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What is This?

Inhibition Drives Early Feature-Based Attention

Jeff Moher[1], Balaji M. Lakshmanan[2], Howard E. Egeth[1], and Joshua B. Ewen[2,3]

[1]Department of Psychological and Brain Sciences, Johns Hopkins University; [2]Neurology and Developmental Medicine, Kennedy Krieger Institute; and [3]Department of Neurology, Johns Hopkins University School of Medicine

Abstract

Attention can modulate processing of visual input according to task-relevant features, even as early as approximately 100 ms after stimulus presentation. In the present study, event-related potential and behavioral data revealed that inhibition of distractor features, rather than activation of target features, is the primary driver of early feature-based selection in human observers. This discovery of inhibition consistent with task goals during early visual processing suggests that inhibition plays a much larger role at an earlier stage of target selection than previously recognized. It also highlights the importance of understanding the role of inhibition (in addition to activation) in attention.

Because the visual system is limited in its capacity for higher-order processing, engaging in appropriate behavioral responses to external stimuli depends critically on the efficient selection of goal-relevant visual input. This selection process can occur on the basis of several stimulus properties, including location (e.g., Posner, 1980) and color (e.g., Green & Anderson, 1956). A recent study (Zhang & Luck, 2009) using event-related potential (ERP) recordings demonstrated that early processing of task-relevant features throughout the entire visual field can be influenced by current behavioral goals even as early as approximately 100 ms following stimulus presentation, independent of stimulus location. It is unknown, however, whether this early, global, feature-based selectivity operates by activating task-relevant features or by inhibiting competing distractor features.

Feature-based attention is typically described in terms of activation of task-relevant features (e.g., Wolfe, 1994), often through an increase in the gain of neurons preferentially tuned to target features (e.g., Saenz, Buracas, & Boynton, 2002). More recently, inhibition has also been shown to play a role in feature-based attention; features can be deprioritized depending on factors such as recent experience (Braithwaite & Humphreys, 2003; Lleras, Kawahara, Wan, & Ariga, 2008). However, although electrophysiological data indicate that location-based inhibition can occur during early stages of visual processing (~100 ms following stimulus presentation; Luck & Hillyard, 1995; Luck et al., 1994), evidence of feature-based inhibition has typically been found only at later stages of processing (starting ~200–300 ms after stimulus presentation; Andersen & Müller, 2010; Shin, Wan, Fabiani, Gratton, & Lleras, 2008). To our knowledge, there is no evidence that feature-based inhibition can influence earlier stages of visual processing.

We adapted Zhang and Luck's (2009) paradigm to include a baseline task-neutral color in order to determine whether feature-based inhibition influences selection early in visual processing. Observers viewed a continuous stream of two spatially interleaved sets of dots in one visual hemifield while maintaining central

Corresponding Author:
Jeff Moher, Brown University, Cognitive, Linguistic, and Psychological Sciences, 190 Thayer St., Providence, RI 02912
E-mail: jeff_moher@brown.edu

fixation. Observers were instructed to indicate whenever the target-colored dots were simultaneously dimmed for 500 ms, but to ignore occasions when the distractor-colored dots dimmed simultaneously. During each trial, task-irrelevant homogeneously colored sets of dots (probes) were occasionally presented in the opposite hemifield. Within each trial, each set of probe dots was randomly selected to be composed of the target color from the task-relevant side, the distractor color from the task-relevant side, or a neutral color that never appeared on the task-relevant side.

We examined changes in the amplitude of the P1 response to these probe stimuli to clarify the effects of feature-based attention on early visual processing. The P1 is an ERP component that reflects an early sweep of visual processing (approximately 100 ms after stimulus presentation) whose amplitude can be affected by changes in neuronal activity in extrastriate cortex (e.g., Mangun, Buonocore, Girelli, & Jha, 1998; Woldorff et al., 1997) that may reflect top-down attentional control settings (e.g., Hillyard & Münte, 1984). The P1 is typically interpreted to reflect a feedforward wave of sensory processing (e.g., Hillyard, Vogel, & Luck, 1998; Luck & Kappenman, 2012; Zhang & Luck, 2009; but see also Foxe & Simpson, 2002, for an alternative interpretation).

Experiment 1

Method

Twenty-one Johns Hopkins community members (9 male, 12 female; mean age = 25.7 years) participated in sessions lasting 1.5 to 2 hr. Stimulus presentation and data analysis were performed using MATLAB (The MathWorks, Natick, MA) and Psychophysics Toolbox software (Brainard, 1997; Pelli, 1997). Electroencephalogram (EEG) data were recorded at 47 sites covering the whole scalp with approximately uniform density using an elastic electrode cap—Waveguard cap (Advanced Neuro Technology, or ANT, The Netherlands) with 128-channel Duke layout (equidistant electrode placement; Fig. 1)—referenced to the average of all channels during recording. Electrode impedance was kept below 5 kΩ. All EEG channels were recorded continuously in direct-current mode at a sampling rate of 512 Hz from a 128-channel, high-impedance ANT Waveguard amplifier with active cable-shielding technology and an antialiasing low-pass filter with a 138 Hz cutoff.

Stimuli. Throughout every trial, sets of small dots (each dot subtending 0.14° of visual angle) were presented in both hemifields on a black background. The dots in each hemifield were randomly placed within an imaginary circle with a radius subtending 3.34° of visual angle,

centered 6.37° of visual angle (horizontal) and 1.71° of visual angle (vertical) from fixation (Fig. 2a).

In the task-relevant hemifield, 100 spatially intermingled target-colored and distractor-colored dots (50 each) were presented. Target and distractor colors were randomly selected without replacement for each participant to be red, green, or blue throughout the entire experiment; colors were counterbalanced across participants. Each color appeared at a luminance of 8.1 cd/m². On the task-relevant side, the luminance of all of the dots of one color was occasionally reduced to 3.2 cd/m². Throughout each trial, in the opposite (or task-irrelevant) hemifield, probes composed of 50 homogenously colored dots, randomly selected to be entirely red, green, or blue for each presentation, were presented at varied intervals at a luminance of 8.1 cd/m².

Design and procedure. Each trial began with a central arrow, randomly pointed either left or right, indicating the hemifield in which task-relevant dots would appear on the upcoming trial. After 1 s, a fixation cross replaced the arrow. Participants were instructed to maintain fixation throughout each trial. After a 0.5-s delay, target and distractor dots appeared in the task-relevant hemifield. Every 100 ms, 50% of all dots were randomly relocated within the imaginary circle in the task-relevant hemifield, giving the dots a scintillating, motion-like appearance (dot motion parameters were based on those in Zhang & Luck, 2009). During each 15-s trial, the target dots occasionally underwent a brief (500 ms) luminance decrement before returning to their original luminance. Luminance decrements also occurred among the distractor dots, but the two events (target decrements and distractor decrements) were independently timed. These "luminance events" occurred between 2 and 5 times for each color during each trial. Participants were instructed to press the space bar every time a luminance event occurred among the target dots, but not to respond to luminance events among the distractor dots. In the opposite (task-irrelevant) hemifield, probes were presented at interstimulus intervals that varied randomly from 217 to 700 ms. Each probe presentation lasted 100 ms and required no overt response.

Following each trial, a blank black screen was presented for 800 to 1,200 ms. Participants completed a minimum of six blocks of trials. Each block consisted of 16 trials, with a brief rest between Trials 8 and 9. Experimenters provided feedback between blocks on task performance and eye and body movements in order to acquire the cleanest possible signal from EEG recordings.

Data analysis. Three participants were removed from analysis either for poor behavioral performance or for
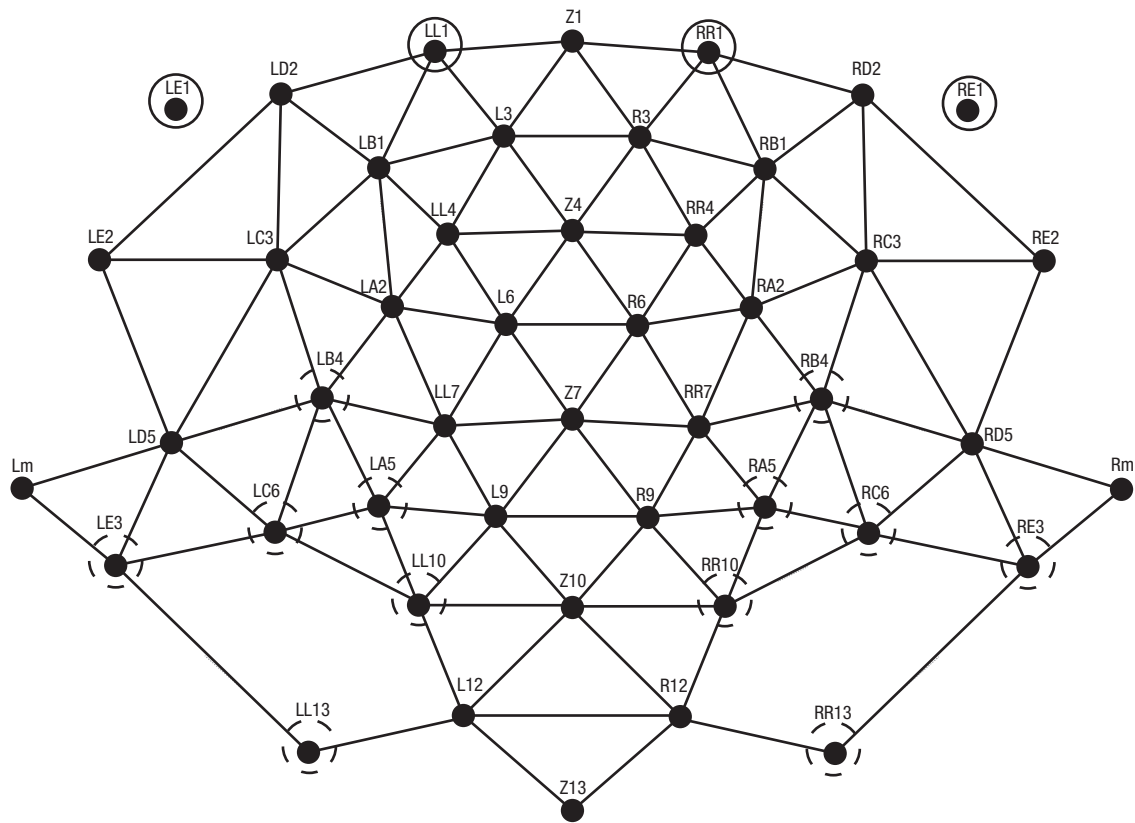
Fig. 1. The electrode layout used in the present experiment. Of the 128 electrodes available, the figure shows the subset of 47 from which data were recorded. A spatially contiguous array of electrodes from the recorded channels was collapsed and examined for P1 analysis (highlighted by dashed circles). The electrodes highlighted by solid circles were used to detect eye movements.

excessive EEG noise (assessed off-line by an experienced electrophysiologist, J. B. E., who was blind to the experimental conditions). EEG epochs were synchronized with the onset of probe dot presentation and analyzed using ANT's ASA software. Vertical electrooculograms were recorded from frontal channels LL1 and RR1 (see Fig. 1), whose locations were designed specifically to capture eye blinks. Horizontal electrooculograms were recorded from channels LE1 and RE1, whose locations were designed specifically to capture horizontal eye movements. Eye blink correction was performed using a principal component analysis method that models the brain signal and artifact subspaces (Ille, Berg, & Scherg, 2002). After eye blink correction, EEG was visually inspected on a trial-by-trial basis to look for any horizontal eye movements. Any trials contaminated with horizontal eye movements were eliminated from averaging. In addition, trials contaminated with excessive muscle artifacts, artifacts due to movements, or trials in which amplifier blocking

occurred were also eliminated. Although it is possible that a few eye movements to the attended side were undetected, there is no reason to expect that this behavior would differentially affect ERP responses to probes depending on the probe color.

An off-line bandpass filter (Butterworth filter, low cutoff frequency = 0.2 Hz, high cutoff frequency = 35 Hz, and linear roll-off = 24 dB/octave) was applied to all channels. ERPs were averaged off-line from 100 ms before to 600 ms after probe stimulus onset. Data were analyzed from six spatially contiguous electrodes in each hemisphere (LA5, LB4, LC6, LE3, LL10, LL13; RA5, RB4, RC6, RE3, RR10, and RR13). These electrodes were selected by experienced electrophysiologists, J. B. E. and B. M. L., on the basis of whether there were discernible P1 patterns present. The electrophysiologists were blind to experimental conditions during this selection process. Finally, ERP waveforms obtained from the selected electrodes were grand averaged using EEGLAB, a MATLAB

toolbox (Delorme & Makeig, 2004). Mean P1 amplitude was calculated for each participant as the mean amplitude from the point in time when the voltage reached 50% of peak amplitude to 50 ms after that point.

Results

Behavior. Task performance was well below ceiling (hit rate = 85.2%, false alarm rate = 8%), which suggests that the task was attention demanding and likely required the use of limited attentional resources. The inclusion of a neutral-colored probe was intended to serve as a baseline measure for feature-based attention effects. However, because the neutral color never appeared in the task-relevant hemifield, observers were not exposed to the neutral color as frequently as to the other colors. Thus, one might be concerned that neutral-colored probes may have captured spatial attention as a result of their relative novelty (e.g., Johnston, Hawley, Plewe, Elliott, & DeWitt, 1990). Although attention can increase the magnitude of the P1 response (e.g., Hillyard & Münte, 1984), this has been demonstrated only in situations in which observers have a preset attentional bias (i.e., attention is biased to a particular location or feature prior to stimulus onset); thus, involuntary capture elicited by stimulus properties should not affect P1 magnitude. Furthermore, there is no evidence, to our knowledge, of novelty affecting any ERP component earlier than the N1 (e.g., Friedman, Cycowicz, & Gaeta, 2001; Parmentier, 2008). Therefore, there is no reason to believe that the magnitude of the P1 to neutral-colored probes would be increased because of their relative novelty.

Nevertheless, to assess any possible probe-induced attentional capture, we analyzed luminance-detection performance according to which type of probe most recently appeared in the task-irrelevant hemifield before each luminance change. If neutral-colored probes capture spatial attention, we would expect more errors when the most recent probe before a luminance change was neutral colored than when it was target colored or distractor colored. We conducted a 3 (probe type) × 6 (block) analysis of variance (ANOVA) on luminance-detection error rate and found main effects of probe type, $F(2, 34) = 9.21$, $p < .01$, and block, $F(5, 85) = 5.45$, $p < .001$, that were mediated by a significant interaction, $F(10, 170) = 3.54$, $p < .001$ (Fig. 2b). Post hoc tests revealed that there was a main effect of probe type in Blocks 1 and 2 ($ps < .01$), and subsequent Tukey's honestly significant difference (HSD) comparisons showed that the error rate was higher following neutral probes compared with other probes in those first two blocks ($ps < .05$). There was no effect of probe type in the remaining blocks ($ps > .05$). These results indicate that the neutral-colored probe likely captured spatial attention early in the experiment, but by the third experimental block,
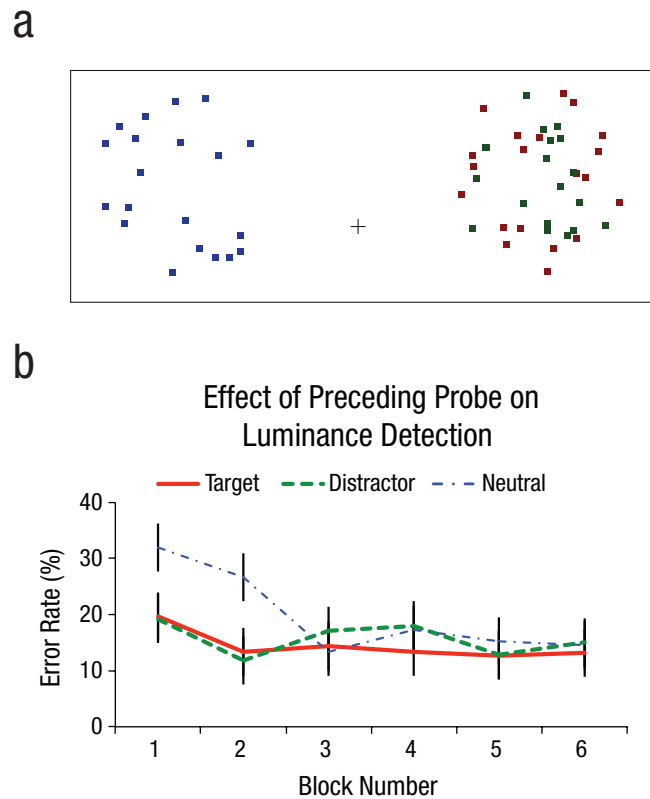

Fig. 2. Sample stimulus display and error rates in Experiment 1. In the sample frame from within a trial (a), the observer would be monitoring for luminance changes among the red (target) dots but not among the green (distractor) dots in the right (task-relevant) hemifield. In the left (task-irrelevant) hemifield, probes would occasionally appear in the target color, distractor color, or neutral color (blue in this example). These probes required no overt response, but we examined event-related potential components elicited by these probes to investigate the influence of feature-based attention on early visual processing. For clarity, the background is presented as white here, but a black background was used in the actual experiment. The graph (b) shows mean error rate as a function of block number and stimulus type. Error bars were calculated using a within-subjects interaction error term (Loftus & Masson, 1994).

observers had experienced a sufficient number of neutral probe stimuli to eliminate novelty-based capture.

EEG. We conducted a 3 (probe type) × 2 (hemifield: left vs. right) ANOVA on mean P1 amplitude in response to probes appearing in the contralateral visual hemifield. As a precaution, the first two blocks were not included in this analysis to avoid novelty effects in the baseline measure. To further reduce the possibility that P1 responses to probes were influenced by shifts of spatial attention, we excluded from analysis any probe for which the observer failed to detect a luminance event in the 2 s before probe onset.

There was a main effect of probe type on P1 amplitude, $F(2, 34) = 6.07$, $p < .01$. There was no effect of hemifield or interaction between hemifield and probe

type (*F*s > .1). Tukey's HSD post hoc tests revealed that the mean P1 amplitude in response to target-colored probes was greater than the mean P1 amplitude in response to distractor-colored probes, *p* < .05 (Fig. 3), which replicates the previous finding of early prioritization of target over distractor features during early visual processing (Zhang & Luck, 2009).

The neutral-colored probes allowed us to determine whether this prioritization reflected activation of target features or inhibition of distractor features. If target activation was the key process, we would expect the mean P1 amplitude in response to target-colored probes to be greater than the baseline mean P1 amplitude evoked by neutral-colored probes. If distractor inhibition was the key process, we would expect the mean P1 amplitude in response to distractor-colored probes to be smaller than the baseline (neutral) P1. We found only the latter to be the case; the mean P1 amplitude in response to distractor-colored probes was smaller than the mean P1 amplitude in response to neutral-colored probes, *p* < .01, but there was no significant difference between neutral-colored probes and target-colored probes, *p* > .1 (Fig. 3). These data suggest that feature-based attention modulates visual input at an early stage of processing via inhibition of distractor features rather than activation of target features.

Experiment 2

We drew conclusions in Experiment 1 by comparing the mean P1 amplitude in response to target- and distractor-colored probes against a baseline P1 obtained from neutral-colored probes. However, a potential concern in our interpretation is that the neutral color appeared less frequently than the other colors globally. That is, whereas all three colors appeared with equal probability as probes on the task-irrelevant side of space, the neutral color never appeared on the task-relevant side of space—only the target and distractor colors ever appeared on that side. As a result, it is possible that the P1 responses to the target- and distractor-colored probes were attenuated as a result of sensory adaptation effects (e.g., Luck & Hillyard, 1994), but that no such reduction occurred in response to the less common neutral-colored probe. This would not account for the difference between target and distractor-colored probes. However, it would affect our interpretation of the neutral, baseline condition. Specifically, it could be the case that the P1 amplitude in response to distractor-colored probes was smaller in magnitude than the P1 amplitude in response to the neutral-colored probes not because of attentional inhibition due to task goals, but instead because of adaptation effects that affected the distractor-colored probe more than the neutral-colored probe.

To rule out the sensory adaptation account, we conducted a control study in which we used the exact same stimuli and procedures as in Experiment 1 but in a passive-viewing task (i.e., no overt responses were required). If the amplitude of the P1 in response to target-colored and distractor-colored probes was attenuated in Experiment 1 because of sensory adaptation effects, we would expect the P1 response to neutral-colored probes in a passive-viewing task to be greater than the P1 amplitude in response to other-colored probes that are rendered in colors that appear on both sides of fixation.

Method

All methods were identical to those in Experiment 1 with the following exceptions. Thirteen Johns Hopkins community members (7 male, 6 female; mean age = 22.9 years) participated. One participant was removed for excessive EEG noise resulting from sleepiness (EEG assessed off-line by B. L. M., who was blind to the experimental conditions). No overt response was required to any event during the course of the experiment; instead, observers were instructed to simply focus on the central fixation cross while stimuli were presented.
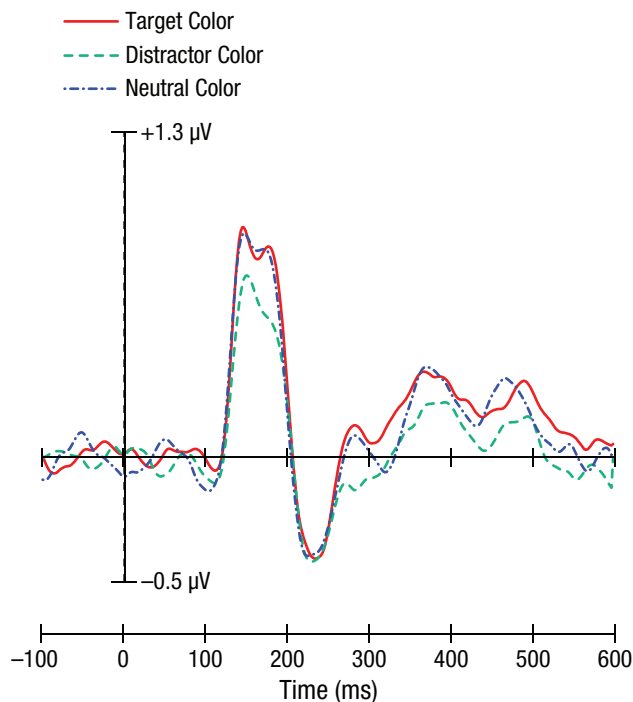

Fig. 3. Results from Experiment 1: event-related potential waveforms from occipital electrodes contralateral to the visual hemifield in which task-irrelevant probes were presented in the target, distractor, and neutral colors. Data for right and left hemifield presentations are collapsed. Stimulus onset occurred at 0 ms.

Electrophysiological data were continuously monitored, and observers were reminded to stay awake and focus on the central fixation cross if there was any indication that they were falling asleep because of the boring nature of the task. All participants completed either five or six blocks of trials.

Data were analyzed from four spatially contiguous electrodes in each hemisphere (LA5, LC6, LE3, LL13; RA5, RC6, RR10, and RR13). As in Experiment 1, these channels were selected based on whether they showed a clear P1 during condition-blind analysis by J. B. E. and B. M. L. The difference in the selected electrode subsets between the two experiments is likely a result of the differences in task demands; previous studies have shown that the P1 component can be affected by factors such as arousal or attentional demands (e.g., Hopfinger & West, 2006; Vogel & Luck, 2000). Finally, to provide the strictest possible test for any effects of stimulus frequency, all runs from each participant were included in the analysis. By including the early runs, we increased the probability of finding any effects of stimulus frequency on P1, including those that might dissipate over time.[1]

On the side of fixation where probes did not appear, referred to as the "task-relevant" side in Experiment 1, two different groups of colored dots were presented, as in Experiment 1. However, unlike in Experiment 1, there was nothing to distinguish either of these colors as the target or distractor color. Therefore, for data analysis, we collapsed the data from all probes into two categories: neutral probes and nonneutral probes. However, we also arbitrarily labeled one color as "target" and the other as "distractor" for each subject, and we present probe data separately for those two conditions in Figure 4 to give the reader a sense of the variability in the data. It is particularly important in this instance to demonstrate low levels of noise, because we hypothesized that there would be no difference in P1 amplitude between results for neutral and nonneutral probes.

Results

We conducted a 2 (probe type) × 2 (hemifield: left vs. right) ANOVA on mean P1 amplitude in response to probes appearing in the contralateral visual hemifield to determine whether probe type had any effect on P1 amplitude in the absence of a task. If global stimulus frequency modulated the amplitude of the P1 in response to neutral-colored probes in Experiment 1, we would expect a main effect of probe type, with greater P1 amplitude in response to neutral-colored probes than to nonneutral (i.e., "target" and "distractor") colored probes. However, we found no main effect of probe type on mean P1 amplitude, $F(1, 11) < 1$, $p = .61$ (Fig. 4). There was a main effect
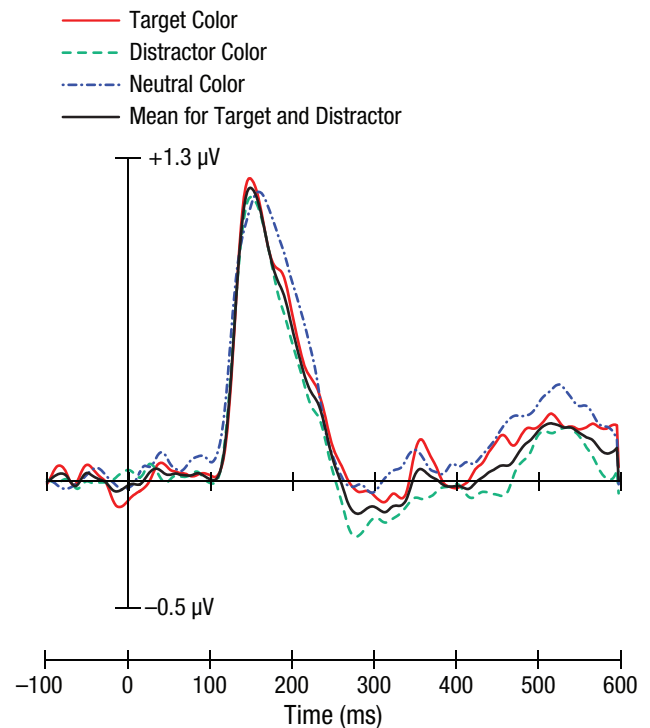

Fig. 4. Results from Experiment 2: event-related potential waveforms from occipital electrodes contralateral to the visual hemifield in which task-irrelevant probes were presented in the target, distractor, and neutral colors. Data for right and left hemifield presentations are collapsed. Probe colors were not distinguished in this experiment, so probes deemed "targets" and "distractors" were selected arbitrarily. Mean results for the "target" and "distractor" colors combined are also shown. Stimulus onset occurred at 0 ms.

of hemifield, $F(1, 11) = 5.13$, $p < .05$, with higher mean P1 amplitude in the right brain hemisphere (in response to probes presented to the left visual hemifield) than in the left brain hemisphere (in response to probes presented to the right visual hemifield), but critically, this did not interact with probe type, $F(1, 11) < 1$.

Proving a negative is difficult; therefore, as additional support to our null results (e.g., de Graaf & Sack, 2011), we also report here the effect size of the probe type factor in Experiment 2 as $\eta_p^2 = .025$. In contrast, the effect size of the probe type factor in Experiment 1 was $\eta_p^2 = .263$, which means that the effect of probe type in Experiment 2 was less than 10% of the size of the effect in Experiment 1.

These data, along with those presented in Figure 4, demonstrate that the adaptation account of Experiment 1 is extremely unlikely. The difference in global frequency among the colors presented in the current paradigm appears to have little effect on P1 amplitude. This provides further support for the distractor-inhibition account of feature-based attention effects found in Experiment 1.

Experiment 3

In Experiment 3, we sought converging behavioral evidence that the luminance-detection task induced an inhibitory (rather than excitatory) feature-based attentional set. Each participant performed a shortened version of the task from Experiment 1 (Task 1) and then immediately performed a visual search task (Task 2), in which the same colors were used. Previous studies have shown that attentional control settings are often robust, continuing to bias selection even when task goals change (e.g., Leber, Kawahara, & Gabari, 2009). Therefore, this design allowed us to measure the effect of attentional control settings induced by the luminance-detection task on later behavior to determine whether they reflect target activation, distractor inhibition, or both.

Method

Eighteen Johns Hopkins community members (5 male, 13 female; mean age = 23.8 years) participated in sessions lasting approximately 1 hr. Stimulus presentation and data analysis were performed using MATLAB and Psychophysics Toolbox software.

Stimuli. Stimuli for Task 1 were identical to those in Experiment 1. For Task 2, 24 letters (each approximately 0.57° of visual angle) appeared on each trial. The target letter was randomly selected for each trial to be "N" or "Z," and the remaining letters were an approximately equal distribution of "H," "I," "V," and "X." The location of each letter was randomly selected from an array of 396 possible locations subtending approximately 19.23° of visual angle. The 24 letters appeared in an equal distribution of four different colors—red, green, and blue, all equivalent to the high luminance versions (8.1 cd/m²) from Task 1, and an equiluminant yellow. The target color was randomly assigned for each trial.

Design and procedure. Participants performed four blocks of Task 1, which lasted approximately 30 min. As in Experiment 1, red, green, and blue were counterbalanced across subjects in their assignment as the target, distractor, and neutral colors. Following completion of Task 1, participants performed three blocks of Task 2. Each block consisted of 100 trials with a brief rest halfway through each block. On each trial, the search display appeared after a 1-s fixation interval. Participants indicated which target letter was present by pressing a key.

Results

We conducted a 3 (block) × 4 (target color) ANOVA with factors of and for Task 2. All response times 2.5 standard deviations above or below the mean in each condition for each participant were removed from analyses (2.9% of all trials). Target color was defined according to what role each color was assigned in Task 1 for each participant: Task 1 target color, Task 1 distractor color, Task 1 neutral color, or novel color.

There was a main effect of block, $F_{(2, 34)} = 5.31$, $p < .05$, explained by a linear trend with faster response times during later blocks, $F_{(3, 51)} = 14.57$, $p < .01$. There was no main effect of target color, $F_{(3, 51)} = 1.46$, $p > .1$.

As Figure 5 shows, there was an interaction between block and target color, $F_{(6, 102)} = 3.91$, $p < .01$. We conducted separate one-way ANOVAs for each block to assess the effect of target color; only Block 1 was significant, $F_{(3, 51)} = 6.7$, $p < .01$. This suggests that feature-based attentional control settings induced by Task 1 affected behavior during Block 1 of Task 2 but did not affect performance on Blocks 2 and 3.

For Block 1, we conducted pairwise comparisons for each color combination. Slower response times to targets appearing in the Task 1 distractor color relative to the neutral and novel colors would suggest that Task 1 induced an inhibitory feature-based attention set. Faster response times to targets appearing in the Task 1 target color relative to the novel and neutral colors would indicate a target activation-based attention set. Response times were slower when the target appeared in the Task 1 distractor color relative to all other colors ($ps < .05$). No other comparisons were significant ($ps > .1$). These data provide converging evidence with Experiment 1, which suggests that the feature-based attentional set induced by Task 1 is defined by inhibition of the distractor color rather than activation of the target color.
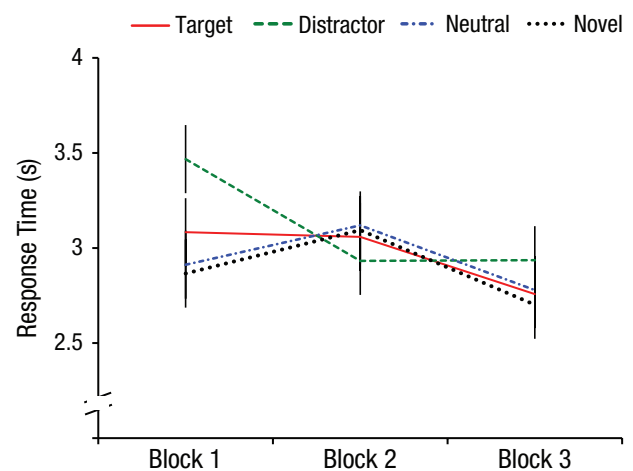

Fig. 5. Results from Task 2 in Experiment 3: mean response time as a function of block number and target color. Error bars were calculated using a within-subjects interaction error term (Loftus & Masson, 1994).

General Discussion

We found that the neural response evoked by distractor-colored probes was reduced relative to the response evoked by neutral-colored probes early in visual processing. Furthermore, we found no evidence for an increased neural response to target-colored probes relative to neutral-colored probes. Together, these data suggest that feature-based attention can modulate incoming sensory input at an early stage of processing via inhibition of distractor features. Converging behavioral evidence indicated that attentional control settings based on distractor inhibition were sufficiently robust to carry over to a novel task.

Neurophysiological studies in monkeys have shown that neuronal responses are suppressed when a neuron's nonpreferred feature is attended (Khayat, Niebergall, & Martinez-Trujillo, 2010; Martinez-Trujillo & Treue, 2004), and other studies have found electrophysiological evidence for inhibitory mechanisms in feature-based attention in humans (Andersen & Müller, 2010; Bridwell & Srinivasan, 2012; Shin et al., 2008; Snyder & Foxe, 2010). However, in the present study, we showed evidence for inhibition of a specific competing distractor feature, rather than inhibition of responses to all nontarget features, occurring during early visual processing in human observers. Furthermore, the data appear to reflect a purely inhibitory mechanism; we found no evidence for target activation during the P1 time frame in the present task.

The absence of selective activation of the target feature was surprising. Previous research has demonstrated that feature-based attentional effects (albeit weak ones) can occur in the absence of direct competition (Saenz, Buracas, & Boynton, 2003); therefore, it remains unlikely that activation plays no role in feature-based attention. However, it appears from the present data that when there is strong competition from distractor stimuli, attention mediates early visual processing primarily through inhibition (and not activation).

Additional research is necessary to understand how higher-level cognitive processes influence early feature-based effects. For example, we previously found that observers are unable to explicitly ignore nontarget features that change on a trial-by-trial basis unless they first select those items (Moher & Egeth, 2012; but see also Woodman & Luck, 2007). Furthermore, several EEG studies in which target and distractor feature values shifted from trial to trial (Andersen & Müller, 2010; Shin et al., 2008) failed to find evidence for feature-based inhibition during early visual processing. To reconcile these previous results with the current findings (in which target and distractor feature values were held constant for each individual participant), we propose that there may be two mechanisms by which feature-based attention biases visual input.

The first is a rapidly initiated attentional set characterized by activation of target features, which can be adjusted to accommodate frequently changing goal states. For example, if a new target feature is cued before a trial, an observer can establish an attentional set to activate visual input matching that feature. This is consistent with ERP data demonstrating activation of target features when the target feature changed frequently (e.g., Andersen & Müller, 2010; Andersen, Müller, & Hillyard, 2009). This type of quickly accessible feature-based set would be especially useful in dynamic visual environments where task goals and task-relevant features change frequently. However, in more stable environments where task-relevant features remain consistent, a different type of feature-based attentional set may be implemented over time. This set effectively modulates visual input at a very early stage via inhibition of distractor features rather than activation of target features. This would be consistent with the findings of the present study, in which the target and distractor features were unchanged throughout the experiments. The shift from an excitatory to an inhibitory mode of operation may reflect a gradual, implicit development of an attentional template in long-term memory as target and distractor feature values are learned over time (e.g., Carlisle, Arita, Pardo, & Woodman, 2011). Why might such a template develop? One speculative possibility is that the inhibitory set is metabolically more efficient (e.g., Buzsáki, Kaila, & Raichle, 2007).

Previous research has demonstrated that a to-be-ignored location (e.g., Serences, Yantis, Culberson, & Awh, 2004) or a single (and thus spatially localized) pop-out distractor (e.g., Ipata, Gee, Gottlieb, Bisley, & Goldberg, 2006) can be inhibited during early visual processing. The present study suggests that distractor features themselves can also be inhibited during an early stage based on current task goals. These findings highlight a critical role for inhibition that merits consideration in future studies and models of attention.

Author Contributions

J. Moher, B. M. Lakshmanan, H. E. Egeth, and J. B. Ewen all contributed to the study design and data analysis. J. Moher and B. M. Lakshmanan collected the data. J. Moher wrote the initial manuscript, and all authors contributed revisions included in the final manuscript.

Declaration of Conflicting Interests

Funding

Note

1. Statistical outcomes did not differ when the first two runs were removed from the analysis, as in Experiment 1.

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