

# Distinct Attention Networks for Feature Enhancement and Suppression in Vision

David A. Bridwell<sup>1,2</sup> and Ramesh Srinivasan<sup>1</sup>

<sup>1</sup>Department of Cognitive Sciences, University of California, Irvine, and

<sup>2</sup>The Mind Research Network, Albuquerque, New Mexico

Psychological Science

23(10) 1151–1158

© The Author(s) 2012

Reprints and permission:

sagepub.com/journalsPermissions.nav

DOI: 10.1177/0956797612440099

http://pss.sagepub.com



## Abstract

Attention biases sensory processing toward neurons containing information about behaviorally relevant events. These attentional biases apparently reflect the combined influence of feature enhancement and suppression. We examined the separate influence of enhancement and suppression in visual processing by determining whether responses to an unattended flicker were modulated when the flicker features matched target features at the attended location, competed with those features, or were neutral. We found that suppression primarily modulated parietal networks with a preferred frequency in the lower alpha band ( $f_2 = 8$  Hz), and enhancement primarily influenced parietal networks with a preferred frequency in the upper alpha band ( $f_2 = 12$  Hz). These responses were coupled with perception, with large responses to the unattended flicker leading to subsequently detected targets when the target features matched the flicker features (i.e., during enhancement). Our results suggest that enhancement and suppression are two distinct processes that work together to shape visual perception.

## Keywords

attention, electrophysiology, visual perception

Received 6/21/11; Revision accepted 2/1/12

Much more information reaches people's senses than they are aware of or that they can effectively process. To overcome this problem, the brain biases sensory processing so that only a subset of information is enhanced and integrated during people's interactions with the environment. These attentional biases often result in positive outcomes, such as an enhanced perceptual representation of visual stimuli containing an attended feature (Carrasco, Ling, & Read, 2004). However, attentional biases may also be maladaptive and can help facilitate certain human psychopathologies. For example, substance abusers demonstrate long-term attentional biases toward addiction-related visual cues, which may help maintain drug dependence (for a review, see Cox, Fadardi, & Pothos, 2006). Trait-anxious individuals demonstrate attentional biases toward threatening stimuli (Derryberry & Reed, 2002), and individuals with negative moods or depression demonstrate attentional biases toward negative stimuli (Joormann, 2004; Mathews & MacLeod, 2005).

Researchers are just beginning to determine whether distinct neural networks facilitate the broad range of early attentional biases. The majority of these studies have examined the influence of attending to visual features or spatial locations over short timescales, such as when individuals suppress irrelevant distractors presented within a stream of visual targets

(Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005) or when suppressing competing information during Stroop, Simon, flanker, or negative-priming tasks. The consensus is that early attentional biases result from activity within frontal and parietal brain locations that are involved in attentional control. For example, previous studies have found increases in parietal responses following cues to direct attention to a feature, such as color or motion (Büchel et al., 1998; Le, Pardo, & Hu, 1998; Shulman, d'Avossa, Tansy, & Corbetta, 2002; Vandenberghe, Gitelman, Parrish, & Mesulam, 2001). These modulations are associated with modulations in early sensory areas that prefer the attended feature, such as V4 for color and middle temporal (MT) gyrus for motion (Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999).

Human imaging and monkey physiology studies have examined how goal-directed attention modulates early sensory processing. These studies primarily focused on attention to color or motion because of the relative ease of isolating

## Corresponding Author:

David A. Bridwell, The Mind Research Network, 1101 Yale Blvd. Northeast, Albuquerque, NM 87106

E-mail: dbridwell@mrn.org

neural responses tuned to these features in unattended regions. Single unit and blood-oxygen-level-dependent functional MRI recordings in area MT show increased responses toward a direction of motion in the unattended visual field when the direction of motion is attended in another region of the display (Serences & Boynton, 2007; Treue & Martinez-Trujillo, 1999). These findings indicate that attending to a feature at one spatial location results in enhanced responses to that feature in unattended regions. However, a distinction between attentional enhancement and attentional suppression has yet to be explored by probing unattended responses. This leaves open the question of whether these opposite biases are subserved by overlapping or distinct attention networks.

In the present study, we examined the influence of parietal areas on both the enhancement and suppression of basic visual features. Individuals performed three different tasks, one which encouraged enhancing the neurons that coded the spatial frequency and orientation spectrum of the background texture at the attended location, one which encouraged suppressing those features, and one which was neutral with respect to those features. In each of these tasks, the subjects detected one feature in one visual field (a target Gabor patch) while a random texture was flickered in the other visual field. The influence of parietal areas on sensory processing was probed by measuring parietal steady-state visual evoked potentials (SSVEPs) to the unattended flickering texture.

We found that responses to the unattended flicker were modulated when the task at the attended location promoted enhancing or suppressing features that matched the flicker feature. These modulations were also sensitive to the frequency of the unattended flicker, with suppression primarily observed at 8 Hz and enhancement primarily observed at 12 Hz. Critically, we also found that the response to the unattended flicker was larger prior to detected targets (hits) compared with undetected targets when the flicker features matched the target features (i.e., during enhancement). Thus, we showed that parietal responses to unattended stimuli reveal the distinct networks for feature enhancement and feature suppression in visual attention.

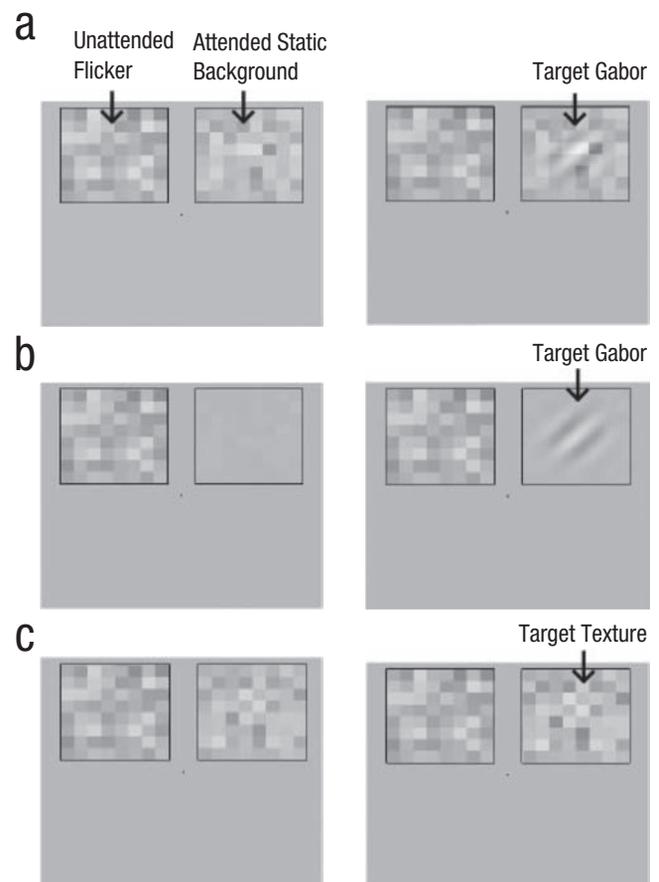
## Method

### Participants

Twenty-six individuals (9 females, 17 males) between the ages of 19 and 33 were recruited to participate in four sessions consisting of two psychophysical (threshold) and two SSVEP sessions. Two SSVEP sessions were discarded from analysis because of participants' inability to maintain alertness, and another SSVEP session was discarded because of excessive eye movements; thus, the final number of participants included in the analysis was 24. Each individual had normal or corrected-to-normal vision, was right handed, and had no family history of epilepsy. Written informed consent was obtained at the start of the first session.

### Stimuli and apparatus

Stimuli were produced with MATLAB (The MathWorks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). They were displayed on a CRT monitor (View Sonic PF790) with a vertical refresh rate of 60 Hz. A hollow black square was present in the top left and top right locations of the display (each side =  $11^\circ$ ; Fig. 1). Targets were displayed inside the attended square, and the flicker was displayed inside the unattended square. The field to which participants attended and the flicker frequency in the unattended field were fixed for each participant. The corner of the square was located  $1.9^\circ$  from fixation. Each square was filled with numerous individual squares of  $1.4^\circ$  each. The pixel luminance of individual



**Fig. 1.** Example stimuli for the three tasks. Each display consisted of two visual fields presented in the upper half of the display, one on the left and one on the right. Participants attended to one visual field in which the background texture remained static throughout each trial (the right visual field in these examples). The background texture of the unattended field always flickered. In the competing condition (a) and the neutral condition (b), participants detected target Gabor patches in the attended field. In the competing condition, targets appeared in a high-contrast background texture, and in the neutral condition, targets appeared in a low-contrast background texture. No Gabor targets appeared in the matching condition (c); instead, participants detected a change in the contrast of the background texture. In all conditions, targets appeared on average once every 10 s across each 40-s trial.

squares of the unattended texture were constructed from a Gaussian distribution with a standard deviation of 43% of the maximum achievable contrast.

The pixel luminance of the attended texture was 43% (high) or 4% (low) contrast at center, with a Gaussian falloff away from center ( $SD = 2.9^\circ$ ). The Gaussian falloff ensured that the attended spatial location overlapped for both the texture and Gabor targets. The attended and unattended textures were equated prior to the experiment to ensure that they contained overlapping spatial frequencies and orientation. Pixel luminance values ranged from .3 to 83  $cd/m^2$  along a linear scale. The target Gabor patch contained a center frequency of .35 cycles per degree with a standard deviation of  $2^\circ$ . Gabor patches were oriented  $45^\circ$  or  $135^\circ$  from the vertical. The frequency of the flicker (square wave, contrast reversal) in the unattended field varied between subjects ( $f_2 = 6, 8, \text{ and } 12 \text{ Hz}$ ). Subjects' ability to maintain fixation was monitored using an iView RED camera (SensoMotoric Instruments, Boston, MA).

## Task

Each participant performed three tasks during both the threshold and SSVEP sessions (Fig. 1). Task order was counterbalanced across individuals. In all tasks, participants attended to a static visual field on one side of the display (left or right side) while the unattended field flickered on the other side of the display.

In the competing (suppression) task, individuals detected a peripheral Gabor patch within a high-contrast background texture. This task promoted suppressing the neurons that code the features of the texture (such as its spatial frequency and orientation spectrum). In the neutral task, individuals detected a Gabor patch within a low-contrast background texture; this task reduced or eliminated the need to suppress the features of the background texture (Doshier & Lu, 2000). In the matching (enhancement) task, individuals detected changes in the contrast of the static background texture. The change in contrast generated energy within the same orientation and spatial frequencies as the texture (see Fig. S1 in the Supplemental Material available online); thus, the relevant target features during the matching condition overlapped with the dominant spatial frequency and orientation information of the unattended texture. All targets were displayed for a duration of approximately 333 ms and had a sudden onset and offset. Trials in all conditions lasted 40 s each, and an average of four targets appeared on each trial.

## Threshold procedure

An initial threshold session was conducted for each individual and each task prior to each SSVEP session. The target level corresponding to the individuals' 65% detection rate was then used in the subsequent SSVEP session. In all sessions, threshold trials had a random duration between 1,517 and 3,267 ms. During each trial, individuals used their right hand to press "1,"

"k," or "j" to indicate whether the target was present with "high," "medium," or "low" confidence, respectively. Individuals used their left hand to press "s," "d," or "f" to indicate whether the target was absent with "high," "medium," or "low" confidence, respectively. The target level presented on each trial was determined using maximum likelihood methods (adapted from the maximum likelihood procedure, or MLP, toolbox; Grassi & Soranzo, 2009). Threshold estimates obtained for each of the three tasks were used to equate performance in the subsequent SSVEP session.

## SSVEP procedure

There were two SSVEP sessions for each participant, which were conducted on separate days. Each SSVEP trial began with instructions to detect either a Gabor patch or a change in background-texture contrast at the attended location, followed by an example of the target and the attended and unattended textures. Targets appeared randomly, but on average once every 10 s. Individuals performed four Gabor-detection trials (two orientations by two background-texture contrast levels) and two trials detecting changes in background-texture contrast within a single block. The six trials were counterbalanced across a total of six blocks for each session.

## SSVEP recording and analysis

Electrodes were placed according to the standard 10-20 placement. Electroencephalogram (EEG) data were recorded with a 128 channel Geodesic Sensor Net (Electrical Geodesics, Eugene, OR; Tucker, 1993). The EEG signals were sampled at 1,000 Hz with a 50-Hz analog low-pass filter and referenced off-line to the average reference. EEG analysis was conducted in MATLAB using custom and built-in functions. MATLAB's Statistics Toolbox was used for parametric statistical tests. The steady-state responses to a contrast-reversal flicker primarily occurred at the second harmonic of the flicker frequency (see Regan, 1989, and Fig. S2 in the Supplemental Material). Steady-state responses were estimated by calculating the signal-to-noise ratio (SNR): the ratio of the power in the second harmonic and the power in the 100 surrounding frequency bins (Sutoyo & Srinivasan, 2009). Significant differences in group SNR between the tasks were assessed using a nonparametric permutation test (5,000 iterations,  $\alpha = .001$ , two-tailed; see SSVEP Analysis in the Supplemental Material).

## Phase-locking analysis

To examine how responses to the unattended flicker related to behavioral performance, we measured the degree of phase locking to the unattended flicker in intervals of approximately 2,000 ms prior to hits (detected targets) and misses (undetected targets) ( $\Delta f = \sim 0.5 \text{ Hz}$ ). The phase-locking index (PLI) approaches 0 if the phases are randomly distributed across intervals, and the PLI equals 1 if the phases are

identical. Intervals were discarded if an eyeblink occurred while the target was displayed (25.3% of intervals). Differences between hits and misses were also examined separately for each task using a permutation test (5,000 iterations,  $\alpha = .05$ , two-tailed). Detailed information on the PLI analysis, the eyeblink exclusion criterion, and the subsequent nonparametric statistical test are described in Phase-Locking Analysis in the Supplemental Material.

## Results

### Behavioral results

In the initial thresholding session, participants had a more difficult time detecting a Gabor patch when it appeared in the high-contrast background texture ( $M = 2.7$ ,  $SD = 0.25$ ) than when it appeared in the low-contrast background texture ( $M = 3.5$ ,  $SD = 0.21$ ). This significant difference in thresholds,  $t(95) = 6.6$ ,  $p < .001$ , suggests that detecting a Gabor patch within a high-contrast background texture encourages suppressing the texture features (such as its orientation and spatial frequency content; Doshier & Lu, 2000). The average texture-detection threshold was 2.4% ( $SD = 0.26$ ).

Performance in the subsequent SSVEP experiment was examined by measuring  $A'$  and  $B''_D$ , nonparametric measures of perceptual sensitivity and response bias, respectively (See, Warm, Dember, & Howe, 1997; Stanislaw & Todorov, 1999). The average  $A'$  was .89 ( $SD = .02$ ) for detecting Gabor patches in a high-contrast background texture, .87 ( $SD = .02$ ) for detecting Gabor patches in a low-contrast background texture, and .92 ( $SD = .02$ ) for detecting changes in the contrast of the background texture. The average  $B''_D$  was .83 ( $SD = .06$ ) for detecting Gabor patches in a high-contrast background texture, .86 ( $SD = .05$ ) for detecting Gabor patches in a low-contrast background texture, and .70 ( $SD = .08$ ) for detecting changes in the contrast of the background texture. A separate one-way analysis of variance revealed significant differences in each measure across the three tasks,  $A'$ :  $F(2, 144) = 5.82$ ,  $p = .0037$ ;  $B''_D$ :  $F(2, 144) = 6.85$ ,  $p = .0014$ . The initial thresholding session was successful at making the subsequent SSVEP experiment sufficiently difficult, with a 66.1% overall target-detection rate. The overall false alarm rate was 1.6%.

### Sustained attention (SSVEPs)

Different flicker frequencies can target functionally distinct brain networks (Ding, Sperling, & Srinivasan, 2006; Srinivasan, Bibi, & Nunez, 2006). Thus, differences in the average SSVEP response among the matching task (detecting a change in the contrast of the background texture), neutral task (detecting a Gabor patch in a low-contrast background texture), and competing task (detecting a Gabor patch in a high-contrast background texture) were examined separately for the three different flicker frequencies ( $f_2 = 6, 8, \text{ and } 12 \text{ Hz}$ ). To determine whether the combined influence of enhancement and

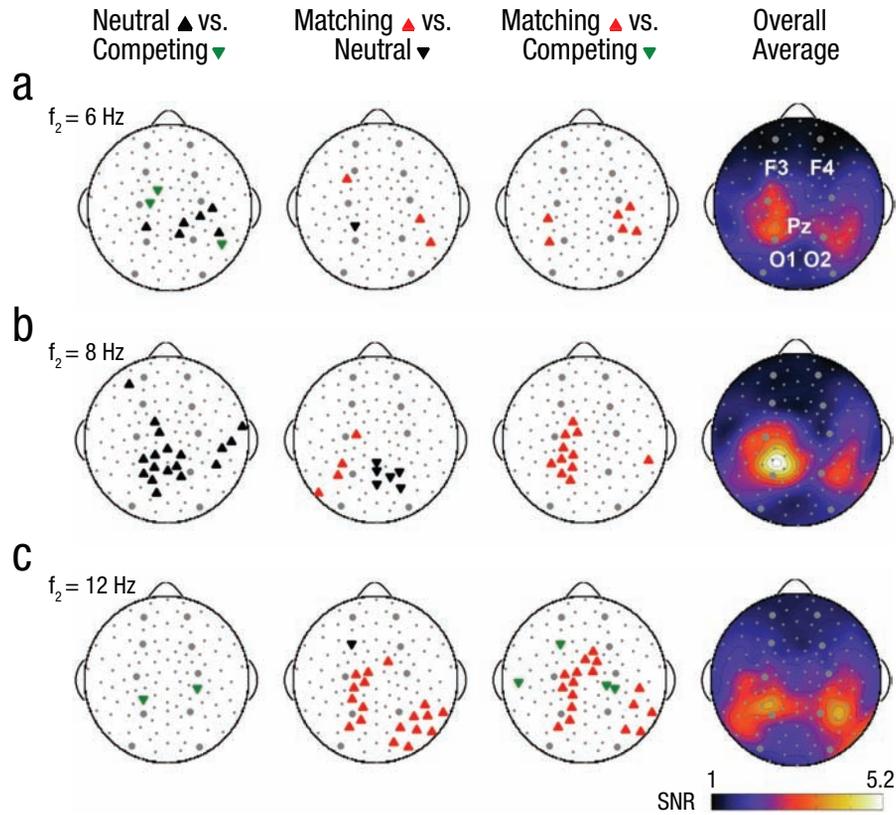
suppression modulated unattended responses, we compared the SNR of the 40-s SSVEP response to the SNR during the unattended flicker during the matching and competing tasks. Responses were larger for the matching task than for the competing task for all three frequencies (6 out of 6 significantly modulated electrodes for 6 Hz, 11 out of 11 electrodes for 8 Hz, and 17 out of 21 electrodes for 12 Hz;  $p < .0005$ ; Fig. 2). These results are consistent with previous findings demonstrating a widespread influence of feature-based attention on unattended responses.

Next, we determined whether this widespread influence was a shared characteristic of both feature enhancement and suppression by comparing the SSVEP responses during the matching and competing tasks to those in the neutral task. We found that 75% of the electrodes that showed suppression were restricted to the 8-Hz flicker frequency, in which responses at all 18 of the significantly modulated electrodes were larger in the neutral than in the competing task (displaying up to a 17% increase in SNR; Fig. 2b). In contrast, 72% of the electrodes that showed enhancement were activated at the 12-Hz flicker frequency, in which responses at 18 out of 19 electrodes were larger in the matching task compared with the neutral task (displaying up to an 18% increase in SNR;  $p < .0005$ ; Fig. 2c). These modulations were also present in individual subjects' data (see Fig. S3 in the Supplemental Material). The results demonstrate that enhancing or suppressing a feature at one location enhances or suppresses the response to a flicker with that feature in an unattended region. However, this widespread influence of enhancement and suppression is observed in dynamically segregated parietal networks with preferred frequencies within the lower and upper alpha bands, respectively.

### Behavioral relevance (PLIs)

To determine whether the sustained modulations were functionally involved in attentional control, we examined whether the response to the unattended flicker was related to participants' ability to subsequently detect targets within each task. We reasoned that large responses to the flicker were associated with an enhanced representation of the flicker feature at the attended location. In accordance with this hypothesis, we predicted that increased responses to the unattended flicker may lead to hits when the target feature matches the flicker feature (i.e., during enhancement) but may lead to misses when the target feature is the competing feature at the attended location (i.e., during suppression). These results can be characterized by an interaction between flicker responses as a function of behavior (hits vs. misses) and task (competing, neutral, and matching).

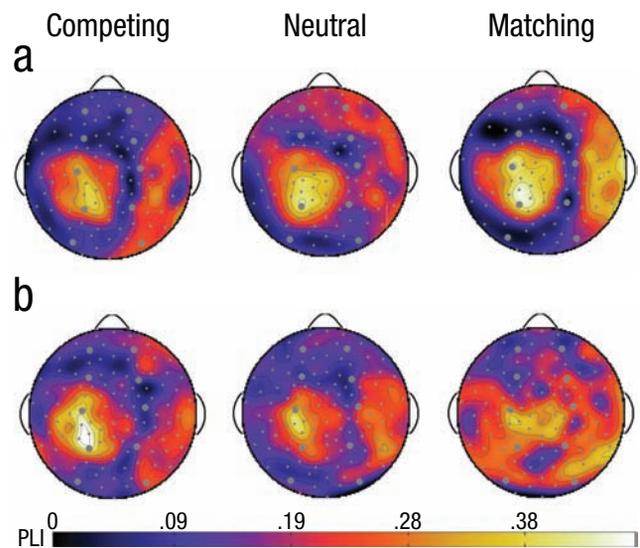
To assess this, we measured the degree of phase locking (the PLI) to the unattended flicker within intervals of approximately 2 s prior to hits and misses. The analysis focused on the 8- and 12-Hz flicker frequencies because the majority of sustained modulations were observed at those frequencies. We



**Fig. 2.** Average signal-to-noise ratios (SNRs) in the three conditions. The three columns on the left show results of comparisons between pairs of conditions at the three frequencies. The black, green, and red triangles indicate the locations where SNRs were larger in the indicated condition than in the comparison condition. Subjects attended to the left and right visual fields, and results are collapsed across these two conditions. The topographic maps in the right column show overall averages across conditions at each of the three frequencies. The large gray circles indicate electrode placements using the 10-20 system.

focused the analysis on the electrodes that showed significant SSVEP modulation due to both feature enhancement and suppression (i.e., in the matching vs. competing conditions). A separate analysis was conducted for the two attended locations (attending left with a flicker in the right visual field and attending right with a flicker in the left visual field), because the average PLI response appeared to lateralize with the attended location (and thus the hemifield containing the flicker).

We examined significant differences in PLI prior to hits and misses for each of the three tasks. We found a significant interaction between behavior and task in the attend-right condition with the left visual field at the 8-Hz flicker frequency ( $p = .0100$ ; Fig. 3). This interaction was characterized by a monotonic increase in phase locking as the relevance of the flicker feature increased at the attended location (i.e., going from competing, neutral, and matching) prior to detected targets; this finding was consistent with the 8-Hz SSVEP results. This trend was reversed prior to undetected targets, in which the response to the unattended flicker monotonically declined with increasing relevance. We found no significant interaction for attending right with the left visual field at a 12-Hz flicker frequency ( $p = .1776$ ) or for attending left with the right visual field at a 8-Hz or 12-Hz flicker frequency ( $p = .3540$ , and  $p = .9814$ , respectively). However, we did find a significantly larger PLI prior to hits than



**Fig. 3.** Phase locking in response to the flicker in the unattended visual field during the intervals approximately 2,000 ms prior to (a) hits and (b) misses in the attended visual field, in each of the three conditions. Results are presented for subjects who attended to the right visual field while an 8-Hz flicker was presented in the left visual field because the spatial location of these responses strongly overlapped with the average steady-state visual evoked potential response at this frequency. The large gray circles indicate electrode placements using the 10-20 system. PLI = phase-locking index.

misses in the matching condition when attending right, with the left visual field at a 12-Hz flicker frequency ( $p = .0204$ ). This significant difference was also present for the 8-Hz flicker frequency ( $p = .0022$ ).

## Discussion

In the experiment reported here, we examined whether enhancing or suppressing a visual feature at one location modulates responses to an unattended flicker containing the enhanced or suppressed feature. We found evidence that sustained enhancement and suppression both have a widespread influence on unattended responses. However, their influence is partially segregated in different brain networks, as reflected by their separate influence on the distinct cortical networks targeted with different flicker frequencies. We found that suppression primarily modulates parietal networks with a preferred frequency within the lower alpha band ( $f_2 = 8$  Hz), and enhancement primarily influences parietal and occipital networks with a preferred frequency in the upper alpha band ( $f_2 = 12$  Hz). The flicker responses appear to reflect the enhanced representation of the target features at the attended location. When the flicker features matched the target features (i.e., when the flicker features were enhanced at the attended location), larger responses to the unattended flicker led to correctly detected targets. Thus, responses to the unattended flicker appear to represent brain processes that are involved in shaping visual processing of features at the attended location.

In the current experiment, individuals performed a task at the attended location that encouraged enhancing or suppressing background-texture features. These modulations likely extended to unattended regions of the visual field, modulating the early sensory response to the flickering texture (Bichot, Rossi, & Desimone, 2005; Martinez-Trujillo & Treue, 2004; Maunsell & Treue, 2006; Saenz, Buracas, & Boynton, 2002; Serences & Boynton, 2007; Treue & Martinez-Trujillo, 1999). Attentional-control regions were integrated with this flickering visual input, because they are tightly coupled with early sensory areas in order to modulate sensory processing. Thus, the cortical responses to the flicker, which were primarily observed over parietal brain areas, may provide a window on the influence of attentional gain at the interface where early sensory biases are integrated with current behavioral goals.

The finding that enhancement is primarily restricted to visual inputs at 12 Hz and suppression is primarily restricted to inputs at 8 Hz suggests that enhancing a feature does not modulate the same processing pathway as suppressing a feature. For example, a subset of the connections between early sensory areas and parietal areas responded preferentially to a 12-Hz flicker, but a partially distinct subset responded preferentially to the 8-Hz flicker. These results presumably reflect differences in the intrinsic time constant and transmission delays between occipital and parietal populations (Nunez, 1995). It is important to note that neurons that responded to the

8-Hz flicker may have been intermixed with neurons that responded to the 12-Hz flicker. This spatial mixing would render it difficult for certain imaging modalities to separate the influence of enhancement and suppression (e.g., if the two populations were intermixed within functional MRI voxels). Moreover, the spatial mixing of distinct brain networks emphasizes the importance of alternative mechanisms, such as temporal synchronization, to segregate distinct brain networks. The spatial overlap between the influence of enhancement and suppression is consistent with the view that brain networks that subserve distinct functions (and that act on different perceptual representations) may be segregated by their dynamic properties (for a review, see Singer & Gray, 1995).

Feature-based attention is regarded as a spatially global phenomenon; attending to a feature (such as color, motion, or orientation) at one location modulates neural responses to that feature in unattended regions of the display. These unattended modulations may reflect the combined influence of enhancement and suppression, depending on the degree to which features compete at the attended location. For example, attending to a direction of motion in the presence of a competing orthogonal direction of motion may encourage enhancing the attended direction and suppressing the unattended direction (Saenz et al., 2002). Attending to a direction of motion in the absence of a distractor encourages a lesser degree of enhancement at the attended location (depending on the degree of task difficulty), even though the orthogonal direction of motion is no longer attentionally suppressed at the attended location.

However, previous studies have demonstrated that enhancing a feature appears to result in a corresponding suppression of nonmatching dimensions of that feature even if they are not attentionally suppressed (by their competing presence) at the attended location (Treue & Martinez-Trujillo, 1999). In the current experiment, it is likely that detecting a Gabor patch in a low-contrast texture resulted in suppression of the nonmatching spatial frequency and orientation components of the texture. Increasing the contrast of the texture features increases the amount of competition and encourages suppressing the texture features at the attended location. The current study extends these findings by demonstrating that attentional suppression of texture features results in a further suppression of neural responses to those features in unattended visual locations. To the best of our knowledge, this is the first study to demonstrate the distinct influence of feature suppression on unattended responses.

The current experiment demonstrated attentional suppression by comparing the SSVEP responses to an unattended flicker during trials in which the flicker feature competes at the attended location (e.g., when it was suppressed during the competing condition) with the SSVEP responses on trials when the flicker was neutral. The behavioral influence of suppression has predominantly been explored in the negative-priming literature, which demonstrates that individuals are slower at responding to a target when that target had served as a distractor in the previous trial.

One contribution to the reduced reaction time in negative priming may be prolonged suppression of the stimulus features on the previous trial, which disrupts the ability to subsequently detect the target (Tipper, 1985). However, the influence of memory phenomenon (e.g., episodic retrieval) in negative priming is obtaining increasing support over attention-based accounts (for a review, see Mayr & Buchner, 2007). The relative complexity of the task (e.g., the second-by-second changes in target features or location) likely contributes to the influence of episodic memory in negative priming. The current experiment demonstrates attentional suppression when individuals detect a fixed target presented at the same spatial location over longer timescales (e.g., the 40-s SSVEP trial). Refraining from changing the target feature or spatial location on a second-by-second basis may have reduced the memory demands in the current task, which allowed a clearer isolation of the brain networks that are uniquely involved in early attentional biases.

The current study demonstrates the partially distinct influence of attentional enhancement and suppression in SSVEP responses. It is important to note that the brain networks that facilitate enhancement and suppression to early sensory features may potentially play distinct roles in the early attentional biases that result when individuals perform more complex tasks, such as detecting shapes (Stokes, Thompson, Nobre, & Duncan, 2009) or categorizing faces (Schyns & Oliva, 1999). In addition, it will be interesting to determine whether overlapping brain networks are involved in the state- and trait-based attentional biases that underlie depression, anxiety, and addiction. Further studies may thus help delineate the potentially distinct role that attention networks play in the range of attentional biases that are involved in complex tasks and human psychopathologies.

### Acknowledgments

We thank J. Serences for comments on the manuscript, E. Hecker for assistance collecting data, and S. Thorpe for assistance programming stimuli.

### Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

### Funding

This work was supported by National Institutes of Health Grant No. 2 R01 MH68004.

### Supplemental Material

Additional supporting information may be found at <http://pss.sagepub.com/content/by/supplemental-data>

### References

- Bichot, N. P., Rossi, A. F., & Desimone, R. (2005). Parallel and serial neural mechanisms for visual search in macaque area V4. *Science*, *308*, 529–534.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*, 433–436.
- Büchel, C., Josephs, O., Rees, G., Turner, R., Frith, C. D., & Friston, K. J. (1998). The functional anatomy of attention to visual motion: A functional MRI study. *Brain*, *121*, 1281–1294.
- Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nature Neuroscience*, *7*, 308–313.
- Cox, W. M., Fadardi, J. S., & Pothos, E. M. (2006). The Addiction-Stroop test: Theoretical considerations and procedural recommendations. *Psychological Bulletin*, *132*, 443–476.
- Derryberry, D., & Reed, M. A. (2002). Anxiety-related attentional biases and their regulation by attentional control. *Journal of Abnormal Psychology*, *111*, 225–236.
- Ding, J., Sperling, G., & Srinivasan, R. (2006). Attentional modulation of SSVEP power depends on the network tagged by the flicker frequency. *Cerebral Cortex*, *16*, 1016–1029.
- Doshier, B. A., & Lu, Z. L. (2000). Noise exclusion in spatial attention. *Psychological Science*, *11*, 139–146.
- Gazzaley, A., Cooney, J. W., McEvoy, K., Knight, R. T., & D'Esposito, M. (2005). Top-down enhancement and suppression of the magnitude and speed of neural activity. *Journal of Cognitive Neuroscience*, *17*, 507–517.
- Grassi, M., & Soranzo, A. (2009). MLP: A MATLAB toolbox for rapid and reliable auditory threshold estimation. *Behavior Research Methods*, *41*, 20–28.
- Joormann, J. (2004). Attentional bias in dysphoria: The role of inhibitory processes. *Cognition & Emotion*, *18*, 125–147.
- Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, *22*, 751–761.
- Le, T. H., Pardo, J. V., & Hu, X. (1998). 4 T-fMRI study of nonspatial shifting of selective attention: Cerebellar and parietal contributions. *Journal of Neurophysiology*, *79*, 1535–1548.
- Martinez-Trujillo, J. C., & Treue, S. (2004). Feature-based attention increases the selectivity of population responses in primate visual cortex. *Current Biology*, *14*, 744–751.
- Mathews, A., & MacLeod, C. (2005). Cognitive vulnerability to emotional disorders. *Annual Review of Clinical Psychology*, *1*, 167–195.
- Maunsell, J. H. R., & Treue, S. (2006). Feature-based attention in visual cortex. *Trends in Neurosciences*, *29*, 317–322.
- Mayr, S., & Buchner, A. (2007). Negative priming as a memory phenomenon: A review of 20 years of negative priming research. *Zeitschrift für Psychologie/Journal of Psychology*, *215*, 35–51.
- Nunez, P. (1995). *Neocortical dynamics and human EEG rhythms*. New York, NY: Oxford University Press.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442.
- Regan, D. (1989). *Human brain electrophysiology: Evoked potentials and evoked magnetic fields in science and medicine*. New York, NY: Elsevier.

- Saenz, M., Buracas, G. T., & Boynton, G. M. (2002). Global effects of feature-based attention in human visual cortex. *Nature Neuroscience*, *5*, 631–632.
- Schyns, P. G., & Oliva, A. (1999). Dr. Angry and Mr. Smile: When categorization flexibly modifies the perception of faces in rapid visual presentations. *Cognition*, *69*, 243–265.
- See, J. E., Warm, J. S., Dember, W. N., & Howe, S. R. (1997). Vigilance and signal detection theory: An empirical evaluation of five measures of response bias. *Human Factors*, *39*, 14–29.
- Serences, J. T., & Boynton, G. M. (2007). Feature-based attentional modulations in the absence of direct visual stimulation. *Neuron*, *55*, 301–312.
- Shulman, G. L., d'Avossa, G., Tansy, A. P., & Corbetta, M. (2002). Two attentional processes in the parietal lobe. *Cerebral Cortex*, *12*, 1124–1131.
- Singer, W., & Gray, C. M. (1995). Visual feature integration and the temporal correlation hypothesis. *Annual Review of Neuroscience*, *18*, 555–586.
- Srinivasan, R., Bibi, F. A., & Nunez, P. L. (2006). Steady-state visual evoked potentials: Distributed local sources and wave-like dynamics are sensitive to flicker frequency. *Brain Topography*, *18*, 167–187.
- Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures. *Behavior Research Methods, Instruments, & Computers*, *31*, 137–149.
- Stokes, M., Thompson, R., Nobre, A. C., & Duncan, J. (2009). Shape-specific preparatory activity mediates attention to targets in human visual cortex. *Proceedings of the National Academy of Sciences, USA*, *106*, 19569–19574.
- Sutoyo, D., & Srinivasan, R. (2009). Nonlinear SSVEP responses are sensitive to the perceptual binding of visual hemifields during conventional “eye” rivalry and interocular “percept” rivalry. *Brain Research*, *1251*, 245–255.
- Tipper, S. P. (1985). The negative priming effect: Inhibitory priming by ignored objects. *The Quarterly Journal of Experimental Psychology*, *37*, 571–590.
- Treue, S., & Martinez-Trujillo, J. C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature*, *399*, 575–579.
- Tucker, D. M. (1993). Spatial sampling of head electrical fields: The geodesic sensor net. *Electroencephalography and Clinical Neurophysiology*, *87*, 154–163.
- Vandenberghe, R., Gitelman, D. R., Parrish, T. B., & Mesulam, M. M. (2001). Location- or feature-based targeting of peripheral attention. *NeuroImage*, *14*, 37–47.