Is Covert Attention Necessary for Programming Accurate Saccades? Evidence From Saccade-Locked Event-Related Potentials

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Abstract

For decades, researchers have assumed that shifts of covert attention mandatorily occur prior to eye movements to improve perceptual processing of objects before they are fixated. However, recent research suggests that the N2pc component—a neural measure of covert attentional allocation—does not always precede eye movements. The current study investigated whether the N2pc component mandatorily precedes eye movements and assessed its role in the accuracy of gaze control. In three experiments, participants searched for a letter of a specific color (e.g., red) and directed gaze to it as a response. Electroencephalograms and eye movements were co-registered to determine if neural markers of covert attention preceded the initial shift of gaze. The results showed that the presaccadic N2pc only occurred under limited conditions: when there were many potential target locations and distractors. Crucially, there was no evidence that the presence or magnitude of the presaccadic N2pc was associated with improved eye movement accuracy in any of the experiments. Interestingly, ERP decoding analyses were able to classify the target location well before the eyes started to move, which likely reflects a presaccadic cognitive process that is distinct from the attentional process measured by the N2pc. Ultimately, we conclude that the covert attentional mechanism indexed by the N2pc is not necessary for precise gaze control.

Keywords

covert attention
eye movements
co-registration
N2pc
visual search

1. Introduction

Traditionally, vision researchers distinguish between two mechanisms of attention: overt and covert attention. Perhaps the most obvious is overt attention, in which the eyes rotate to bring an object of interest into the fovea. During scene viewing, humans make about 2–3 rapid eye movements per second (i.e., saccades), and it has been estimated that we make over 100,000 saccades in a typical day (Irwin et al., 1995). We can also generate shifts of covert attention to enhance the perceptual processing of objects without making eye movements (Eriksen & Hoffman, 1972; Posner, 1980). These shifts of covert attention are often compared to a spotlight that moves throughout a visual scene (Posner et al., 1980).

Shifts of covert attention are widely thought to occur prior to eye movements (Deubel & Schneider, 1996; Posner, 1980; Rizzolatti et al., 1987). But, there are many mechanisms of covert attention (Luck & Vecera, 2002), and relatively little research has asked why covert attention might precede eye movements.

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The current study therefore sought to examine the relationship between a neurophysiological measure of covert attentional allocation—the N2pc component—and eye movements.

The N2pc Component

One technique to measure covert attention has come from ERP studies of the N2 posterior-contralateral (N2pc) component (see review by Luck, 2012). The N2pc is a negative-going deflection that is larger over the hemisphere contralateral to a covertly attended location compared to the ipsilateral hemisphere. It is typically observed in electrode sites over posterior occipital cortex (PO7/PO8) approximately 200–300 ms after the onset of a search stimulus. For example, Luck and Hillyard (1994b) had participants search displays for a target bar (e.g., horizontal bar) amongst nontarget stimuli while refraining from making eye movements. An N2pc component was observed at electrode sites that were contralateral to the target stimulus, which was interpreted to index covert attentional allocation to the target. In subsequent studies, variations in the presence or absence of the N2pc across different experimental conditions has led to a general agreement that the N2pc component reflects a covert attentional process involved in the selection of a target item (Hickey et al., 2009; Luck & Ford, 1998; Luck & Hillyard, 1994b; Tan & Wyble, 2015; Woodman & Luck, 1999, 2003; Zivony & Eimer, 2021), although it is still debated what exact mechanism of covert attention is measured by the N2pc component (see review by Luck, 2012).

The relationship between the N2pc component and eye movements is not well understood. This is because most ERP studies using the N2pc component prohibit eye movements to avoid artifacts arising from the corneoretinal potential inside each eyeball. This potential shifts its orientation when the eyes rotate, and volume conduction of the voltage produces a negative-going deflection over the hemisphere contralateral to the direction of the eye movement (Lins et al., 1993). This artifactual voltage can easily be confused with the N2pc component. Participants in N2pc experiments are therefore instructed to maintain central fixation, and trials with eye movements are either excluded (e.g., Luck et al., 1997; Woodman & Luck, 2003) or corrected using independent component analysis (e.g., Drisdelle et al., 2017; Plöchl et al., 2012). As a result, little is known about the relationship between eye movements and the mechanism of covert attention indexed by the N2pc component. This is a lost opportunity, because the N2pc component would otherwise provide a very straightforward means of monitoring covert attention across a wide variety of eye-movement paradigms. By contrast, behavioral approaches have generally required complex dual-task approaches that combine an eye-movement task with an independent discrimination task.

The Relationship Between Covert and Overt Attention

Many previous studies have asked how covert and overt attention are coordinated during visual search, with the assumption that shifts of covert attention are automatically and obligatorily directed to the saccade destination before the eye movement is generated. For example, Deubel and Schneider (1996) investigated whether covert perceptual processing preceded saccade execution in a dual-task paradigm. At the beginning of a trial, a central arrow cue informed the participant of the location to which they needed to prepare an eye movement. After a long delay (500–1000 ms), the arrow cue disappeared, serving as the go-signal to initiate the prepared eye movement. Before the saccade could be generated, a character (an E or a 3) was briefly presented at the saccade destination or at an adjacent location and then was immediately removed. After the eye movement was completed, participants were asked to report the identity of this character. Critically, discrimination accuracy for the character was much higher when it was presented at the saccade-target location compared to other locations. This presaccadic enhancement effect was taken to suggest that covert attention had shifted to the saccade-target location immediately prior to the eye movement, improving perceptual processing at this location (see also Hoffman & Subramaniam, 1995; Kowler et al., 1995; Schneider & Deubel, 1995; Shepherd et al., 1986).

Not all agree, however, that a shift of covert attention mandatorily precedes eye movements (see reviews by Hunt et al., 2019; Li, Hanning, et al., 2021). First, many studies have failed to find presaccadic enhancement effects under certain conditions (Hunt & Kingstone, 2003b, 2003a; Klein, 1980; Klein & Pontefract, 1994; MacLean et al., 2015; Remington, 1980), which suggests that covert attention might not always precede eye movements. Second, Li, Pan, and colleagues (2021) have questioned whether presaccadic enhancement effects observed in dual-task paradigms are truly due to a shift of covert attention, or instead reflect some other kind of cognitive process (see also Huber-Huber et al., 2021). Specifically, the authors compared contrast-response functions for presaccadic enhancement effects and shifts of covert attention. Shifts of covert attention resulted in both contrast-gain changes and response-gain changes, consistent with predictions made by models of covert attention (Reynolds & Heeger, 2009). Yet, presaccadic enhancement effects only resulted in response-gain changes and failed to produce contrast-gain changes. These results were taken to suggest that presaccadic enhancement effects may rely on an attentional mechanism that is conceptually distinct from covert attention.

In sum, there has been mixed evidence of presaccadic enhancement effects at saccade target locations. Furthermore, there is some evidence that such presaccadic enhancement effects, when present, may be mediated by conceptually distinct cognitive processes from those involved in shifts of covert attention. As a result, it is unclear whether covert attentional processes mandatorily occur before every eye movement.

The Presaccadic N2pc Component

Most investigations into how covert and overt attention are coordinated have come from behavioral studies using dual-task paradigms. These paradigms have typically combined eye movement tasks and probe discrimination tasks to provide a snapshot of where covert attention had been allocated before an eye movement began. However, these dual-task paradigms are often highly demanding and may encourage attentional strategies that are not utilized under more naturalistic visual search conditions. By contrast, the N2pc can be used to monitor attention without a secondary task and could therefore be used to assess whether the mechanism of covert attentional selection indexed by this ERP component occurs prior to eye movements in tasks with simpler designs. However, as noted above, it is difficult to isolate the N2pc component in eye movement tasks due to ocular artifacts.

Recently, Weaver and colleagues (2017) devised an innovative technique to overcome the problem of ocular artifacts during visual search tasks. Participants searched displays of vertical lines for a uniquely oriented line (e.g., 20°) and directed their eyes to it as the response. Instead of time-locking to the onset of a search array (as in most previous N2pc studies), the EEG data were time-locked to the onset of the first saccade (see Dimigen et al., 2011, for a methodological overview). As a result, the ERP data before time zero (i.e., saccade onset) were largely free of ocular artifacts. Crucially, an N2pc-like negativity was detected prior to saccades that were directed to the target, and this presaccadic N2pc component was taken as evidence that covert attention had been allocated to the target before the eye movements were initiated (see also Huber-Huber et al., 2016, 2021; van Zoest et al., 2021).

There is also evidence that eye movements can be directed to search targets without an accompanying presaccadic N2pc component. For example, Talcott and Gaspelin (2021) had participants search for a target-colored square (e.g., red) amongst distractor squares and make a speeded response about the location of the gap in the target (top or bottom). When participants were prohibited from making eye movements during the task, a large N2pc component was found, in line with many prior studies. However, when participants were allowed to move their eyes to the target (which they did on almost every trial), no presaccadic N2pc component was observed. A control experiment revealed that a presaccadic N2pc component did occur when participants were forced to covertly attend the target prior to generating an eye movement. Altogether, these results suggest that the presaccadic N2pc component does not mandatorily occur before eye movements. Rather, the covert attentional process indexed by the N2pc component may be conditionally deployed before eye movements depending on task demands.

The above findings suggest that the mechanism of covert attention indexed by the N2pc component does not mandatorily occur prior to all eye movements, but it may still be necessary for some types of eye movements. This parallels the fact that some but not all behavioral studies have found evidence for a presaccadic shift of covert attention (Hunt & Kingstone, 2003b, 2003a; Klein, 1980; Klein & Pontefract, 1994; MacLean et al., 2015; Remington, 1980). This raises an important question: Why is covert attention observed prior to eye movements in some experiments but not others? To answer this question, it might be fruitful to consider how shifts of covert attention might be used to aid shifts of gaze.

One possibility is that covert attention is used to improve the precision of eye movements, and this might be particularly likely to occur in certain search tasks. For example, observers might deploy covert

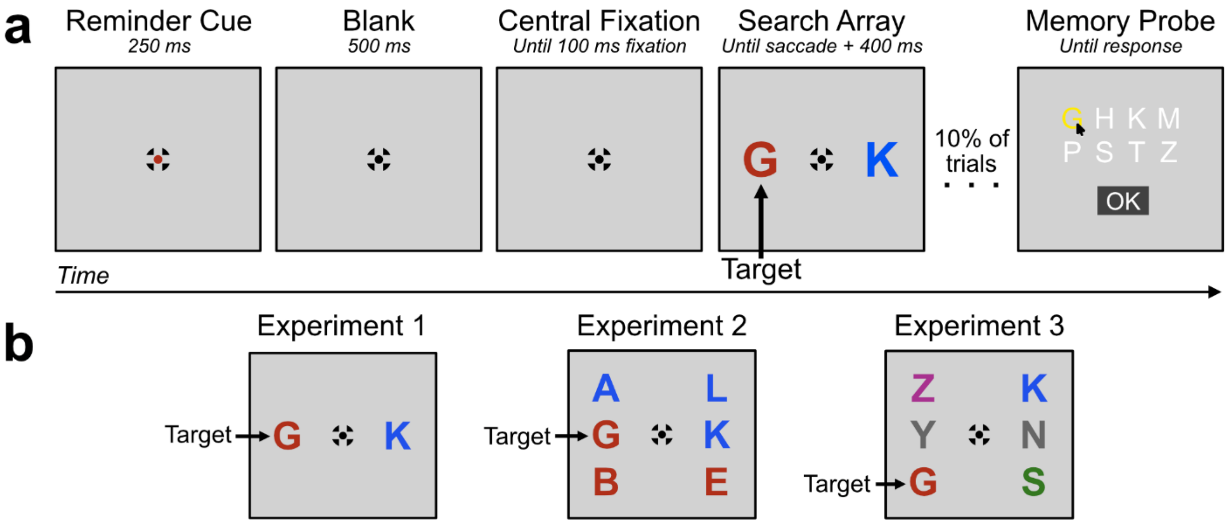

Figure 1. Stimuli and procedure for Experiments 1–3. (A) The trial sequence for the experiments. Participants searched for a letter of a specific target color (e.g., red) and generated a saccade to it. On memory probe trials (10% of trials), participants were then asked to report the identity of the target letter. (B) Search displays for the experiments. In Experiments 1 and 2, the target could appear at either of the two locations on the horizontal midline. Dummy distractors were added above and below each potential search location to encourage filtering around the attended location in Experiment 2. In Experiment 3, the target could appear at any of the four corner locations. See the online article for the color versions of all figures in this article.

attention before eye movements to assess whether an object is likely to be the target or distractor to minimize the number of locations that need to be overtly searched (e.g., as proposed by Luck, 2009). This would be especially important when the target is accompanied by nearby distractors. By selecting the target and suppressing the distractors, the location of the target can be more accurately determined and used to guide the saccade programming system. In line with this hypothesis, many of the studies that have found a presaccadic N2pc component used relatively difficult search tasks that maximized the need for careful gaze control (e.g., Huber-Huber et al., 2016, 2021; Talcott & Gaspelin, 2021, Experiment 2; Weaver et al., 2017). However, there were many other uncontrolled differences between previous studies, making them challenging to directly compare.

The Current Study

The current study used a saccade-to-target paradigm (Figure 1). Participants searched for a letter of a specific target color (e.g., red) and generated an eye movement to it. We then examined whether these eye movements were preceded by an N2pc component. We started with an extremely simple eye movement task, similar in design to our previous task that did not elicit a presaccadic N2pc (Talcott & Gaspelin, 2021). We then added elements designed to increase the likelihood that a presaccadic shift of covert attention would be helpful in making a fast and accurate saccade. We predicted that a presaccadic N2pc would be observed when the target was accompanied by nearby distractors and could appear at several different locations. We further predicted that the N2pc component would be especially evident prior to saccades that were fast and accurate.

To preview the results, the data did not support our predictions: we found no evidence that the N2pc component was associated with improved gaze control. An initial experiment (Experiment 1) found no evidence of a presaccadic N2pc component even though shifts of gaze were rapidly and accurately directed to the target. In a follow-up experiment (Experiment 2), we added distractors around the target to increase the importance of distractor filtering. We still found fast and accurate eye movements with no presaccadic N2pc component. In a final experiment (Experiment 3), we increased the number of potential target locations and finally observed a presaccadic N2pc component. However, when we examined trial-to-trial variations in gaze performance, we found no evidence that the N2pc was associated with saccadic speed or accuracy.

In addition, we also examined electrophysiological markers of presaccadic processing using ERP decoding (Bae & Luck, 2018). Specifically, support vector machines were trained to predict the target location from ERP scalp data before eye movements were generated. Any above-chance decoding accuracy would indicate that some information predictive of the target location was present in the ERP scalp data prior to an eye movement. Interestingly, the decoder was able to accurately classify the target location about 100 ms prior to an eye movement in all experiments, regardless of whether an N2pc was observed. These results are important because they suggest that some kind of cognitive process occurred before eye movements that was independent of the covert attentional process measured by the N2pc component. These decoding results might reflect processes other than spatial attention, such as motor preparation or feature-based attention (for more, see the General Discussion). In any case, ERP decoding may offer important future insights into the cognitive processes that occur before eye movements.

Experiment 1

Experiment 1 used an easy saccade-to-target task with the aim of reproducing the prior finding of no presaccadic N2pc in an easy visual search task (Talcott & Gaspelin, 2021). In the prior study, the task was to find a uniquely colored square and report the location of a tiny gap on this square; the gap was too small to be perceived parafoveally, so eye movements were implicitly required. In the present study, eye movements were explicitly required: participants searched displays of two letters for a target-colored letter (e.g., red) and were instructed to generate an eye movement to it as the response (Figure 1A). On some trials (10% of trials), participants were then asked to complete a memory probe task in which they reported the identity of the target letter after fixating it. [1]

Method

Participants

Twenty undergraduate students from the State University of New York at Binghamton participated for monetary compensation (Mage = 19.9 years; 6 men and 14 women). The sample size was determined a priori to be similar to prior studies of the presaccadic N2pc component (Talcott & Gaspelin, 2021, Experiment 2; Weaver et al., 2017). With our planned analytic approach, this sample size provides 99% power to detect a presaccadic N2pc based on the effect sizes observed in prior presaccadic N2pc studies (ηp2 = 0.70, reported in Weaver et al., 2017). All participants had normal neurological history, normal or corrected-to-normal visual acuity as assessed by a Snellen test, and normal color vision as assessed by an Ishihara test.

Apparatus

Stimuli were presented using PsychToolbox (Brainard, 1997) for MATLAB and were presented on an Asus VG248QG LED monitor placed at a viewing distance of 100 cm in a dimly lit room. A photosensor was used to measure the timing delay of the monitor (12 ms), and all data were adjusted offline to compensate for this delay.

Stimuli and Procedure

The basic task is illustrated in Figure 1A. Each display consisted of two letters that were presented in Arial font (1.0° in width and height) that appeared 4° to the left and right of the center of the screen. Letters were presented on a light gray background (100.0 cd/m2, x = .296, y = .330). One letter was red (30.0 cd/m2, x = .148, y = .070) and the other was blue (30.0 cd/m2, x = .631, y = .331), which were photometrically isoluminant and similar in color saturation. An optimal fixation stimulus (Thaler et al., 2013), which consisted of a black circle (0.7° diameter) that contained a gray crosshair (0.7° in height and width; 0.1° thick) and a small inner dot (0.1° diameter), was continually present except during the probe stimuli. The letter set consisted of eight consonants that were chosen from a subset of the Latin alphabet (G, H, K, M, P, S, T, and Z). The identities of the target and distractor letters were selected at random and without replacement within each display, and all potential pairings of the target and distractor identities were equiprobable.

At the beginning of each block of trials, the participant was told that either red or blue would be the target color for that block. In addition, the color of the inner dot of the fixation stimulus was briefly changed at the beginning of each trial to remind the participant of the target color in the current block. The target color alternated every block, and the order of blocks was counterbalanced across participants. Participants

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[1] We had initially planned on assessing ERP decoding of the target and distractor letter identity, and the memory probe task was meant to make the letter identity task relevant. However, we found that decoding accuracy for letter identity was very low, so the letter decoding accuracy results are found in the Supplementary Materials.

were instructed to respond by making an eye movement to the target-colored letter as quickly as possible while maintaining a high accuracy.

Each trial began with the reminder cue of the target color for 250 ms. Next, the fixation display appeared for 500 ms. Participants were then required to maintain fixation within 1.5° of the center of the screen for an additional 100 ms to initiate a trial. The search array then appeared. A response was recorded as soon as gaze moved within 2° of a letter. After a response was made, the search array remained on the screen for 400 ms and then terminated. If the response was too slow (slower than 2000 ms) or the response was incorrect (i.e., gaze was directed to the distractor-colored letter), a 200-Hz tone sounded for 300 ms.

On memory probe trials (10% of trials), participants were next asked to report the identity of the target letter from the immediately preceding search array. All eight potential letters were displayed on the screen in white Arial font (1.0° each) and participants clicked on a letter with a mouse to select it. Once a letter was selected, it turned yellow. Participants were only allowed to select one letter. Participants confirmed this selection by clicking on an “OK” button at the bottom of the screen, thereby advancing the experimental program to the next trial. The intertrial interval was randomly selected between 0 and 500 ms to prevent entrainment of the EEG to the stimulus stream.

After receiving instructions on the task, each participant first completed two practice blocks of 56 trials. Participants then completed ten blocks of 112 trials. The first five trials of each block were removed from all analyses to eliminate any potential feature priming of the target color from the previous block.

Eye Tracking

An SR Research Eyelink 1000+ desk-mounted system recorded gaze position monocularly from the right eye at 500 Hz. The eye tracker was used in remote mode (i.e., with a specialized lens that can operate without a chinrest) to reduce discomfort throughout the experimental session. The eye-tracking and stimulus-presentation systems were interfaced using the EyeLink Toolbox (Cornelissen et al., 2002). The onset of a saccade was determined using minimum velocity threshold of 30°/s and an acceleration threshold of 9500°/s2. Participants completed a nine-point calibration procedure at the beginning of each block. If a participant failed to meet the fixation requirement for more than 5 seconds on a given trial, the eye-tracking system was recalibrated before restarting the trial. An online drift correction procedure was additionally implemented to help maintain the eye tracker calibration accuracy within a block.

The eye-tracking analyses focused on the destination of the first saccade on each trial. The destination of the first eye movement was classified offline as the first saccade to land outside the 1.5° central fixation region and within 3° of either letter. The average first saccade end position was ±0.8° (SD = 0.2°) from the center of a letter. Trials were excluded from analyses if they contained an incorrect response (i.e., gaze was shifted to a distractor; 1.3%) or abnormal saccadic latencies (less than 50 ms or greater than 1000 ms; 0.2%). Additionally, 2.3% of all trials were excluded for having abnormal first saccade destinations (i.e., the first saccade started outside the 1.5° central fixation region or ended at a distance greater than 3° from either search item) and 0.5% of all trials were excluded due to miscellaneous issues (e.g., no eye movement was generated, or any shifts of gaze did not meet the a priori saccade thresholds).

EEG Recordings

The EEG was recorded using a 32-channel set of active Ag/AgCl electrodes (Brain Products actiCHamp) from a set of 27 standard scalp sites (FP1, FP2, F3, F4, F7, F8, C3, C4, P3, P4, P5, P6, P7, P8, P9, P10, PO3, PO4, PO7, PO8, O1, O2, Fz, Cz, Pz, POz, Oz). Recordings were also obtained from left and right mastoids, and their average was used to reference the data offline. Vertical eye movements and blinks were measured in the EEG system using the vertical electrooculogram (VEOG), and horizontal eye movements were measured using horizontal EOG. The EOG signals were used to verify that the eye tracker data were perfectly synchronized with the EEG data.

During the experimental session, impedances were kept at or below 10 kΩ for all electrodes. Brain Vision Recorder software was used to record the EEG data online with a 500-Hz sampling rate. The data were analyzed offline using EEGLAB Toolbox (Delorme & Makeig, 2004) and ERPLAB Toolbox (Lopez-Calderon & Luck, 2014). A noncausal Butterworth high-pass filter (half-amplitude cutoff: 0.1 Hz, slope: 12 dB/octave) was applied to the data offline for analyses of traditional ERPs, but not for analyses of ERP decoding (to avoid artifactual temporal spreading of decoding accuracy; van Driel et al., 2021).

Data from the EEG and eye tracking systems were measured concurrently, and event codes were

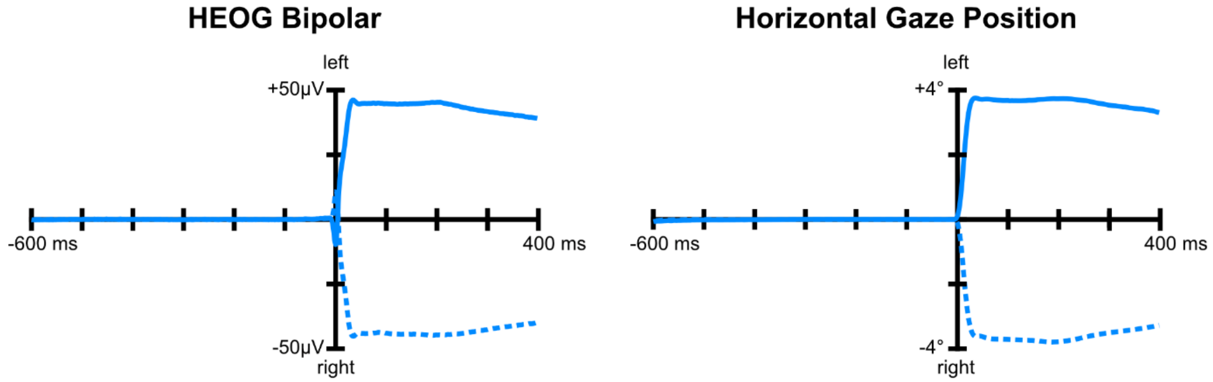

Figure 2. Bipolar horizontal electrooculogram (HEOG) and horizontal gaze position time-locked to the onset of the first saccade in Experiment 1. Both plots depict only trials where the first saccade was directed to the target. Leftward eye movements are shown as positive values and rightward eye movements are shown as negative values. Crucially, both measures deviate at the time-lock point.

simultaneously sent to both systems via a parallel port splitter. The data were then combined offline using the EYE-EEG Toolbox (Dimigen et al., 2011). The timing of event codes in the EEG and eye tracking files were perfectly correlated (R2 = 1.00 for all participants). Nearly all events had a 0-ms latency difference between data types, and all other events that were identified as having a latency difference between data types were separated by no more than a single sample (i.e., +/- 2 ms). To provide additional confirmation that the EEG and eye-tracking data were properly synchronized, we examined HEOG signals and horizontal gaze position time-locked to the onset of the eye movement, as determined by the eye tracker. A figure of these plots is included in Figure 2. Importantly, both HEOG and horizontal gaze position deviated from the center of the screen precisely at the time-locking point, confirming that the synchronization was successful.

Separate analyses were conducted to examine the EEG data (a) time-locked to the onset of the search array (stimulus-locked), and (b) time-locked to the first eye movement during the search array (saccade-locked). Stimulus-locked waveforms were computed as in prior studies of the N2pc component (Luck & Hillyard, 1994a, 1994b; Woodman & Luck, 1999, 2003). An 800-ms epoch was established, beginning 200 ms prior to stimulus onset. Then the EEG signal was baselined using the 200-ms prestimulus period and screened for artifactual signals. Saccade-locked waveforms were generated using a two-stage process, similar to previous studies (Huber-Huber et al., 2016, 2021; Krebs et al., 2012; Talcott & Gaspelin, 2021; Weaver et al., 2017). First, the EEG data were time-locked to the onset of the search array using a large 2500-ms epoch that began 500 ms before the onset of the search array. The data were then baselined to the 200-ms window immediately preceding the onset of the search array. Next, the data were re-epoched into 1000-ms epochs beginning 600 ms before the onset of the first saccade. These saccade-locked epochs were then screened for artifactual signals. This made it possible to use the 200 ms immediately prior to search array onset as the baseline for the saccade-locked averages as well as for the stimulus-locked averages. After artifact rejection was completed, only trials with first saccades that were directed to the target were used in analyses (which was 98.7% of trials; see also Behavioral Performance).

Trials with common artifacts (i.e., eyeblinks and large voltage deflections) were rejected from the epoched data using an automatic routine. Due to the nature of how saccade-locked epochs were generated, the saccade-locked epochs likely contained data that was not included in the stimulus-locked epochs. Thus, the artifact rejection routine was conducted separately for stimulus-locked and saccade-locked data. Eye blinks were characterized as step-like voltage changes that exceeded 80 µV in any 200-ms window within the epoch and the threshold for large voltage deflections was set at □100 µV in any electrode channel. Because our analyses focused on ERP signals preceding eye movements, artifacts created by the eye movements were neither rejected nor corrected. Participants were replaced if the number of trials rejected for artifacts in the EEG signal exceeded 25% of trials in either the stimulus-locked or saccade-locked data. One participant was replaced for this reason. For one participant, electrodes F7 and F8 were interpolated using the remaining scalp electrodes for all analyses. In the final sample, an average of 2.7% of trials in the stimulus-locked data and 4.3% of trials in the saccade-locked data were excluded for artifacts.

The measurement windows and electrode sites were chosen a priori based on previous studies of the N2pc component in the stimulus-locked data (Gaspelin & Luck, 2018; Hickey et al., 2009; Woodman & Luck, 1999, 2003) and in saccade-locked data (Huber-Huber et al., 2016; Talcott & Gaspelin, 2021; Weaver et al., 2017). This was done to prevent Type I errors as a result of post-hoc data selection procedures. (Luck & Gaspelin, 2017). The N2pc component in the stimulus-locked data was measured as the mean amplitude in the contralateral-minus-ipsilateral difference waveform relative to the location of the target at the PO7/PO8 electrode sites during the 200–300 ms time window. The presaccadic N2pc component in the saccade-locked data was measured as the mean amplitude in the contra-minus-ipsi difference waveform at the PO7/PO8 electrode sites in the 50 ms window leading up to the onset of the saccade (i.e., -50–0 ms). This time window was chosen to match prior studies investigating the presaccadic N2pc component (Huber-Huber et al., 2021; Talcott & Gaspelin, 2021; Weaver et al., 2017). Significance was assessed using a one sample t test against 0 μV in the a priori time window for both the stimulus-locked and saccade-locked data.

ERP Decoding Analysis

The ERP decoding analyses were based on the methods of Bae and Luck (2018, 2019). As an overview, this approach created averaged ERPs for left-target and right-target trials, and a machine learning algorithm was trained to predict the target side from the distribution of voltage over all the scalp electrodes. To avoid issues related to overfitting, we used a cross-validation procedure in which a subset of trials was left out of the averaged ERPs that were used for training the decoder, and averaged ERPs from these left-out trials were used to test whether the decoder could accurately predict the target side. This process was repeated many times with different random subsets of trials used for training and testing, and the percentage of correct predictions was computed across these repetitions. To increase the speed of the decoding analysis, the EEG signals were resampled to 50 Hz (i.e., one data point every 20 ms). In addition, whereas Bae and Luck (2018) used a low-pass filter at 6 Hz to focus on slow brain activity during the maintenance period of a working memory task, we low-pass filtered the data at 20 Hz using the EEGLAB eegfilt() routine to attain greater temporal resolution. Because there were only two possibilities (left and right), chance-level decoding was 50%. Decoding was performed separately at each time point relative to either stimulus onset (for stimulus-locked averages) or saccade onset (for saccade-locked averages), making it possible to assess the amount of decodable information in the ERP signal at each point in time following the stimulus or preceding the saccade. The decoding procedures were nearly identical between stimulus- and saccade-locked analyses, differing only in their respective epoch time windows. Decoding was performed separately for each participant and mean decoding accuracy across participants was compared to chance (50%) at each time point with correction for multiple comparisons. For an in-depth description of the ERP decoding analysis, see the Supplemental Materials.

If information about the target location is represented in the scalp ERP data, then decoding accuracy for those aspects of the target should be greater than chance (50%). One-sample t tests comparing decoding accuracy with chance were conducted for all time points after stimulus onset in the stimulus-locked data (20–580 ms) and after the average stimulus onset in the saccade-locked data (-200–380 ms). One-tailed tests were used because below-chance decoding accuracy is meaningless with the present procedure. Corrections for multiple comparisons were achieved by using the Benjamini-Yekutieli false discovery rate procedure that accounts for arbitrary dependencies (Benjamini & Yekutieli, 2001). This method allows greater interpretive precision than the nonparametric cluster-based technique used in prior ERP decoding studies (Bae & Luck, 2018, 2019) and makes fewer assumptions than the original false discovery rate procedure (Benjamini & Hochberg, 1995).

Data and Code Availability

The data, stimulus presentation scripts, and data analysis scripts for all experiments are available on the Open Science Framework repository, https://osf.io/umfdj/?view_only=46c7b3bfa1a74b3295f77f7ac8fb4c34. Those interested in further analyses not reported in the current study are welcome to download the data and analyses scripts. None of the experiments were preregistered.

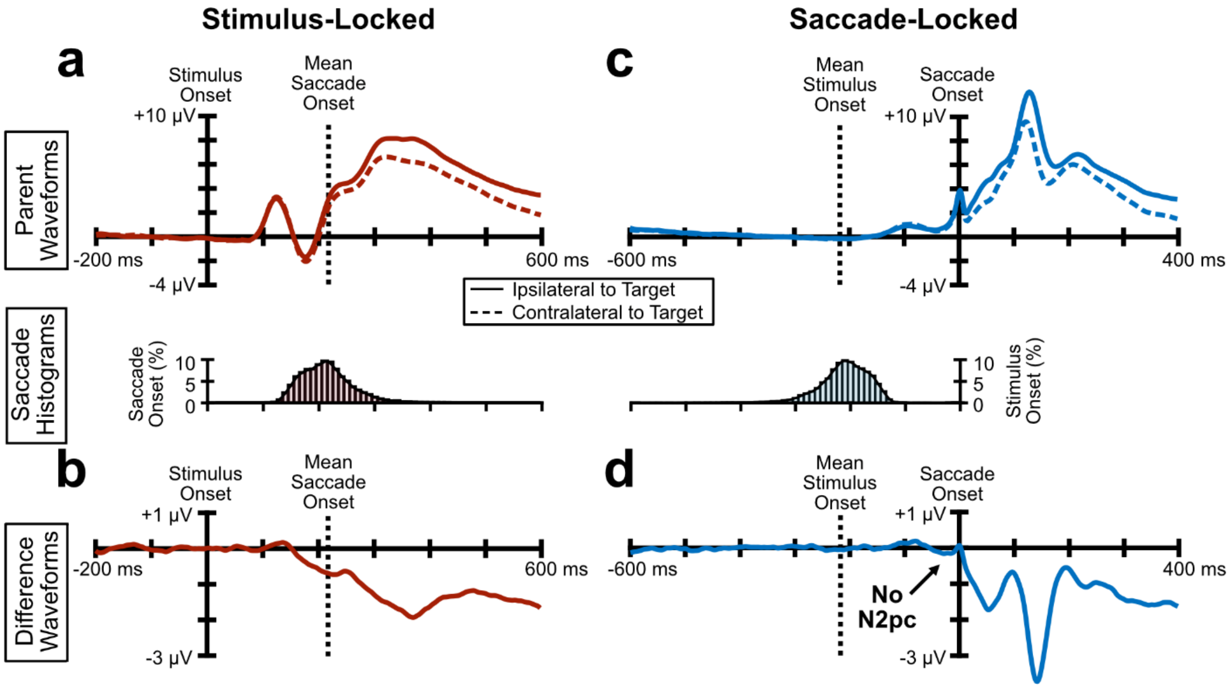

Figure 3. ERP results from Experiment 1. (A) and (C) depict grand-averaged ERP waveforms time-locked to the onset of the search array and the onset of the first saccade, respectively. (B) and (D) depict contralateral-minus-ipsilateral difference waveforms for stimulus-locked and saccade-locked ERPs, respectively. Histograms of saccade-onset and stimulus-onset are included along the horizontal axis. ERP waveforms in all figures in this paper were low-pass filtered to improve visibility (Butterworth noncausal filter, half-amplitude cutoff = 30 Hz, slope = 12 dB/octave).

Results

Behavioral Performance

Shifts of gaze were generally quick and accurate in this task. The first saccade was almost always directed to the target stimulus (M = 98.7%, SD = 0.8%) and these eye movements occurred with a mean latency of 217 ms (SD = 28 ms). Additionally, probe report accuracy was also highly accurate (M = 96.9%, SD = 3.2%), indicating participants identified the target letter after fixating it and held this representation in working memory. The critical question is whether these fast and highly accurate eye movements were preceded by an N2pc component.

Stimulus-Locked ERPs

Figure 3A shows grand-average stimulus-locked ERP waveforms on trials where the eye movement was directed to the target. These waveforms were time-locked to the onset of the search array and were computed using lateral occipital scalp sites (PO7/PO8). Separate waveforms are plotted for electrodes that were ipsilateral versus contralateral to the target location. A histogram of saccade onset is depicted below the ERP waveforms. Figure 3B shows the contralateral-minus-ipsilateral difference waveform, which isolates the N2pc from nonlateralized brain activity.

A contralateral negativity can be seen beginning approximately 150 ms poststimulus. A one-sample t test of the mean amplitude from 200–300 ms (-0.82 µV) revealed that it was significantly more negative than zero, t(19) = 3.51, p = .002, dz = 0.79. However, this negative-going deflection is likely not a true N2pc and is instead likely to be an artifact of the rotation of the eyes, which causes a change in the scalp distribution of the volume-conducted corneoretinal potential. Scalp topography maps are included in the Supplemental Materials and show that the lateralized negativity was largest at electrodes closest to the eyes, supporting this interpretation.

Saccade-Locked ERPs

To minimize ocular artifacts and assess whether shifts of covert attention occurred prior to saccade onset, we created saccade-locked averages in which time zero is the onset of the eye movement. These averages were made using only trials where the first saccade was directed to the target. We then looked for an N2pc immediately prior to time zero (which was, by definition, before the corneoretinal potential began). Figure 3C shows the grand-average ERP data, with separate waveforms for electrodes sites that were contralateral and ipsilateral to the target. A histogram showing the distribution of stimulus onset times relative to the saccade onset is included below the ERP waveforms; this histogram is the mirror image of the saccade onset latency histogram in Figure 3A. Figure 3D shows the corresponding contralateral-minus-ipsilateral difference waveform. In both Figures 3C and 3D, the voltages to the left of time zero correspond to EEG activity leading up to the eye movement, whereas voltages to the right of time zero correspond to EEG activity following the eye movement.

There was little or no contralateral negativity in the difference wave prior to saccade onset (i.e., no presaccadic N2pc component). This was formally assessed by calculating the mean amplitude of the difference waveform from -50 to 0 ms (-0.09 µV). A one-sample t test confirmed that there was no significant negative-going deflection prior to the eye movement, t(19) = 0.70, p = .494, dz = 0.16. To provide positive evidence for the lack of an N2pc, we computed the Bayes factor for this effect using the default prior of 0.707 (Rouder et al., 2009), which yielded BF01 = 3.46. This indicates that there was more evidence for the null hypothesis (N2pc absence) than there was for the alternative hypothesis (N2pc presence).

It is also possible that an N2pc was generated on only a subset of trials and served to speed the eye movements to the target on those trials. By this logic, the covert attentional process measured by the N2pc would be used as a scout for shifts of gaze to improve eye movement accuracy. To examine this, we conducted an exploratory analysis in which we performed a median split on saccadic latencies for each participant and compared the presaccadic N2pc on the averaged ERPs from the fast-latency trials (M = 185 ms) and from the slow-latency trials (M = 250 ms). No significant presaccadic N2pc component was observed for fast-latency trials (-0.15 µV), t(19) = 1.24, p = .232, dz = 0.28, or for slow-latency trials (-0.10 µV), t(19) = 0.62, p = .542, dz = 0.14. In addition, the presaccadic N2pc voltage did not differ between fast-latency and slow-latency trials, t(19) = 0.43, p = .657, dz = 0.10, and the corresponding Bayes factor provided support in favor of the null, BF01 = 3.97. Saccade accuracy was near ceiling for both fast-latency trials (98.1%) and slow-latency saccades (99.1%). Together, these results provide no evidence that the mechanism of covert attention reflected by the N2pc component was used to improve gaze control.

ERP Decoding of Target Location

The results described so far provide an interesting dissociation: saccades were quickly and accurately directed to the target but were not preceded by a shift of covert attention, at least as measured by the presaccadic N2pc component. However, some set of processes must have identified the target location and programmed the eye movement vector prior to saccade onset. As an exploratory analysis, we asked whether we could detect these processes from the scalp ERP signal by attempting to decode the target location from the distribution of voltage over the scalp at a given moment in time relative to stimulus onset (stimulus-locked decoding) or relative to saccade onset (saccade-locked decoding).

The stimulus-locked decoding results are shown in Figure 4A. Decoding accuracy exceeded chance beginning approximately 160 ms poststimulus and approached 100% after the mean saccade onset. This strong decoding accuracy after the eye movement was presumably driven, at least in part, by the artifactual voltages produced by the eye rotation. One-sample one-tailed t tests were used to compare decoding accuracy at each time point following stimulus onset to chance-level performance (50%) and were corrected for multiple comparisons. All time points beginning at 160 ms until the end of the epoch window were statistically significant after correction (p's < .01). These results indicate that information about target location was present in the scalp ERP signal beginning shortly after stimulus onset.

We next repeated the procedure on saccade-locked data to determine whether target location could be decoded prior to saccade onset, ruling out contributions from ocular artifacts. For the saccade-locked data (Figure 4B), decoding accuracy rose above chance more than 100 ms prior to saccade onset and reached nearly perfect accuracy immediately following the saccade. Decoding accuracy from -120 ms until the end of the epoch window was significantly above chance after correction for multiple comparisons (p's < .05). These results indicate that the decodable information about the target location was present in the scalp ERP signal well before the first saccade (and before the signal was contaminated by ocular artifacts). To ensure our chosen low-pass filter (20-Hz cutoff) did not spuriously induce these results, the

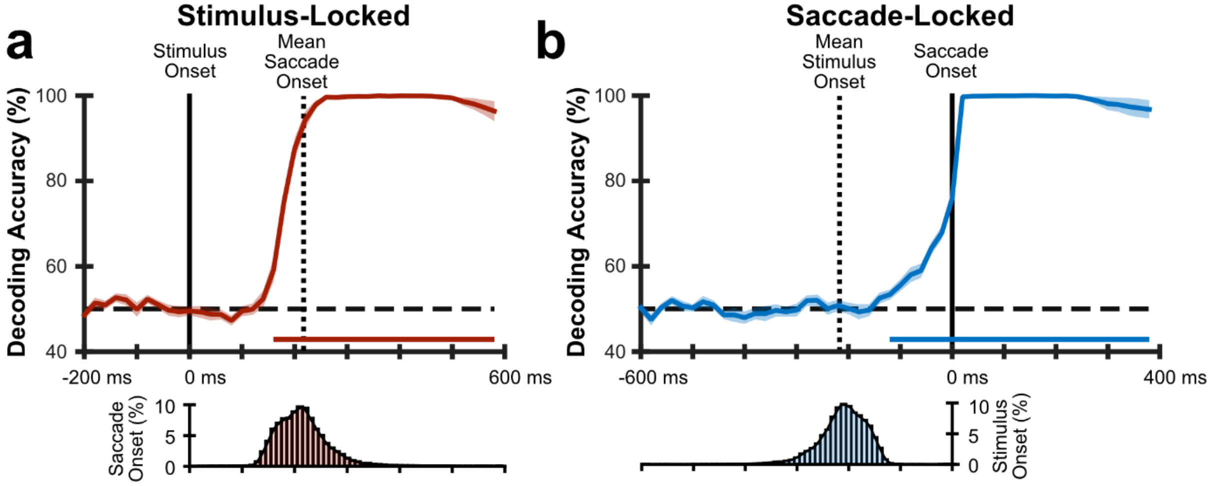

Figure 4. ERP decoding results from Experiment 1. Decoding accuracy of target location for (A) stimulus-locked and (B) saccade-locked data. Chance-level performance is depicted by a dashed horizontal line (50%). Horizontal lines along the x-axis indicate statistically significant time points (*p* < .05) after correcting for multiple comparisons. Shading indicates standard error of the mean. Histograms of saccade-onset and stimulus-onset are shown below each plot, respectively.

saccade-locked decoding analyses were rerun using low-pass filter cutoffs set at 10 Hz, 30 Hz, and 50 Hz. There were no changes in the pattern of results across the different filters.

Because the source of the decoding accuracy is unclear, an additional analysis was conducted that only used data from posterior electrode sites (Pz, P3, P4, P5, P6, P7, P8, P9, P10, POz, PO3, PO4, PO7, PO8, Oz, O1, O2). If the above-chance decoding accuracy was primarily driven by motor preparation processes in the frontal eye fields or subthreshold motor activity from the extraocular muscles, decoder performance should decrease, or even be eliminated, when only posterior electrode sites are used. Crucially, we still found robust classification accuracy prior to an eye movement, providing stronger evidence that this decoding accuracy was not driven by oculomotor activity. This is consistent with the notion that some kind of covert process had identified the target location and/or prepared a saccade to the target location, but these processes are distinct from the covert attentional process measured by the N2pc component.

Discussion

Experiment 1 evaluated whether the N2pc component occurred before eye movements in a saccade-to-target paradigm. Saccades were quickly and accurately guided to the target, and yet there was no evidence of a presaccadic N2pc component. This indicates that the mechanism of covert attention indexed by the N2pc component was not allocated to the target prior to the eye movement (see also Talcott & Gaspelin, 2021). Interestingly, an ERP decoding analysis showed that information about the target location was present in the scalp ERP signal before the eye movement was generated. This could reflect some previously undiscovered mechanism of covert attention that cannot be detected with conventional ERP analyses. However, this might instead reflect some kind of cognitive process involved in motor preparation of eye movements. For example, saccade preparatory cells in the frontal eye fields and supplementary eye fields may start firing up to 100 ms prior to saccade onset (Hanes et al., 1995).

Experiment 2

One plausible explanation for the lack of a presaccadic N2pc component in Experiment 1 was that there was little need to engage in distractor filtering. Search displays contained only two items, and these items were separated by 8° of visual angle. Many previous studies have shown that the N2pc component is substantially weakened when there are no distractors around the target object (Bacigalupo & Luck, 2015; Hickey et al., 2009; Luck, 2012; Luck & Ford, 1998; Luck & Hillyard, 1994b). Although some evidence has accumulated against the hypothesis of Luck and Hillyard (1994b) that the N2pc reflects distractor filtering per se (e.g., Hickey et al., 2009), it is still plausible that the N2pc reflects an attentional process that is applied only when the target is accompanied by nearby distractors (Luck, 2012).

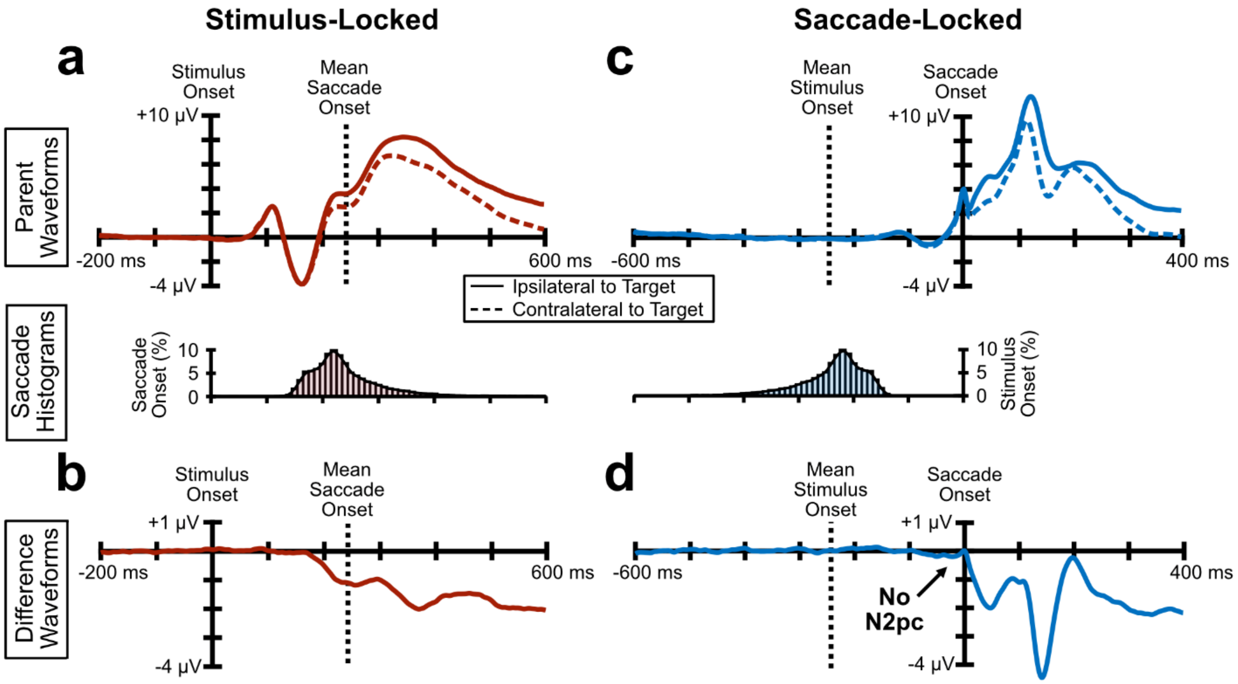

Figure 5. ERP results from Experiment 2. (A) and (C) show grand-averaged ERP waveforms time-locked to the onset of the search array and to the first saccade, respectively. Histograms of saccade-onset and stimulus-onset are shown below these waveforms, respectively. (B) and (D) show contralateral-minus-ipsilateral difference waveforms.

Experiment 2 therefore used the same task as in Experiment 1, but distractors were added above and below the two potential target locations (Figure 1B). If the lack of a presaccadic N2pc in Experiment 1 was due to the lack of nearby distractors, then a presaccadic N2pc component should be detected in Experiment 2 because distractors were added around the target. Note that Experiment 2 used “dummy distractors” at locations that could never contain a target; however, the addition of dummy distractors close to a target has been shown to increase the N2pc when participants are forced to use covert rather than overt attention (Bacigalupo & Luck, 2015).

Method

All methods were identical to those in Experiment 1 except for as follows.

A new sample of 20 students were recruited from State University of New York at Binghamton (Mage = 21.9 years; 8 women, 10 men, and 2 nonbinary). No participants were replaced for being performance outliers.

The search displays are illustrated in Figure 1B. Participants performed the same basic task as in Experiment 1, except that dummy distractors were added to increase filtering demands. The target could appear at one of two locations on the horizontal midline, and the dummy distractors were centered 2.5° above and below each potential target location (with a gap of 1.5° between the edges of the letters). This distance was chosen to maximize the N2pc mean amplitude (Bacigalupo & Luck, 2015). To keep the stimulus energy of the displays consistent, each hemifield always contained one red and one blue dummy distractor. The arrangement of dummy distractor colors (e.g., red above, blue below) was chosen at random and independent of the other hemifield. The identities of the dummy distractors were randomly selected without replacement from letters in the alphabet that were not included in the target letter set. In addition, exceptionally wide or narrow letters (i.e., I, O, Q, and W) that would be easy to filter on the basis of shape were excluded from the dummy distractor letter set.

Trials were excluded from analyses if they contained an incorrect response (2.0%) or had abnormal saccadic latencies (less than 50 ms or greater than 1000 ms; 0.2%). Additionally, trials were excluded if abnormal saccade activity was detected (i.e., the start and end positions of the first saccade on a trial did not meet our a priori criteria; 2.0%) or if no saccade event was found (0.1%). In addition, common

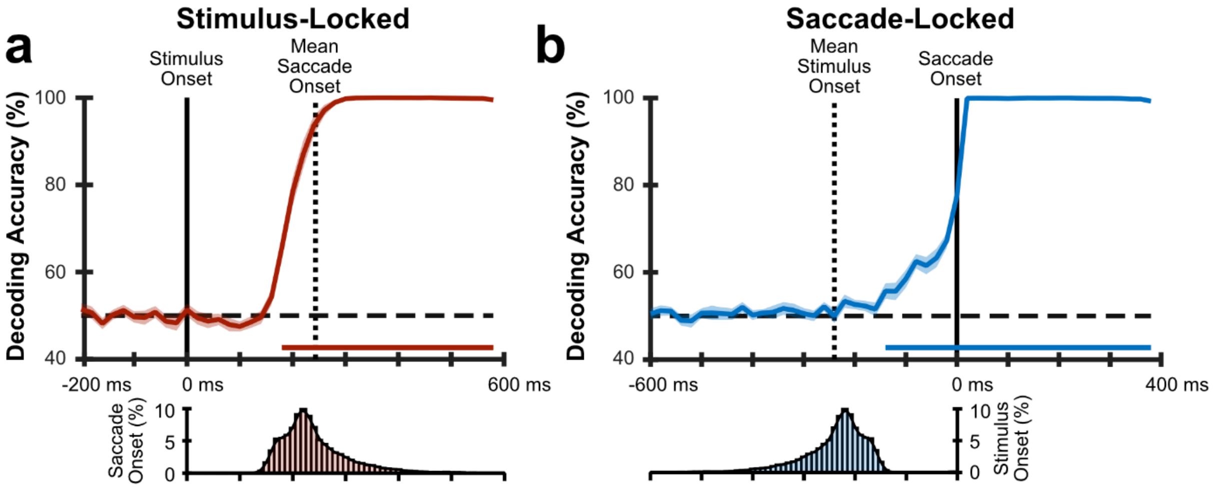

Figure 6. ERP decoding results for Experiment 2. Target-location decoding accuracy for (A) stimulus-locked data and (B) saccade-locked data. Histograms of latencies are plotted beneath. Chance-level performance is depicted by a dashed horizontal line (50%).

ERP artifacts were excluded from the epoched data using the same routines as in Experiment 1. On average, 2.5% of trials were rejected for containing artifacts in the stimulus-locked data and 3.9% of trials were excluded in the saccade-locked data.

Results

Behavioral Performance

Eye movements were fast (M = 243 ms, SD = 38 ms) and accurate (98.0% correct), similar to Experiment 1. Saccadic latencies were significantly slower in Experiment 2 (243 ms) than in Experiment 1 (217 ms), t(38) = 2.45, p = .019, d = 0.78. This provides evidence that adding the dummy distractors made it more difficult to rapidly find the target stimulus. Probe report accuracy was also high (M = 96.4%, SD = 3.7%), suggesting that the participants stored the target identity in working memory.

Stimulus-Locked ERPs

Figure 5A shows grand average ERPs stimulus-locked waveforms from electrode sites ipsilateral and contralateral to the target location, along with the probability distribution of saccadic latencies. Figure 5B depicts the corresponding contralateral-minus-ipsilateral difference waveform. A contralateral negativity in the difference waveform began approximately 180 ms after search array onset. To formally analyze this negativity, a one-sample t test assessed the mean amplitude of the difference wave from 200–300 ms poststimulus (-1.00 μV). The negativity was significantly different from zero, t(19) = 4.65, p < .001, dz = 1.04. As in the previous experiment, it is unclear how much of this negativity was the result of ocular artifacts.

Saccade-Locked ERPs

The key question in this experiment was whether adding distractors around the attended location would lead to a presaccadic N2pc component. Figure 5C shows ERP waveforms ipsilateral and contralateral to the target, time-locked to the onset of the first saccade, and Figure 5D shows the corresponding contralateral-minus-ipsilateral difference waveform. As in Experiment 1, there was no clear N2pc component prior to saccade onset. The voltage mean amplitude from -50 to 0 ms (-0.13 μV) did not significantly differ from zero, t(19) = 1.07, p = .297, dz = 0.24, and the Bayes factor was in favor of the null hypothesis, BF01 = 2.60. Thus, the mere presence of nearby distractors to filter was insufficient to elicit a presaccadic N2pc.

As in Experiment 1, we conducted an exploratory median-split analysis of the presaccadic N2pc by creating separate averages for fast-latency trials (M = 205 ms) and slow-latency trials (M = 283 ms). As in Experiment 1, no presaccadic N2pc was found on slow-latency trials (-0.19 μV), t(19) = 1.34, p = .195, dz = 0.30, or on fast-latency trials (-0.14 μV), t(19) = 1.27, p = .218, dz = 0.29. These mean amplitudes did not differ from each other, t(19) = 0.37, p = .713, dz = 0.08, and the Bayes factor was in favor of the null hypothesis, BF01 = 4.04. Saccades were highly accurate on both fast-latency trials (96.9%) and slow-latency trials (99.0%).

ERP Decoding of Target Location

Target location decoding accuracy for stimulus-locked and saccade-locked data are shown in Figure 6. In the stimulus-locked data, decoding accuracy increased above chance beginning approximately 180 ms poststimulus and reached ceiling approximately 300 ms poststimulus. Decoding accuracy was significantly greater than chance (50%) from 180 ms poststimulus until the end of the epoch (p's < .001 after correction for multiple comparisons). In the saccade-locked data, decoding accuracy rose above chance beginning 140 ms prior to saccade onset, and all time points beginning at 140-ms before saccade onset through the end of the epoch window were significantly above chance level (p's < .05 after correction for multiple comparison). The significant presaccadic decoding indicates that information about the target location was present in the ERP signal before the first saccade.

Discussion

Adding distractors above and below the potential target locations slowed saccadic latencies, confirming that they were indeed effective distractors. Nonetheless, no presaccadic N2pc was detected, indicating that the specific mechanism of covert attention indexed by the N2pc was not allocated to the target before the eye movement was generated. This suggests that the lack of a presaccadic N2pc component in Experiment 1 was not simply due to a lack of nearby distractors and expands the range of conditions under which gaze can shift without a preceding N2pc. Once again, other presaccadic processes could be detected in the ERP decoding, reflecting other cognitive or premotor processes that help guide eye movements but are distinct from the specific attentional mechanism measured by the N2pc.

Experiment 3

No presaccadic N2pc component was observed in Experiments 1 and 2, providing strong evidence that the specific covert attentional mechanism measured by the N2pc is not required for saccade programming (see also Talcott & Gaspelin, 2021). However, other previous studies have observed a presaccadic N2pc component (e.g., Huber-Huber et al., 2016, 2021; Weaver et al., 2017). One potential explanation is that these previous studies used multiple target locations (e.g., four or six), whereas there were only two potential target locations in Experiments 1 and 2 and in the study of Talcott and Gaspelin (2021). Presaccadic covert attention may be more important when the location of the target is more variable. For example, behavioral studies have shown that covert attention contributes to precision of the initial saccade and facilitates corrective saccades if a saccade is misdirected (e.g., Hollingworth et al., 2008; Van der Stigchel & de Vries, 2015). Therefore, in an effort to elicit a presaccadic N2pc component, Experiment 3 modified the paradigm of Experiment 2 to increase demands on gaze control by increasing the number of potential target locations (i.e., the relevant set size). Specifically, the target in Experiment 3 could appear at one of the four corner locations (Figure 1B)[2]. We predicted that a presaccadic N2pc would now be observed.

Method

All methods were identical to those in Experiment 2, except as follows.

A new sample of 20 participants was recruited (Mage = 20.6 years, 13 women, 7 men). One participant was replaced for abnormally slow saccadic latencies (>2.5 SDs from the mean), and another was replaced for abnormally low probe report accuracy (<2.5 SDs from the mean).

The stimuli are shown in Figure 1B. Letters were presented at the same six locations as in Experiment 2, but the target could now appear at any of the four corner locations (i.e., the dummy-distractor locations in Experiment 2). The letter identities at the four search letters were chosen randomly and without replacement from the target letter set (G, H, K, M, P, S, T, and Z), with the constraint that each target letter appeared equally often at each location. The two dummy letters along the midline were chosen randomly and without replacement from the remaining letters in the alphabet (except for I, O, Q, and W). In addition to red and blue, two new distractor colors—purple (30.0 cd/m2, x =

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[2] We realize that Experiment 3 differed from Experiment 2 in other ways as well. In particular, the location of the targets differed in respect to the horizontal meridian. However, this should have no effect on the ability to detect an N2pc. The magnitude of the N2pc is increased for targets below the horizontal meridian but reduced for those above the meridian (Luck et al., 1997; Perron et al., 2009). Thus, when averaged together, this should be equivalent to presenting the target on the horizontal midline. Another change was the addition of new colors. However, this likely increased the efficiency of color search from Experiment 2 and may have slightly reduced demands on gaze control. Thus, we believe these changes were unlikely to induce a presaccadic N2pc component in Experiment 3.

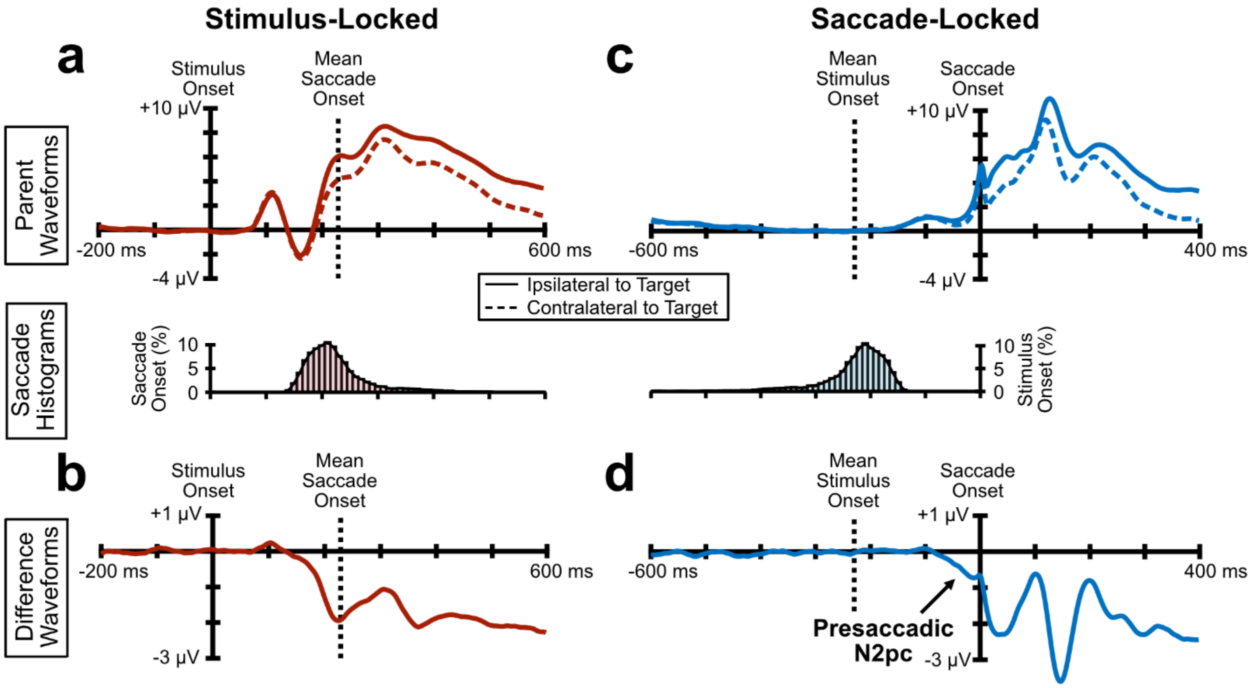

Figure 7. ERP results for Experiment 3. (A) Stimulus-locked and (C) saccade-locked grand-averaged ERP waveforms. Histograms of latencies are plotted beneath these ERP waveforms. (B) and (D) show contralateral-minus-ipsilateral difference waveforms.

.316, y = .149) and green (30.0 cd/m2, x = .273, y = .638)—were used at the potential target locations. The arrangement of the four colors across the four potential target locations within a search display was random but with a constraint that the probability of the target color appearing at each of the four potential target locations was equal within each block. The two dummy distractor letters presented on the horizontal midline were always presented in dark gray (30.0 cd/m2, x = .282, y = .293).

Participants completed two practice blocks of 64 trials, followed by 10 blocks of 128 trials. Trials were excluded from all analyses (except behavioral accuracy) if they contained an incorrect response (2.1%) or abnormal saccadic latencies (0.1%). Trials were excluded from ERP and ERP decoding analyses if they contained abnormal first saccade start or end positions (2.7%) or if no first saccade event was detected (0.4%). Additionally, the EEG data were screened for common artifacts. In the stimulus-locked analysis, 2.9% of trials were rejected for containing artifacts. In the saccade-locked analysis, 4.4% of trials were rejected.

Target location decoding procedures were similar to those used in the previous experiments but were updated to account for the increased number of possible target locations. Four SVMs were trained, each classifying one potential location against the other three potential target locations at each time point, and the location that minimized the cost function across the four SVMs was chosen as the decoded location. Chance-level decoding accuracy performance was now 25%. Because the number of target locations were doubled while the total number of trials was kept similar to the prior experiments, a 20-fold cross validation procedure was used instead of the 40-fold procedure of the two prior experiments to keep the number of trials within each subset equivalent (i.e., 10–20 trials per subset).

Results

Behavioral Performance

Eye movements were fast and accurate, as in the prior experiments. Almost all first saccades were directed to the target (M = 97.9%, SD = 1.4%) and these eye movements were initiated quickly (M = 229 ms, SD = 31 ms). Interestingly, the saccades were not significantly slowed relative to Experiment 1 (217 ms), t(38) = 1.33, p = .192, d = 0.32, BF01 = 1.62, nor were they significantly speeded relative to Experiment 2 (243 ms), t(38) = 1.25, p = .220, d = 0.39, BF01 =

1.75. Probe report accuracy was very high as well (M = 96.7%, SD = 3.3%).

Stimulus-Locked ERPs

Figure 7A depicts grand average ERP waveforms time-locked to stimulus onset for ipsilateral and contralateral electrode sites relative to the target location, and Figure 7B shows the corresponding difference wave. A large contralateral negativity can be observed in the N2pc time window (200–300 ms). A planned one-sample t test confirmed that the mean amplitude of this negative-going deflection (-1.57 μV) was significantly different from zero, t(19) = 7.54, p < .001, dz = 1.69. As in the previous experiments, it is unclear how much of this negativity can be contributed to ocular artifacts and how much is a true N2pc component.

Saccade-Locked ERPs

The key question was whether a presaccadic N2pc component would be visible in the saccade-locked waveforms. These waveforms are presented in Figure 7C, and the difference waveform is shown in Figure 7D. Crucially, a clear contralateral negativity can be observed before the saccade. Formal assessment confirmed that the mean amplitude of this negative deflection (-0.55 μV) differed from zero, t(19) = 3.71, p = .001, dz = 0.83. The Bayes factor was strongly in favor of the hypothesis of the presence of a non-zero N2pc, BF10 = 26.03. In addition, we compared the amplitude of this presaccadic N2pc with the data from Experiments 1 and 2 using independent-samples t tests. We found that the presaccadic N2pc in Experiment 3 (-0.55 μV) was significantly more negative than the presaccadic activity in Experiment 2 (-0.13 μV), t(38) = 2.21, p = .033, d = 0.70, and in Experiment 1 (-0.09 μV), t(38) = 2.29, p = .028, d = 0.72. Scalp topography maps are included in the Supplemental Materials and show that this negativity is centralized over posterior occipital electrode cites.

If saccade programming relied upon the presaccadic N2pc component for target acquisition, then eye movements should have been fastest and most accurate on trials when covert attention had rapidly selected the target. This would predict that the N2pc component would precede the fastest saccades, and thus the N2pc should have onset earlier than the fastest saccades. However, as can be seen by comparing the negativity in Figure 7B to the histograms of saccadic latencies, this was not the case. An alternative explanation might be that covert attention was deployed to support saccade programming on trials where the initial attempt to locate the target using preattentive features had failed. In other words, the eyes might have waited until the covert attentional mechanism indexed by the N2pc had localized the target before shifting gaze. According to this logic, slow-latency saccades should therefore have a large presaccadic N2pc and high saccade precision. Fast-latency saccades, on the other hand, should be associated with a small-amplitude N2pc, if one is present at all, and these saccades should be less accurate. Thus, the presaccadic N2pc component in Figure 7D should primarily reflect activity on trials with slow eye movements.

An exploratory median-split analysis was conducted on the saccade-locked ERP data by separating the data relative to each participant's mean saccadic latency. In the ERPs from slow-latency trials (M = 266 ms), a robust presaccadic N2pc component was observed (-0.65 μV), t(19) = 3.53, p = .002, dz = 0.79. In the ERPs from fast-latency trials (M = 194 ms), a significant presaccadic N2pc component was also detected (-0.34 μV), t(19) = 2.63, p = .016, dz = 0.59. A paired-sample t test confirmed that the presaccadic N2pc was larger in magnitude for slow-latency trials (-0.65 μV) than for fast-latency trials (-0.34 μV), t(19) = 2.19, p = .041, dz = 0.49.

Saccades were highly accurate on both fast-latency trials (96.5%) and slow-latency trials (98.2%). As a more sensitive index of saccade accuracy, we computed the distance between the saccade destination endpoint and the middle of the target letter for saccades directed to the target, and we then computed the average error for each participant's slow-latency and fast-latency trials. The amount of error was nearly identical for the slow-latency trials (0.98° from the target) and the fast-latency trials (0.93° from the target). If anything, the saccade error was smaller on fast-latency trials than on slow-latency trials, although the difference was not statistically significant, t(19) = 2.05, p = .054, dz = 0.46.

In sum, even though the magnitude of the presaccadic N2pc was larger for slow-latency trials than for fast-latency trials, eye movements were no more precise on slow-latency trials than on fast-latency trials. Thus, despite our best efforts and contrary to our expectations, we could find no evidence that the presence of an N2pc component was associated with faster or more accurate eye movements.

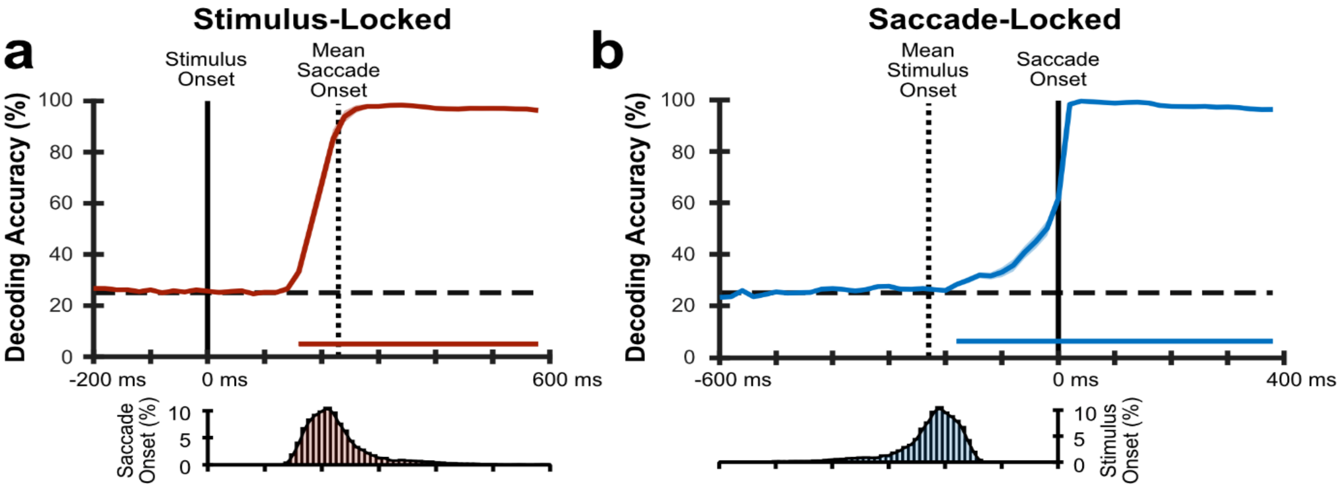

Figure 8. ERP decoding results for Experiment 3. Target location decoding accuracy for (A) stimulus-locked and (B) saccade-locked data. Chance-level performance is depicted by a dashed horizontal line (25%).

ERP Decoding of Target Location

Figure 8A shows target location decoding accuracy time-locked to the onset of the stimulus display. Because the target could appear at one of four locations, chance accuracy was 25%. Decoding accuracy was significantly greater than chance for all time points from 160 ms until the end of the epoch (p’s < .05 after correcting for multiple comparisons). Target location decoding accuracy for saccade-locked data is shown in Figure 8B. Decoding accuracy was significantly above chance from -180 ms through the end of the epoch (p’s < .05 after correcting for multiple comparisons).

Discussion

In Experiment 3, the target could appear at four locations instead of only two, as was the case in Experiments 1 and 2. This change was done in an attempt to increase demands on gaze control by more closely aligning the search task with those used in prior studies that found a presaccadic N2pc component. Crucially, a presaccadic N2pc component was observed. Interestingly, the magnitude of the presaccadic N2pc was not associated with behavioral markers of gaze control, suggesting that—even when present—the specific processes of covert attentional selection measured by the N2pc did not contribute to saccade planning. Target location decoding accuracy was also strong prior to saccade onset, suggesting that target location information that is extracted from a display prior to the saccade may be sufficiently precise to differentiate between stimuli in the same visual field (see also Fahrenfort et al., 2017, Experiment 2).

General Discussion

Covert and overt attention have largely been studied in isolation, making it unclear how they are coordinated during visual search. A common assumption is that shifts of covert attention mandatorily precede eye movements to aid in gaze control. That is, covert attention may assist saccade programming by inspecting potential targets before eye movements are generated to improve saccade speed or accuracy. The current study used a saccade-to-target paradigm to evaluate whether the mechanism of covert attention indexed by the N2pc component occurs before eye movements to produce faster or more accurate eye movements.

In Experiment 1, participants searched displays of two letters for a target-colored letter (e.g., red) and made an eye movement to it. Most saccades were quickly and accurately directed to the target. However, there was no presaccadic N2pc component, suggesting that the corresponding mechanism of covert attention is not required for a fast and accurate eye movement under these conditions. Experiment 2 added dummy distractors to the displays to increase the filtering demands of the task, which typically increases N2pc amplitude (see Luck, 2012). Nevertheless, no presaccadic N2pc was detected. Finally, Experiment 3 further increased demands on gaze control by increasing the number of possible target locations from two to four. A robust presaccadic N2pc component was observed in this experiment, suggesting that the presence of a presaccadic N2pc depends on variability in the location of the target. This is consistent with prior studies in which 4–6 target locations were used and a presaccadic N2pc was observed (e.g., Huber-Huber et al., 2016, 2021; Weaver et al., 2017). The presence of a presaccadic N2pc under some conditions but not others is consistent with research using dual-task behavioral approaches, some of which found evidence that preparing a saccade led to a shift of covert attention (e.g., Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995) and others of which did not (e.g., Hunt & Kingstone, 2003a; Klein, 1980).

Even when a presaccadic N2pc was observed (Experiment 3), we found no evidence that the magnitude of the presaccadic N2pc component was associated with improved gaze control. The N2pc was actually larger on trials with slow saccades than on trials with fast saccades, which is the opposite of what would be expected if the N2pc was associated with faster target acquisition. It is, however, consistent with prior findings that the latency of the N2pc component is closely tied to stimulus onset (Töllner et al., 2012) and stimulus intensity (Brisson et al., 2007), suggesting that the latency of the presaccadic N2pc is sensitive to stimulus onset rather than saccade onset. Moreover, saccade accuracy was very similar on trials with fast or slow saccades, providing no evidence that the larger N2pc on the slow-latency saccades led to a benefit in saccade accuracy. These results suggest that the mechanism of covert attention indexed by the N2pc was not used to aid saccade planning in Experiment 3, and the presence of the N2pc may have been epiphenomenal. Weaver et al. (2017) also found a dissociation between the N2pc and saccadic performance: a presaccadic N2pc to the target was present even on trials where the eye movement was directed to the distractor. Thus, the pattern of results across the existing behavioral and N2pc studies is consistent with models that propose covert attention and eye movements are separate but related systems (Hunt et al., 2019; Posner, 1980).

Interestingly, ERP decoding was able to classify the target location at above-chance levels well before the first eye movement in all experiments, regardless of whether a presaccadic N2pc was observed. This indicates that information about target location was present in the presaccadic ERP signal, an indication that some localization process distinct from the N2pc component was present. This exciting result suggests that there are cognitive or premotor processes which aid in saccade preparation but are conceptually distinct from the specific attentional process measured by the N2pc component. This could reflect, for example, some other kind of rapid attention than what is typically studied by covert attention (e.g., see Hickey et al., 2019; Li, Pan, et al., 2021). However, the ERP decoding could be due to some other kind of neural process. As mentioned, several studies have shown saccade preparation processes occur in the frontal eye fields about 100 ms before a saccade is initiated (e.g., Hanes et al., 1995), and this could be what the decoder was utilizing. This will be an important issue for future research.

It is important to remember that covert attention consists of many separable subprocesses (Luck & Vecera, 2002), and it may be impossible to definitively rule out the possibility that some kind of shift of covert attention precedes every shift of overt attention. One could always posit that the current methods are insensitive to detect some hypothetical mechanism of covert attention. This issue is further complicated in the current study by uncertainty regarding what exact attentional subprocess is measured by the N2pc component. Without definitive knowledge of what the N2pc measures, it is difficult to explain exactly what kinds of covert processes will and will not proceed eye movements.

One possibility suggested by Lamy, Zivony, and colleagues is that the N2pc component may measure the engagement of attention on a target stimulus rather than an orienting process per se (Zivony et al., 2018; Zivony & Lamy, 2018). This dichotomization is similar to Prinzmetal et al.'s (2005) classic distinction between channel enhancement (i.e., boosting the perceptual representation of the attended item) and channel selection (i.e., determining the location of the to-be-attended item). In the current study, the N2pc may have measured something akin to channel enhancement, while the ERP decoding may have measured something akin to channel selection (i.e., determining which location is the target). However, this interpretation is merely speculative. Ultimately, more research is needed to definitively determine what the N2pc and ERP decoding techniques are measuring, and this may help resolve which cognitive processes do occur before eye movements.

The current findings do fit well with the conclusions of recent studies of reading using concurrent EEG and eye-tracking. For example, Milligan et al. (2023) had participants read sentences of text in a gaze-contingent task in which the critical parafoveal preview word was sometimes changed before it could be fixated. The depth of processing of this target word was assessed using fixation-related potentials (FRPs). The results showed that these parafoveal preview words were partially processed before an eye movement was generated to it, as evidenced by an overall increase in fixation durations on these target words on change-display trials. However, this effect of display change was only found when the preview word was a high-frequency word, and there was no such cost on change-display trials for low-frequency preview words. Similarly, an FRP index of word recognition was only modulated by display changes with high-frequency preview words but was unaffected by display changes with low-frequency preview words. The authors concluded that parafoveal words may only be subject to shallow processing during reading, with the bulk of linguistic processing occurring well after they become fixated (see review by Schotter, 2018). In other words, these results suggest that only a limited amount of low-level information can be extracted from parafoveal objects during reading, and the low-level information that was extracted was only sufficient to support downstream word recognition for high-frequency words well-after the eyes had fixated the critical object, but it was not sufficient for low-frequency words. This idea is broadly consistent with the findings of the current study: covert attention may not always enhance the processing of parafoveal objects before an eye movement is generated and this might limit the amount of information that can be obtained about an object (or word) before an eye movement is executed. However, future research on how shifts of covert attention are executed during reading would be needed to make more definitive conclusions.

An alternate explanation for why no presaccadic N2pc was observed in Experiments 1 and 2 may be that participants had randomly selected one location to search, used covert attention to determine whether that location contained the target or the nontarget color, and then made a prosaccade if the location contained the target color or an anti-saccade if that location contained the nontarget color. The N2pc would have been opposite in polarity on these two types of trials, canceling out in the averaged ERP waveform. Although this alternative explanation is logically possible, we believe it is unlikely. Anti-saccades are more difficult to control, take longer to initiate than pro-saccades, and often show bimodal saccade latency distributions of rapid but inaccurate prosaccades and slow but accurate anti-saccades (Dafoe et al., 2007; Munoz & Everling, 2004). Given that saccadic latencies in Experiments 1 and 2 were quick and highly accurate, it is unlikely that participants had adopted this strategy. Additionally, this strategy would predict consistent differences in N2pc between fast- and slow-latency saccades, because fast-latency trials should primarily consist of pro-saccades while slow-latency saccades should primarily consist of anti-saccades. Thus, an N2pc should be observed on fast-latency trials while an inverted N2pc should be observed on slow-latency trials. This was not the case.

It is also worth noting that the current study examined the relationship between neural markers of covert attention and eye movements using relatively easy visual search tasks. It is likely that the relationship between covert attention and eye movements would differ under other conditions, such as during a more difficult visual search task. Although the results of the current study do not directly implicate search difficulty as the critical factor for the presence of a presaccadic N2pc component (i.e., eye movements in Experiment 3 were numerically faster and just as accurate as in Experiment 2), it is likely that more difficult search tasks will require participants to slow down and covertly identify the target before making an eye movement (e.g., scout search; Talcott & Gaspelin, 2021, Experiment 2). Ultimately, additional research is needed to understand when a presaccadic N2pc will or will not precede eye movements in tasks that emphasize different covert attentional subprocesses.

Finally, it is possible that the appearance of a presaccadic N2pc in Experiment 3 was a consequence of something other than the larger number of potential target locations. As previously explained, the N2pc was unlikely to be a consequence of moving the target locations off the horizontal meridian. However, it would be useful for future research to more fully test the hypothesis that the number of potential target locations is the key variable. Additionally, future research with more complex and realistic scenes would help determine if there are conditions where a presaccadic N2pc is helpful in making saccades faster or more accurate. Even if the presaccadic N2pc was epiphenomenal in Experiment 3, it may have been triggered by the similarity between the task used in Experient 3 and real-world tasks in which this mechanism of covert attention plays an important functional role. More broadly, it would be useful for future research to consider and test the specific ways in which shifting covert attention prior to overt attention might be worth the time and neural energy needed.

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Appendix A

Supplemental Material

Supplemental data to this article can be accessed online at [link TBD; request a copy early by contacting ttalcot1@binghamton.edu].

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