure are shown in yellow. The higher level visual areas give rise to the P1 component. Image from studyblue.com
Given the advantages of using ERPs to study the effects of attention on the processing of a stimulus, we have decided to use this method to examine the neural correlates of pre-saccadic attention. There are certain challenges associated with measuring ERPs in tandem with saccades. The main problem is the introduction of electrical activity associated with the activation of the eye muscles. These artifacts are most intrusive in the frontal electrodes in EEG and are less pronounced in the occipital electrodes (Zhou & Gotman, 2009). If the saccade occurs soon after the presentation of a stimulus, then the response elicited by the stimulus, the ERP, will be interrupted by the electrical activity of the eye muscles. This would distort the EEG signal and cloud the response to the stimulus. But in order to observe the effects of attention right before a saccade is made, when attentional facilitation is thought to be greatest, stimuli would have to be presented close to the onset of the saccade. Careful signal processing can be used to remove the eye movement artifacts that may interfere with ERPs.

Based on this information, we decided to carry out experiments that would elucidate the neural mechanisms of pre-saccadic attention by analyzing modulations of early ERP components. The findings of this study will hopefully lead to a better understanding of pre-saccadic attention and spatially specific facilitation of perception which has implications for treating disorders in children associated with attentional malfunctioning such as anxiety disorders and ADHD (Munoz, Armstrong, Hampton, & Moore, 2003; Pine, Helfinstein, Bar-Haim, Nelson, & Fox, 2009).

METHODS

Three psychophysical experiments were carried out in order to elucidate the neural correlates of presaccadic attention and whether the underlying mechanisms responsible for these shifts of spatial attention differ from those employed in covert attention. One experiment consisted of the subject making eye movements in the absence of a perceptual task, the second required the subject to make saccades while simultaneously completing a discrimination task. This entails a two alternative forced choice in response to every stimulus presented. The third was a covert attention and stimulus detection task in which there were no eye movements. All psychophysical experiments were coded in MATLAB using Psychtoolbox. Sixteen blocks were carried out for
every experiment for two subjects, AB and LG, with the exception of the covert task for which subject AB had only 9 blocks. Every block for the eye movement experiments consisted of 384 trials and the covert attention experiment consisted of 380 trials per block.

_Electroencephalography and Eye Tracking_

Electroencephalography (EEG) and eyetracking data was recorded for every experiment. The EyeLink 1000 (SR Research) eye tracker, sampling at a rate of 1000Hz, with an accuracy of 0.25°-0.5° was used in conjunction with a 96-channel, low-noise/active electrode Brain Products EEG system.

_Visual Field Mapping_

Before conducting any experiments, the best locations for stimulus presentation for each subject were selected. These were based on the idea that we would be assessing the C1 component of the visually evoked event related potential. Using flickering checkerboard stimuli following an M-sequence, we were able to map the visual field of our subjects to find the best locations to elicit the largest C1 component. This was an important step as it has been shown that there are striking differences among the morphology of the calcarine sulcus (the location of this structure in cortex is indicated in Figure 1) of different individuals, which leads to variable responses among subjects to the same stimuli in the same locations (Vanegas, Blangero, & Kelly, 2013).

_Experiment 1: Paced Saccades Task_

The first paradigm consisted of the subject making regularly paced saccades without having any perceptual task to complete. Subjects were asked to make saccades every 800ms between targets continuously displayed on a screen in a diamond pattern in either a clockwise or counterclockwise fashion, alternating every block. Targets were spaced 5 degrees of visual angle apart and the angle between the targets was 40° for subject AB and 25° for LG, as seen in Figure 2 (right). Locations 1 through 4, relative to fixation, are up and to the right, up and to the left, down and to the left, and down and to the right, respectively.
Subjects were instructed to focus on maintaining a constant pace throughout the experiment. The probes used were Gabor patterns with a spatial frequency of 5Hz and they were flashed for 100ms. We attempted to present probes at either 100, 200, 300, 400, or 600 ms prior to the execution of the next saccade, which was estimated online and based on the subject's current pace. As the subject was making saccades, a probe was flashed at a target location adjacent to their current fixation point. The location at which a saccade was being planned was considered the attended location. The opposite location was considered unattended.

No perceptual task was employed in this case because we wanted to examine pre-saccadic shifts of attention in isolation. If a task had been used, then the subject would have likely recruited their top-down attentional processing in order to optimize their performance. Asking the subject to solely focus on planning their saccades would ensure that the event related potentials examined were a reflection of involuntary shifts of attention tied to eye movements, and not a reflection of endogenous attention.

A trial was considered to have begun when the subject’s saccade landed on the target and ended when they arrived at the next target. Thus, every trial includes one probe and one saccade. For every trial, auditory feedback was presented to let the subject know whether their timing was correct, or whether they were executing their saccades too early or too late. The tone for a saccade that was 800ms ± 50 ms after the last saccade was 800 Hz. For saccades that occurred too late it was 1100 Hz and the frequency for saccades that occurred too soon was 450 Hz. During the first ten trials, the tone for correctly timed saccades was automatically played every 800ms and subjects were told to make saccades when they heard the tone. This was done to aid the subject in developing the correct timing.

**Experiment 2: Paced Saccades + Discrimination Task**

The second experiment that was conducted required that the subject carry out regularly paced saccades, like in the first paradigm, but they also had to report on a property of the probes that were presented. The purpose of this experiment was to be able to compare neural activity when the subject must perform a perceptual task while making saccades to that which occurs when saccades alone are executed. We asked the subject to report on whether or not they saw a dark ring present in the Gabor pattern. The Gabors were the same as those used in the first experiment.
and were also only presented for 100ms. The ring was created by a decrement in luminance. The reduction for AB was 70% while the reduction for LG was 60%. These values were chosen so that both subjects performed at about 70% accuracy when detecting the ring. This specific stimulus had been used previously in a study that demonstrated modulation of the C1 component in an attended versus unattended condition (Kelly et al., 2008) and is shown in the left of Figure 2. Thus, we used the same stimulus in hopes of effectively inducing a C1 modulation, which, until recently, was believed to be a component that is unaffected by attention.

Subjects were again instructed to make a saccade every 800ms and probes were presented 100, 200, 300, 400, or 600 ms prior to the execution of the next saccade. Upon landing on the next target after completing a saccade, the subject had to provide a response indicating whether they believed that the probe presented contained a ring or not. The subject clicked the left mouse button when they saw a probe without a ring and clicked the right mouse button when they believed they saw a ring. The subject could take as much time as needed to submit their response. The likelihood of a ring being present in any given probe was 50% and it was equally likely to be presented at the attended or unattended location. After inputting their reply, the subject had to wait 800ms, during which time the probe was flashed, and then make a saccade again. Auditory feedback was also provided in this task.

Performance was calculated based on the subjects correct identification of a Gabor with no ring or a Gabor with a ring. Incorrect responses were the lack of detection of a ring or the report of a ring being present when there was none.
Figure 2: (Left) Setup of the four saccade targets for Experiment 1. X is the best angle for that subject. (Right) The Gabor pattern is shown in the top panel and the Gabor with a ring is shown on the bottom. Image from Kelly et al., 2008.

**Experiment 3: Covert Attention in a Detection Task**

The third and final experiment that we conducted did not involve eye movements. This was done in order to characterize the neural signature of covert attention to compare with that for presaccadic attention.

The same four locations that were used in the first two experiments were again used for this task. However, the subject fixated on the center of the screen and the target locations were situated relative to this fixation point. For every trial only two adjacent locations were used for probe presentation. At the beginning of every block the subject was asked to fixate on a dot in the center of the screen. A cue was then flashed for 500ms indicating the location at which a probe with a ring was 70% more likely to be presented. Of all the stimuli presented, 25% contained rings. This information was intended to motivate the subject to focus their attention at the cued location. The probe and ring parameters were the same as those used in Experiment 2. Probes were flashed for 100ms every 700-900ms for a total of 30s. After this time, the subjects were
allowed to rest before continuing with the next trial. The task required that the subject respond by clicking the left mouse button only when they saw a Gabor pattern with a ring, but they had to report on stimuli appearing at both the cued and uncued location.

Performance in this task was calculated based on whether the subject clicked within 500ms of the presentation of a probe with a ring.

**Data Analysis**

The eye tracking data was examined to classify useable trials. A GUI (shown in Figure 3) was programmed in MATLAB to facilitate the analysis of the eye movement data. Bad trials, like those containing blinks, were identified as well as the time of saccade onset and probe occurrence for every trial. This information was critical when parsing the EEG data.

EEG was average referenced and low pass filtered with a cutoff frequency of 50Hz. It was then analyzed to extract ERPs. A segment of data 50ms before and 250ms after the presentation of the probe was chosen. This data was then collapsed across trials for the four different locations and this resulted in ERP waveforms. The procedure is illustrated in Figure 4.

The best electrode for every location was also chosen to maximize the amplitude of the signals. This was accomplished by inspecting topoplots created using the EEGLAB toolbox for MATLAB. Topoplots show the voltage at a given point in time for every electrode as a topographical map of the scalp. The best electrodes were different for each subject, for each location, and for each component examined. These are listed in Table 1. One electrode was used for the C1 component and the P3 component, but a group of electrodes was used for the P1 component. The same electrodes were used for analyzing data from each experiment, however.

Statistical analysis included a three-way ANOVA test to check for statistically significant differences among the component magnitudes based on task, attention, and location. This analyses was conducted separately for the two subjects and for each component of the VEP.
Figure 3: The graphic user interface that was created for examining eye tracking data. This shows data from Experiment 2 for subject LG. The blue and red traces are the x and y position, respectively, of the gaze. Green vertical lines indicate the beginning of a trial, pink lines show when the subject clicked, and the black vertical line indicates the time of probe presentation. The black bold lines on the position traces highlight the saccade that initiates the next trial. This was classified as a bad trial due to the blink occurring near 1000ms.
Table 1: The electrodes chosen for each component. They are listed in order for locations 1 through 4.

<table>
<thead>
<tr>
<th>Subject</th>
<th>C1 Component</th>
<th>P1 Component</th>
<th>P3 Component</th>
</tr>
</thead>
<tbody>
<tr>
<td>AB</td>
<td>PO8, POz, PO8, PO3</td>
<td>Loc1: CPP3h, P7, P5, P3, PO3, PPO1h, O1, Loc2: P5, P3, P1, Pz, PO7, CPP4h, PO3, POz, O1, PPO2h Loc3: CPP3h, P7, P5, P3, PO3, PPO1h, O1 Loc4: P4, P6, P8, PO4, P10, PO8, PO10, PPO10h</td>
<td>CPz, CPz, Pz, Pz</td>
</tr>
<tr>
<td>LG</td>
<td>P6, PO3, PO4, PO3</td>
<td>Loc1: P4, P6,P8,POz, PO4, P10, PO8, PPO2h, Oz,PPO10h, O2 Loc2: CPP3h, P7, P5, P3, PPO9h, TPP7h, PO9, PO7, PO3, POz,P9,PPO1h, OI1h, O1, OI2h, PPO2h, Oz, PPO10h, O2 Loc3: CPP3h, P7, P5, P3, PPO9h, TPP7h, PO9, PO7, PO3, PPO1h, OI1h, O1, OI2h</td>
<td>P2, Pz, Pz, P2</td>
</tr>
</tbody>
</table>

Figure 4: The method for extracting an ERP from EEG data. (a) The EEG signal is taken in segments time-locked to stimulus presentation. (b) Those segments are averaged. Image from Luck et al., 2000.
RESULTS

Visual Field Mapping

The results of the visual field mapping can be seen in Figure 5. The topoplots show the response to checkerboard stimuli presented at the same locations at which the plots are situated. The topoplots are for activity occurring 82ms after the presentation of the stimulus, which is around the time at which the C1 component peaks. The best locations for each subject are highlighted with an arrow. The angles chosen were 25° for AB and 40° for LG. These were the angles between two vertical targets and they were used for all experiments.

C1 Modulation

A typical ERP wave can be seen in Figure 6. The different components that were assessed are highlighted. We found no difference between the amplitude of the C1 component of the visually evoked event related potentials for attended and unattended stimuli in all tasks as seen in Figures 7 and 8 (ANOVA values provided in Figure 12). This was the case for stimuli presented in all four locations. There was no attentional modulation of the C1 component.

However, a spatially specific difference in performance was observed in Experiment 2 (Figure 9). The performance on the task varied for stimuli in unattended and attended locations based on when and where the stimulus was presented. Subject AB performed better when stimuli appeared in the lower visual field around 300ms before saccade onset. Subject LG showed a similar behavioral facilitation in the same time range of 300ms before the saccade, but the effect was more pronounced for locations in the upper visual field.

For Experiment 3, the average performance for stimuli at the attended location better than that for stimuli at the unattended location. Reaction times for attended stimuli were also faster for both subjects. These values are presented in Table 2.

The difference in the behavioral performance for the attended and unattended conditions in the absence of a C1 amplitude difference led us to believe that later components could be responsible for these results.
Table 2: Results of Experiment 3.

<table>
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<tr>
<th>Subject</th>
<th>Unattended Performance (percent correct)</th>
<th>Attended Performance (percent correct)</th>
<th>Unattended Response Reaction Time (ms)</th>
<th>Attended Response Reaction Time (ms)</th>
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<tr>
<td>AB</td>
<td>93%</td>
<td>98%</td>
<td>383</td>
<td>355</td>
</tr>
<tr>
<td>LG</td>
<td>90%</td>
<td>96%</td>
<td>366</td>
<td>356</td>
</tr>
</tbody>
</table>

**P1 Modulation**

We next examined whether there were any differences among the P1 component. There was a statistically significant difference for the component based on the condition of attention, task, and location for both subjects (Figure 12).

Interestingly, there was an increase in the overall amplitude of the component across experiments, as seen in Figures 7 and 8. The P1 component was larger when the subject was required to perform a perceptual task than when they were solely focused on making saccades. As seen in Figures 10 and 11, this was also true across the timecourse of saccade preparation. The P1 component is consistently greater when tasks require more resources. Additionally, there appears to be a larger difference between the P1 component for attended and unattended conditions immediately preceding the saccade.

Also of note, was the result that the value of the P1 component in Experiment 3 was usually in between that of the two saccade experiments. It was generally lower than that of the experiment that involved both eye movements and saccades, but greater than the task which only required eye movements.

**P3 Component**

The P3 component was modulated by attention in Subject LG but not in Subject AB. The magnitude of this component was significantly different among experiment type and location for both subjects.
Figure 5: Scalp topographies for both subjects created using multifocal mapping. The best location for presenting stimuli that elicit a strong C1 component is labeled with an arrow.
Figure 6: ERPs for AB from Experiment 1. The four plots correspond to the four locations tested. The components of the ERP that were later assessed are highlighted.
Figure 7 (continued on following page)
The C1 Component:

The P1 Component:
The P3 Component:

Figure 7: The absolute value of the magnitude of the three ERP components for each location and for each experiment for Subject AB. Red bars represent responses to unattended stimuli and blue represents attended.
Figure 8 (continued on following page)

The C1 Component:

The P1 Component:
Figure 8: The absolute value of the magnitude of the three ERP components for each location and for each experiment are shown for Subject LG. Red bars represent responses to unattended stimuli and blue represents attended.
Figure 9: Performance, in Experiment 2, for probes presented at different times relative to saccade onset. The red lines indicate unattended stimuli and the blue lines are attended.
Figure 10: The absolute value of the amplitude of the C1 component (left) and the P1 component (right) are shown for probes occurring at different times relative to saccade onset, which would be at time zero, in Subject AB. Dashed lines are for Experiment 1, solid lines are for Experiment 2, and the stars show the magnitude of the component in Experiment 3 (magenta=attended, green=unattended for stars). Red and blue signify unattended and attended stimuli, respectively.
Figure 11: The absolute value of the amplitude of the C1 component (left) and the P1 component (right) are shown for probes occurring at different times relative to saccade onset, which would be at time zero, in Subject LG. Dashed lines are for Experiment 1, solid lines are for Experiment 2, and the stars show the magnitude of the component in Experiment 3 (magenta=attended, green=unattended for stars). Red and blue signify unattended and attended stimuli, respectively.
**Figure 12 (continued on following page)**

### Analysis of Variance

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<tr>
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### Analysis of Variance

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### Analysis of Variance

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DISCUSSION

We did not observe any significant modulation of the C1 component for attended and unattended stimuli in any experiment. We had hypothesized that we would see modulation of this component in Experiment 1 due to the isolation of pre-saccadic attention from top-down processing effects. The lack of modulation of the C1 component indicates that processing in the early visual cortex is likely not affected by pre-saccadic attention. Furthermore, there was no saccade-dependent differences in component amplitude for attended and unattended conditions across tasks (Figure 10 and 11). The C1 amplitude did not change as the impending saccade became imminent. If activity in V1 was tied to pre-saccadic shifts of attention, then one would
expect to see larger amplitudes or larger differences between attended and unattended conditions as saccade onset approaches.

The locus of these attentional shifts is probably in higher visual areas since later components did show attentional effects. While an attentional modulation of the P1 component was observed for both subjects, the modulation of the P1 component is not as pronounced as the modulation of the P3 component in Experiment 1 for Subject LG (Subject AB does not show significant attentional modulation of P3). This suggests that perceptual facilitation at saccadic targets could be attributed to an increase in the P3 amplitude which has been shown to be related to the accumulation of evidence towards making a decision (Kelly & O’Connell, 2013). It is also possible that the extrastriate cortex, which gives rise to the P1 component, may play a role in pre-saccadic facilitation because this component also displayed attentional modulations in the absence of a psychophysical task. However, the effect in the parietal cortex is more conspicuous and this area has been shown to be tied to perception by way of accumulating sensory evidence (O’Connell et al., 2012). But on the other hand, the P1 component shows a saccade-specific attentional effect (Figure 10 and 11). Note that at 100ms before the saccade is executed, the P1 magnitude for an attended stimulus rises sharply above that for an unattended stimulus. This effect is present in most locations for both subjects and it is also interesting that it is not present at other times. Long before saccade onset, there is no attentional effect on the P1 component. This analysis of attentional effects relative to eye movement initiation was not carried out for the P3 component, so it is unknown whether it displays this type of facilitation as well. It is difficult to discern which component is governing pre-saccadic attentional shifts, though it is possible that both play a role in the modulation of visual processing.

The increase of the P1 among our different experiments is indicative of the ability of this component to reflect the cognitive load imposed by a task (T. C. Handy, Soltani, & Mangun, 2001; T.C. Handy & Mangun, 2000). The P1 amplitude consistently increased as task difficulty increased, which is exemplified more clearly by Subject LG in Figure 8. Here, Experiment 1 can be considered to impose the lightest load because no perceptual task is employed; the subject is simply making saccades. Experiment 2 can be considered to be more difficult than Experiment 3 because not only did the subject have to assess and report on a feature of a briefly presented stimulus, as in Experiment 3, but they also had to be cognizant of their pace when making saccades.
Finally, we’d like to relate the behavioral effects that we observed to the component amplitudes we measured. The perceptual facilitation of stimuli in certain locations is likely due to increased processing of sensory information at that location. So we would attribute better performance to increases in ERP component amplitudes because that is indicative of more attention. In Experiment 2, subject AB showed better performance at locations 3 and 4, in the lower visual field, but only 200-400ms before saccade onset (Figure 9). The P1 component does not follow this pattern and the C1 component did not change relative to saccade onset at all. In fact, the P1 component shows larger responses to attended vs unattended stimuli right before the saccade, which is exactly when the behavioral facilitation drops off for this subject. Therefore, neither of these components can be said to be responsible for the behavioral enhancements seen in Subject AB, but the P1 component may actually contribute to a decrease in perception right before a saccade. However, in Experiment 3, this same subject exhibited better performance and faster reaction times at the attended locations and the P1 component in this experiment was larger for attended stimuli. Similarly, Subject LG showed behavioral facilitation at locations 1 and 2 in the upper visual field. This facilitation cannot be attributed to the P1 component either, but the inhibition of perception right before saccade onset occurs just as the P1 component amplitude increases.

CONCLUSION

The locus of pre-saccadic attention is likely not in striate cortex but in higher visual areas such as the extrastriate or parietal cortex. Enhanced performance at attended locations in tasks with saccades seems to be attenuated right before saccade onset due to increased activity in the extrastriate cortex. However, better performance in covert tasks not involving eye movements occurs in conjunction with attentional modulation of P1, suggesting that this area of the brain can have different effects on perception based on whether or not an eye movement is being planned.

FUTURE DIRECTIONS

Moving forward with this study, we would like to record data from more subjects to determine which of the effects we are seeing are consistent across subjects, especially those of task and attention on the P1 and P3 components.


