The effects of spatial attention in early human visual cortex are stimulus independent

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Although visual spatial attention has been shown to increase activity as measured with both fMRI and electrophysiological techniques, significant differences in the results have been shown. fMRI studies have routinely demonstrated large signal increases to an attended versus unattended stimulus in early visual areas (V1–V3) whereas some previous electrophysiology research has either shown very small or no differences in spike rate. One possible explanation for this discrepancy is that most previous fMRI studies have not differentiated between stimulus-evoked and baseline-shift changes in the response to an attended stimulus. Here, fMRI was used to separately measure stimulus-evoked and baseline-shift responses. In the first experiment, contrast–response functions to grating stimuli that were either attended or unattended were measured. The results show that the increases in fMRI signal associated with spatial attention are accounted for by a baseline shift. In a second experiment, spatial attention was fixed in a single location that isolated possible stimulus-evoked changes with attention. Consistent with the first experiment, no stimulus-evoked changes were found. These results potentially reconcile previous discrepant findings between fMRI studies and some neurophysiology studies of attention by demonstrating that the effects of spatial attention in early visual areas can be dominated by stimulus-independent shifts in baseline responses.

Keywords: fMRI, attention, contrast, V1, vision, functional imaging

Introduction

Visual spatial attention has long been known to enhance neural processing. There are two primary ways that this enhancement is thought to occur. The first is a general increase in the baseline firing rate of neurons with receptive fields at the retinotopic position of the focus of spatial attention. These "baseline shifts" are independent of the presence of a stimulus—directing attention to one part of the visual field versus another is all that is necessary to evoke a change in firing rate. Electrophysiology measurements in the monkey have shown significant baseline shifts as early as V2 (Luck, Chelazzi, Hillyard, & Desimone, 1997).

A second way in which spatial attention is thought to enhance neural processing is dependent on stimulus selectivity. These changes are characterized by an increase in firing rate of neurons that have a stimulus-evoked response to a particular stimulus, after any change in baseline firing rate is removed from the response. There is electrophysiological evidence of stimulus-evoked increases in spike rate with attention in later retinotopic areas (e.g., V4; McAdams & Maunsell, 1999; Moran & Desimone, 1985; Reynolds, Pasternak, Desimone, 2000; Willford & Maunsell, 2006). However, in early visual areas (e.g., V1), stimulus-evoked increases have either been nonexistent (Luck et al., 1997; Marcus & Van Essen, 2002; Moran & Desimone, 1985), very small (e.g., 6%; McAdams & Maunsell, 1999), or highly dependent on

stimulus configuration (Ito & Gilbert, 1999; Motter, 1993; Roelfsema, Lamme, & Spekreijse, 1998).

In apparent contradiction to the findings from electrophysiology, fMRI studies of spatial attention have routinely demonstrated large signal increases in V1 to a stimulus that is attended versus unattended (e.g., Breczynski & DeYoe, 1999; Gandhi, Heeger, & Boynton, 1999; Martínez et al., 1999; Somers, Dale, Seiffert, & Tootell, 1999). However, it is not currently known if these changes are due to baseline shifts, differences in the stimulus-evoked response, or some combination of two. While previous fMRI studies have identified baseline shifts in early visual cortex (Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Ress, Backus, & Heeger, 2000; Silver, Ress, & Heeger, 2007), purely stimulus-evoked changes with attention—that do not also potentially include baseline shifts—have yet to be isolated with fMRI.

The current study uses event-related fMRI to separately measure the contribution of baseline-shifts and stimulus-evoked changes with spatial attention. In the first experiment, the response to brief presentations of gratings that were either attended or unattended was measured across a range of stimulus contrasts. We show that the change in the contrast response function (CRF) with spatial attention can be completely accounted for by a baseline shift. In a second experiment, spatial attention was fixed in a specific location and CRFs were measured in attended and unattended locations. Because the location of attention was fixed, only stimulus-evoked changes were measured. Consistent with previous electrophysiological results in

early visual cortex—and predicted by the results from the first experiment—no attention-related differences were observed. Together these experiments demonstrate that baseline shifts are the predominant effect of spatial attention in early visual cortex measured with fMRI.

Methods

Subjects

Four subjects (one female) participated in Experiment 1. Three of the four subjects participated in Experiment 2, which was conducted in a separate session. All subjects had normal visual acuity and all indicated informed written consent in accordance with the University of Washington Human Subjects Institutional Review Board.

Stimuli and task

Subjects performed identical threshold-level spatial-frequency discrimination tasks in the laboratory and in the scanner. Sinusoidal gratings windowed by a circular aperture of diameter 6° were positioned in the four visual quadrants, 8° laterally and 8° vertically. For each trial, one side (left or right) was randomly chosen as the "attended" side and the other was the "unattended" side. Subjects were instructed which side to attend to by a small arrow cue at the central point of fixation (details about the cue are described below). Eye movements were not recorded during scanning. However, all subjects were very experienced psychophysical observers and were instructed about the importance of maintaining eye fixation at all times. Moreover, as described in the fMRI data analysis section below, data were analyzed in small regions-of-interest that represented the precise retinotopic position of the stimuli. Any consistent shift in eye position would have resulted in greatly attenuated or nonexistent fMRI responses.

A "standard grating" with a spatial frequency of 2.0 cycles/deg was shown in either the top or bottom position (randomly determined on each trial) on the attended side. A "test grating" of a slightly higher spatial frequency was shown in the other position on the attended side. The unattended side had the same stimuli but the top and bottom positions of the standard and test were separately and randomly determined. Subjects indicated which grating on the attended side had the higher spatial frequency using one of two buttons. Six contrast levels were used (3%, 6%, 12%, 25%, 50%, and 75%). Stimuli were presented for 300 ms with a 2700-ms response interval.

All subjects received extensive practice (minimum 2 hours) and participated in a psychophysical experiment (an additional 2–3 hours) in the laboratory 1–3 days prior to scanning. The psychophysical experiment measured the spatial-frequency increment threshold using a standard 3-down 1-up double-interleaved staircase procedure (50 trials for each staircase). Weibull functions were fit to the psychometric data using a maximum likelihood procedure to estimate the spatial frequency difference that would produce 80% correct performance. Thresholds were measured separately for each contrast level and for each attended side (left and right). In general, increment thresholds were constant across the 12% to 75% contrasts and ranged across subjects from 0.10 to 0.125 cycles/deg above the baseline of 2 cycles/deg. The 3% and 6% contrast levels had slightly higher increment thresholds for all subjects ranging across subjects from 0.15 to 0.20 cycles/deg. Increment thresholds obtained in the laboratory for each subject were used in the MRI scanner resulting in constant task difficulty at approximately 80% correct.

fMRI experimental design, Experiment 1

We assume that there are two potential effects of spatial attention on the contrast response function: (1) an effect on the stimulus-evoked response and (2) a baseline shift in the overall neural response that is independent of the stimulus. The responses to an attended and unattended stimulus as a function of stimulus contrast x can be expressed as:

$$R_A = A(x) + b_A \text{ and } R_U = U(x) + b_U, \qquad (1)$$

where b_A and b_U are the baseline responses in retinotopic positions that represent the attended and unattended locations, and $A(x)$ and $U(x)$ are the stimulus-evoked responses to the attended and unattended stimuli as a function of contrast, respectively. Note that by this convention, $A(0) = U(0) = 0$ which simply says that when there is no stimulus, there will be no stimulus-evoked response.

In Experiment 1, there were three trial types: (1) reference trials, (2) 0% contrast trials (no stimulus), and (3) stimulus trials containing a range of contrast levels. Figure 1 shows a schematic example of the three different trial types. In addition, Table 1 shows the different attention components that contribute to the signal for each condition. During the reference trials, which established the reference-point for calculating percent signal change (see fMRI data analysis section), no cue or stimulus was presented. Subjects were simply asked to maintain their attention on the central fixation mark and await the presentation of the next trial. Thus, as illustrated in Table 1, there was no stimulus-evoked component associated with spatial attention, $A(0)$. In addition, because attention was focused centrally, there was no baseline-shift component (which is why a "0" is present in Table 1 in place of the baseline shift).
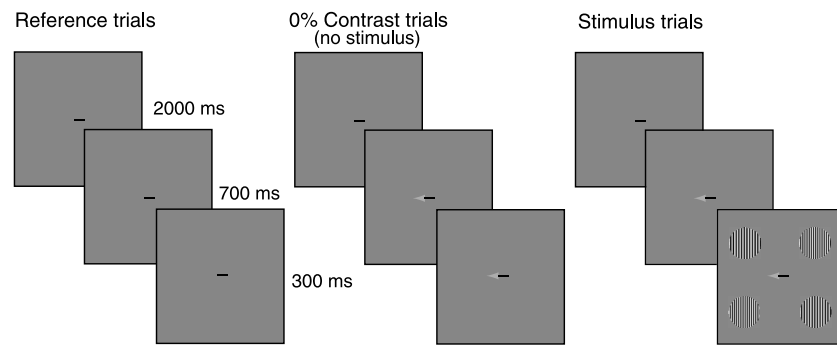
Figure 1. Experiment 1. There were three trial types: (1) Reference trials where subjects maintained attention on a central fixation mark. (2) Zero percent contrast (no stimulus) trials in which a low-contrast cue appeared but no stimulus. The difference between the 0% contrast trials and the reference trials measured baseline shifts associated with spatial attention. (3) Stimulus trials in which the presentation of the cue was followed by the presentation of a sinusoidal grating which differed in luminance contrast from trial to trial.

From the subject's perspective, the reference "trials" simply appeared as an extended intertrial interval. It was important that subjects maintained their spatial attention on the central fixation mark during reference trials (i.e., during the intertrial interval). This provided a reference point that did not include any baseline shifts associated with spatial attention at the attended and unattended locations. The reference trials had a central fixation mark while the zero-contrast and stimulus trials had a low-contrast arrow next to the fixation mark. To help ensure that attention was directed centrally during the reference trials, the small arrow instruction cue that initiated trials in the zero-percent and stimulus conditions was low contrast (6%, see Figure 1). Thus, after a trial was completed, subjects were motivated to move their attention back to the central fixation mark in order to be able to see the instruction cue for the next trial. (Although thresholds were not determined for the central arrow cue, it was very difficult to see if attention was not directed centrally.) All subjects reported maintaining attention centrally during the reference/intertrial period.

During the 0% contrast trials, which occurred on 12.5% of trials, only the instruction cue was presented. Subjects shifted their attention to the cued side in expectation of a stimulus presentation. The attended side could be either left or right with equal probability. Subjects were well-practiced and informed beforehand about these "no-stimulus" trials so that if no stimulus was observed, attention was shifted back to the center to await the next instruction cue. The no-stimulus trials were used to measure baseline shifts associated with changing spatial

attention from the center to the cued side. Specifically, the signal measured during the zero-percent contrast trials was compared to the reference trials in order to isolate baseline shifts. For example, using the convention presented in Table 1, in the attended condition the signal was measured by subtracting the reference condition from the zero-percent contrast condition: $(A(0) + b_A) - (A(0) + 0)$, and since $A(0) = 0$, we are left with a measure of b_A. The same logic results in the measurement of the baseline shift at the unattended locations, b_U.

During the stimulus trials, following the instruction cue, a stimulus of a particular contrast was shown for 300 ms. Again, left and right attended directions occurred with equal probability. The stimulus trials had two separate potential contributions to the measured signal: (1) baseline changes associated with the shift of attention to the cued side and (2) stimulus-evoked changes associated with attention to the cued side. The signal during stimulus trials was measured by subtracting the reference condition from the stimulus trials. For example, in the attended condition, the signal was measured by $(A(x) + b_A) - (A(0) + 0)$, and since $A(0) = 0$, we are left with $A(x) + b_A$. The same logic applies to the measurement of the unattended condition.

The central question will be whether the baseline changes, b_A and b_U, that are measured with the no-stimulus (zero-percent contrast) trials can account for the differences observed between the attended and unattended stimuli, $A(x) + b_A$ and $U(x) + b_U$. In other words, we will have a direct measure of the baseline response in the zero-percent contrast condition, which we can then subtract away from the stimulus trials, $(A(x) + b_A) - b_A$ in the attended condition, $(U(x) + b_U) - b_U$ in the unattended condition. We can then evaluate whether $A(x)$ equals $U(x)$. If they are equal, this would indicate that baseline shifts entirely account for the attention effects. Alternatively, if they are not equal, it would be indicative of a stimulus-evoked difference between the two conditions.

There were a total of 16 separate conditions: seven contrast levels (counting 0%) times two attention conditions (left and right) plus two reference trials (both were

	Reference trials	0% Contrast trials	Stimulus trials
Attended	$A(0) + 0 = 0$	$A(0) + b_A = b_A$	$A(x) + b_A$
Unattended	$U(0) + 0 = 0$	$U(0) + b_U = b_U$	$U(x) + b_U$

Table 1. The different attention components present in each of the three trial types of Experiment 1 using the conventions of Equation 1.
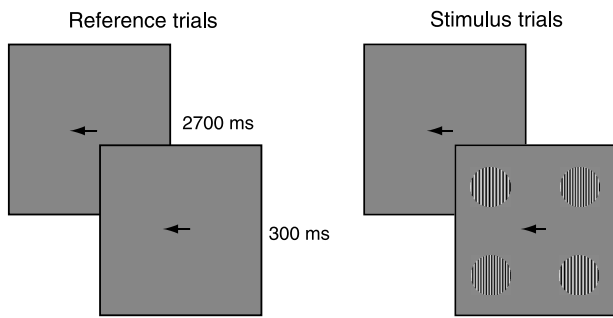
Figure 2. Experiment 2. This experiment differed from Experiment 1 in that attention was directed to one side (left or right) for the entire duration of a scan so that during reference trials spatial attention remained in the attended location.

identical but for randomization purposes were considered separately). Each fMRI scan consisted of 8 trials per condition. The ordering of trials was determined using an m-sequence (Buracas & Boynton, 2002). A maximum of 8 scans was conducted per session (all subjects completed at least 5 scans). It should be emphasized that for Experiment 1 (and for Experiment 2, described next) the trial onsets were not predictable by the subject. Although a "trial" began regularly every 3 s, because reference trials (during which nothing happened) were randomly inter-mixed in the same counterbalanced order as all other trial types, trial onsets appeared random from the subject's perspective.

fMRI experimental design, Experiment 2

This experiment was designed to only measure potential stimulus-evoked increases due to spatial attention. For the entire duration of a scan, the attention cue remained, directing attention to only one side. During reference trials no stimulus was presented, although unlike Experiment 1, attention was directed to the cued location during reference trials. During stimulus trials, one of the six stimulus contrast levels was presented (Figure 2). Using the convention introduced in describing Experiment 1, Table 2 shows the different contributions to the measured signal.

With spatial attention fixed at the attended location, there is only one potential contribution to the measured signal: stimulus-evoked changes associated with attention to the cued side. With this design, it is not possible to separately measure the baseline shifts. Instead the baseline shifts are incorporated into the reference condition that will be subtracted away from the signal to measure the response on stimulus trials. For example, for the attention condition, the stimulus trials will be measured by subtracting the reference trials from the stimulus trials: $[A(x) + b_A] - [A(0) + b_A]$, leaving only a measure of $A(x)$. Similarly, in the unattended condition, we will be left only with a measure of $U(x)$. The advantage of this design over Experiment 1 is that rather than separately estimating

the magnitude of baseline shifts, baseline shifts are built directly into the reference condition in the experimental design. Thus, any difference between the attended and unattended CRFs will reveal stimulus-evoked changes associated with spatial attention. These stimulus-evoked differences could manifest in a number of different ways, but two commonly discussed possibilities are 'response-gain' or 'contrast-grain' changes (e.g., Reynolds et al., 2000). A similar experimental design was used to demonstrate stimulus-evoked increases with attention in the shape-processing region, lateral occipital complex, in a previous study (Murray & He, 2006).

While there is no guarantee that subjects maintained their attention on the cued side for the entire scan duration, there are several reasons to expect that they did. First, the detection of the low-contrast (3%) stimuli, which were slightly above detection threshold, was easier with attention fixed on the attended side, particularly because trial onsets were unpredictable. Second, the spatial-frequency discrimination task itself was easier if attention was continuously positioned at the attended location rather than shifted after the onset of the stimuli. All subjects reported that for these strategic reasons, they maintained attention at the cued location throughout the scan.

For each scan, there were a total of 8 separate conditions: six contrast levels plus two reference trials (both were identical but for randomization purposes were considered separately). Each functional MRI scan consisted of 16 trials per condition. The ordering of trials within any particular scan was determined using an m-sequence. A total of eight scans—during which attention was directed either to the left or right side for the entire scan duration—were performed. Four scans of attend-left and four scans of attend-right were collected from each subject in an alternating order, counterbalanced across subjects.

fMRI data acquisition

Functional MRI data were acquired using a Philips Achieva 3T scanner using an 8-channel head coil and an echo-planar imaging sequence. During each scan, 400 temporal frames were acquired (repetition time, 1 s; flip angle, 60°; 16 slices of 5 mm thickness and 3.44 × 3.44 mm resolution, field of view, 220 mm). Each scanning session began with a T1-weighted structural scan 1 × 1 × 1 mm used to for visualization of retinotopic visual areas.

Visual cortical areas, V1, V2, and V3 were localized using standard retinotopic mapping and cortical-flattening

	Reference trials	Stimulus trials
Attended	$A(0) + b_A = b_A$	$A(x) + b_A$
Unattended	$U(0) + b_U = b_U$	$U(x) + b_U$

Table 2. The different attention components present in each of the two trial types of Experiment 2 using the conventions of Equation 1.

techniques using BrainVoyager QX. Regions of interest (ROIs) within these visual areas were determined using an on–off block design localizer (40 s period × 5 cycles) alternately displaying flickering checkerboards in the left and right visual field in the same retinotopic position as the grating stimuli. It was not possible to reliably identify the subregions of areas V3A and V4v that correspond to the retinotopic position of the grating stimuli. Thus, these cortical areas were not analyzed.

fMRI data analysis

The analysis of the event-related data was done using methods similar to previous studies (e.g., Kourtzi & Kanwisher, 2000; Murray & Wojciulik, 2004) using custom software written in MATLAB. The time course of MR signal intensity was extracted by averaging the data from all the voxels within the independently defined ROIs identified with the localizer scans. For each scan, the signal intensity across the trials in each condition at each of 12 time points time-locked to the onset of the stimuli was averaged. These event-related time courses of signal intensity were then converted to percent signal change by subtracting the corresponding value for the reference condition and then dividing by that value. The resulting time course for each condition was then averaged across scans. The peak in the average response occurring 5–6 s after stimulus presentation served as the measured response for each condition. Averages in the hemisphere contralateral to the focus of attention were designated "attended" data. Averages in the hemisphere ipsilateral to the focus of attention were designated "unattended" data. Attended data from each hemisphere and unattended data from each hemisphere were averaged.

Results

Experiment 1

This experiment was designed to separately measure baseline-shift and stimulus-evoked changes of the contrast–response function (CRF) due to spatial attention. As illustrated in Figure 1 and explained in the methods, attention was focused centrally during the baseline condition. During the zero-contrast condition, attention shifted to the attended side but no stimulus was presented. The difference in response between the reference condition and the zero-contrast condition measures the baseline shift associated with spatial attention. Behavioral results in the scanner were as expected based on the threshold measurements determined initially in the laboratory before scanning. Percent correct for each of the contrast levels (3, 6, 12, 25, 50, 75) was (77 ± 1.2; 78 ± 1.6; 77 ± 2.5; 79 ± 2.6; 79 ± 3; 79 ± 2).

Consistent with previous fMRI results, baseline shifts were observed in V1, V2, and V3. Specifically, in the absence of any visual stimulus (i.e., at zero-contrast), there was a 0.07, 0.08, and 0.10 increase in the percent change of the fMRI signal caused by the shift of spatial attention to the cued versus uncued side in V1, V2, and V3, respectively. Expressed as percentages of the response on the unattended side, these signal increases correspond to baseline shifts of 28%, 35%, and 83%, respectively. A one-tailed t test testing whether there was an increase in the attended condition was significant in V1 ($p = 0.03$), V2 ($p = 0.004$), and V3 ($p = 0.0001$).

Figure 3 shows the CRFs for each visual area where the filled symbols represent the attended data and unfilled symbols represent the unattended data. The solid lines through the symbols are the best least squares fits of a hyperbolic ratio function, described by:

$$R = r_{max} \times \left(\frac{C^n}{C^n + C_{50}^n} \right) + m, \qquad (2)$$

where R is the predicted fMRI response, c is the contrast, r_{max} is the maximum attainable response, m is the spontaneous activity, c_{50} is the contrast at which the response is half-maximal, and n is the exponent that determine the steepness of the response function. This function has provided good fits to contrast response functions from visual cortex in cat and monkey (Albrecht & Hamilton, 1982) and has also been used to fit the population-based fMRI contrast–response function (Boynton, Demb, Glover, & Heeger, 1999). The fits include data from the zero-contrast condition. Excluding these points had a negligible effect on the accuracy of the fits.

The CRFs are consistent with previous studies (Boynton et al., 1999; Buracas & Boynton, 2007) in that there is a monotonic increase in the fMRI signal as a function of contrast in each visual area. In addition, a significantly larger fMRI signal was measured for each contrast level in the attended versus the unattended conditions (Figure 3, top row). The central question is whether this increase in the CRF with attention can be accounted for by a baseline shift or whether additional stimulus-evoked changes are also present. The data unequivocally show that the baseline shift can account for the magnitude difference between the attended and unattended CRFs. This is demonstrated in two ways. First, a constant, additive offset term, k, was added to Equation 2:

$$R = k + \left(r_{max} \times \left(\frac{C^n}{C^n + C_{50}^n} \right) + m \right). \qquad (3)$$

The best-fitting parameters for the unattended data derived from Equation 2 were held constant and the least-squares solution for k was found that best fit the attended data. The
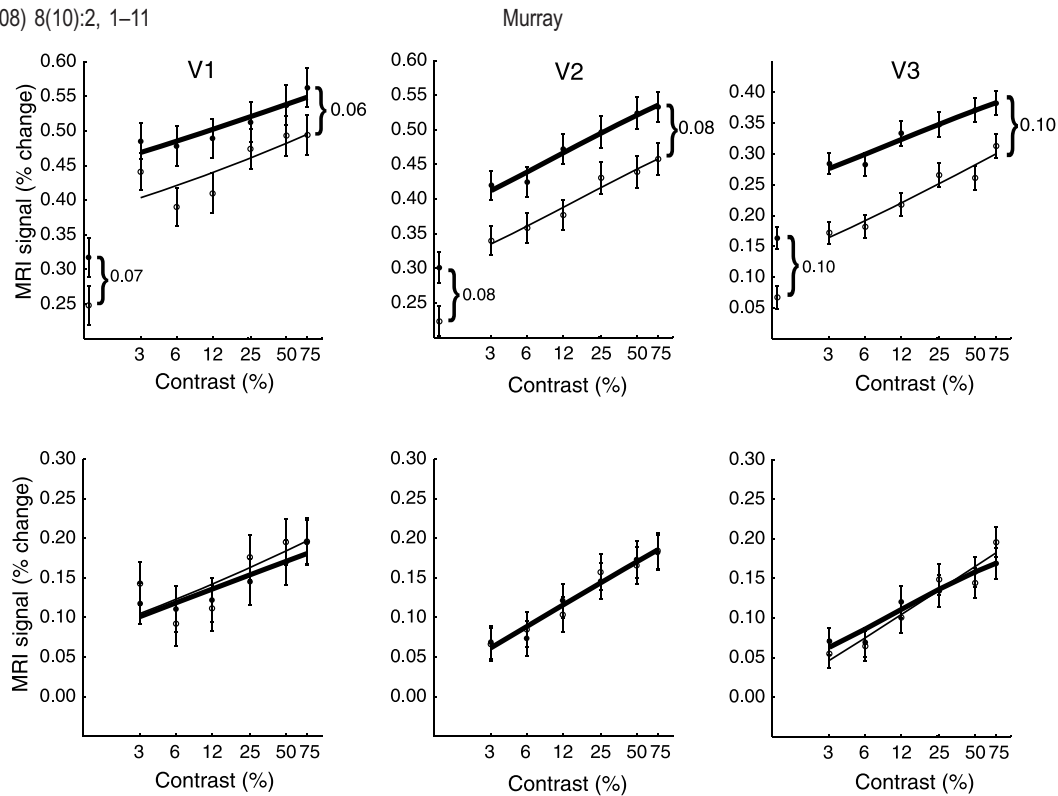
Figure 3. Results from Experiment 1. Top row, The fMRI response is plotted as a function of contrast for the attended (filled circles) and unattended (unfilled circles) stimuli in three different visual areas. Solid lines are the best fits of a hyperbolic ratio function (Equation 2 in text). The points on the far left of each graph show the difference in fMRI signal in the 0% contrast condition as a function of attention and represent that magnitude of the baseline shift. The bracketed numbers to the right of curves are an estimate of an additive constant, *k*, that best accounts for the difference between the attended and unattended curves (Equation 3). Bottom row, the curves are replotted with the baseline shifts (i.e., the zero-percent contrast values for each attention condition) subtracted away from the attended and unattended curves. Error bars are *SE*s of the mean across trials.

magnitude of the baseline shift (i.e., the difference between the attended and unattended data points at zero-contrast) in each area (0.07, 0.08, and 0.10) is nearly equivalent to the derived *k* value (0.06, 0.08, and 0.10) for each area (shown in brackets next to the plotted CRFs in Figure 3).

To further demonstrate that a baseline shift accounts for the increase in the CRF for the attended condition, the bottom row of Figure 3 replots the CRFs after removal of the baseline shift (i.e., the difference at zero-contrast) from the attended and unattended conditions. Specifically, the zero-percent contrast points represent an estimate of the attended and unattended baseline response, b_A and b_U. Using the convention derived in the methods, the curves in the bottom row represent $(A(x) + b_A) - b_A$, which is an estimate of $A(x)$, and $(U(x) + b_U) - b_U$, which is an estimate of $U(x)$. After the removal of the baseline effects, the curves are now nearly identical and show a uniform effect of the baseline shift across different contrast values and that there is no residual stimulus-evoked effect of attention.

Although a constant additive shift (additive model)—which assumes that the effects of attention simply add a constant to the fMRI response—appears to account for the differences between the attended and unattended conditions, there are alternative models to consider. In particular, electrophysiology results have suggested that spatial attention may act to increase response gain (McAdams & Maunsell, 1999) or contrast gain (Martínez-Trujillo & Treue, 2002; Reynolds et al., 2000). Response gain is equivalent to multiplying the firing rate of a neuron by a constant factor. Contrast gain, on the other hand, is equivalent to a leftward shift in the CRF. More recent electrophysiological results have found evidence that both models can account for the change in the CRF with attention (Willford & Maunsell, 2006).

Here we directly compare three models and their ability to account for the change in the CRF with attention: (1) additive model—Equation 3, (2) response gain, and (3) contrast gain. Response gain was modeled by adding a multiplicative scaling term, *a*, to Equation 2:

$$R = a \times r_{max} \times \left(\frac{C^n}{C^n + C_{50}^n} \right) + m, \qquad (4)$$
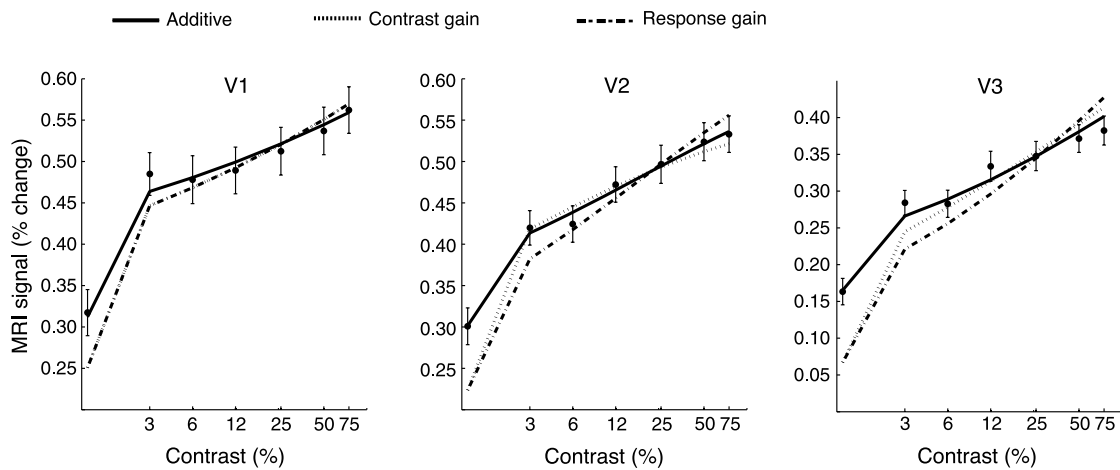
Figure 4. Model comparison. Three models of the effects of attention on the CRF were compared. The additive model (solid line) can account for the change in the CRF due to attention better than contrast gain (dotted) and response gain (dash dotted). Note that contrast gain and response gain provided equivalent fits in V1.

Contrast gain, or a leftward shift, was modeled by including a multiplicative scaling term, *a,* to the contrast-at-half-maximum variable:

$$R = r_{max} \times \left(\frac{C^n}{C^n + a \times C_{50}^n} \right) + m. \qquad (5)$$

To test the three models, parameters were first fit from Equation 2 to the unattended data. These parameter values were held constant and Equations 3, 4, and 5 were fit to the attended data allowing the free parameters k (Equation 2), a (Equation 3), and a (Equation 4) to vary to find the best least-squares fit. The fits to the attended data are plotted in Figure 4. Visual inspection of the best-fitting additive model (solid lines) versus the response-grain and contrast-grain shows that the additive model fits better in each of the visual areas. To compare the fits quantitatively, a Monte Carlo simulation was conducted using 1000 sample data sets derived from the original fMRI measurements. Sums-of-squared errors were computed

between the fits and the simulated data. In V1, the additive model fits better in 88% of sample data sets compared to 8% for contrast gain and 5% for response gain. In V2, the additive model fits better in 93% of data sets compared to 3% and 4% for contrast- and response-gain, respectively. In V3, the additive model fits best in 98% of data sets.

Experiment 2

Experiment 1 separately measured the magnitude of baseline shifts (the difference between that attended and unattended zero-percent contrast conditions) and then compared it to the size of the attention effect across different contrast values. A different way to assess the contribution of baseline shifts is to remove them from the experimental design directly. This was done by having subjects attend to a single location for an entire scan and then measuring the fMRI response to stimuli presented at the attended versus unattended location (Figure 2).
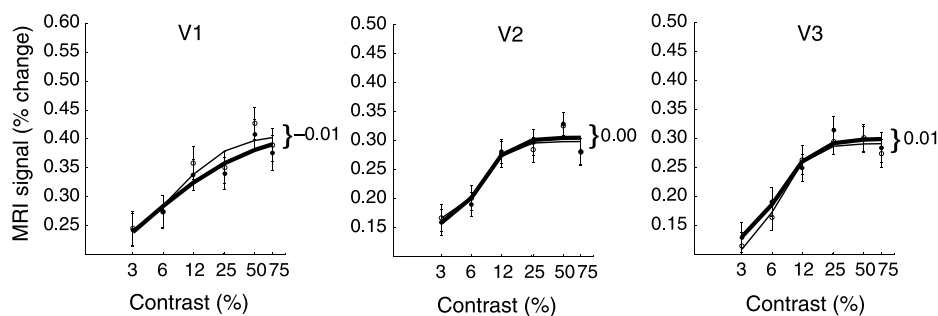

Figure 5. Results from Experiment 2. Filled circles show the fMRI response as a function of contrast for stimuli in the attended location. Unfilled circles show the unattended response. Solid lines are the best fits of a hyperbolic ratio function (Equation 2). The bracketed numbers to the right of curves are an estimate of an additive constant, *k,* that best accounts for the difference between the attended and unattended curves (Equation 3). Error bars are *SE*s of the mean across trials.

Because any baseline shift differences are incorporated into the reference trials, only stimulus-evoked changes are measured. Specifically, using the convention outlined in the methods, the attended data represent $[A(x) + b_A] - [A(0) + b_A]$, leaving only a direct measure of $A(x)$. A similar logic leaves a direct measure of $U(x)$.

Behavioral results were similar to Experiment 1. Percent correct was near the psychophysically measured threshold level for each of the contrast levels (75 ± 1.1; 79 ± 2.4; 75 ± 2.8; 79 ± 1.9; 83 ± 2.7; 83 ± .82). The solid and filled symbols in Figure 5 show the attended and unattended responses across different contrast levels. No differences in the CRF were observed as a function of attention. Average differences between the attended and unattended data points were −0.01, 0.00, and 0.01, respectively, for V1, V2, and V3. The lack of any stimulus-evoked differences in the fMRI signal further demonstrate that baseline shifts are the predominate source of spatial attention effects in early visual cortex.

Discussion

Using two different experimental designs, we show that baseline shifts account for nearly all of the measured change in the fMRI response in early visual cortex to a stimulus that is attended versus unattended. Stimulus-evoked changes, if they are present, are very small. Our results are consistent with previous reports that have measured baseline shifts in early visual cortex (Kastner et al., 1999; Ress et al., 2000; Silver et al., 2007) and are consistent with recent fMRI measurements of CRFs with and without attention (Buracas & Boynton, 2007). The significant contribution here is that we are able to separate the contributions of baseline-shifts and stimulus-evoked changes with attention. The demonstration of minimal stimulus-evoked changes with attention in early visual cortex has significant practical and theoretical implications for understanding the neural mechanisms of visual spatial attention.

First, a central question that has plagued attention research is how such differing results could be obtained in electrophysiological and brain imaging studies of spatial attention in early visual cortex (e.g., reviewed in Heeger & Ress, 2002; Pessoa, Kastner, & Ungerleider, 2003; Posner & Gilbert, 1999). fMRI experiments routinely demonstrate large signal increases whereas electrophysiology studies rarely show increases in spike rate. The differences in the results have been particularly striking in V1 where some electrophysiology has shown either no (Luck et al., 1997; Marcus & Van Essen, 2002) or very small (e.g., 6%, McAdams & Maunsell, 1999) increases with attention. However, see Ito and Gilbert (1999), Motter (1993), Roberts, Delicato, Herrero, Gieselmann, and Thiele (2007), and Roelfsema et al.

(1998) for studies demonstrating considerably larger stimulus-evoked changes with attention in early visual areas. Possible explanations for these apparently conflicting results have ranged from the use of different species (monkey vs. human) to intrinsic differences in the measurements. For example, because the fMRI signal is tied to hemodynamics, it has been suggested that subthreshold or inhibitory processes—which could contribute to blood flow responses but would be less apparent using electrophysiological techniques—are contributing to the fMRI results (Heeger & Ress, 2002). Also, others have suggested that V1 attention effects occur late, as the possible result of feedback from extrastriate areas (Martínez et al., 1999; Noesselt et al., 2002). Since fMRI is integrating the response over long time scales, perhaps the signal incorporates both initial feedforward and longer-latency feedback influences from other areas. Although this may be true, the additional presumption of this explanation is that previous electrophysiology studies have simply missed the hypothesized later occurring effects of attention in V1.

The data presented here suggest an alternative interpretation for the discrepancy between electrophysiology and fMRI results in early visual cortex. By separating the contributions of baseline-shifts and stimulus-evoked changes, our results show that fMRI measures are entirely consistent with the conclusions drawn from electrophysiology experiments—namely, that stimulus-evoked changes with attention are very small or nonexistent in early visual cortex. Instead, the large signal increases typically observed in fMRI studies of attention in early visual cortex are the result of baseline shifts—what others have referred to as sustained "bias" signals (e.g., Martínez et al., 1999). When these baseline shifts are not present, as shown in Experiment 2 in the current study and in previous fMRI experiments (e.g., Liu, Pestilli, & Carrasco, 2005), no differences in V1 are found (although Liu et al., 2005 did observe changes in V2 and V3). This claim is further supported by a very recent finding that recorded intracranial local field potentials (LFP) in human primary visual cortex (Yoshor, Ghose, Bosking, Sun, & Maunsell, 2007). Similar to our Experiment 2, where stimulus-evoked differences were not observed, this study was sensitive only to stimulus-evoked changes with attention and showed only very small, statistically nonsignificant changes in the LFP measured in V1.

Although our results potentially reconcile differences between fMRI and some electrophysiology results in V1, significant stimulus-evoked differences have been measured in V2 (Luck et al., 1997). Why are these stimulus-evoked changes not apparent in our study in V2 and V3? The exact stimulus configuration had a large impact on whether stimulus-evoked responses were measured in the Luck et al. (1997) study. No stimulus-evoked changes were observed when one stimulus was in the receptive field of the neuron and the other stimulus was placed in the other hemifield—a stimulus configuration that is very similar

to the configuration used in our fMRI experiment. A recent electrophysiology study that also used a similar stimulus configuration (gratings on either side of the vertical meridian) and measured contrast response functions in V4, also observed changes in attention that can apparently be accounted for by a baseline shift (see Figures 6A–6C of Willford & Maunsell, 2006). Also consistent with the idea that stimulation configuration plays an important role in determining the influence of attention in early visual areas are electrophysiological studies showing that attention can modify contextual processing as early as V1 (Ito & Gilbert, 1999; Motter, 1993; Roberts et al., 2007). Common to the experimental designs in these studies were the presence of contextual 'flanking' stimuli (Ito & Gilbert, 1999; Motter, 1993) or stimuli that extended beyond the classical receptive field (Roberts et al., 2007; Roelfsema et al., 1998). Thus, it appears that with isolated stimuli (such as in this current experiment), the primary effect of spatial attention in early visual areas is a change in baseline firings rates, but in more complex stimulus configurations, attention may indeed alter the stimulus-evoked response.

A re-examination of a previous study also provides fMRI evidence for purely baseline shifts associated with spatial attention. Buracas and Boynton (2007) used fMRI to measure CRFs with and without attention. This study used a blocked experimental design that required subjects to alternate attention between stimuli in the left and right visual fields. Although the study did not independently measure stimulus-evoked and baseline-shift changes associated with attention, their experiment can be described in those terms. Specifically, the measured response in their experiment represented the *difference* in fMRI signal between (1) the sum of stimulus-evoked and baseline activity in response to the attended stimuli and (2) the sum of the stimulus-evoked and baseline activity in response to the unattended stimuli. The measured response (i.e., the difference between 1 and 2, above) was constant across different contrast values. It follows from this constant response that there was no difference in stimulus-evoked activity between the attended and unattended conditions (Boynton, personal communication), a finding consistent with our explicit measurement of these values.

How can baseline shifts, which are generally on the order of only a few spikes/s when measured in electrophysiology experiments, result in such large fMRI differences? While baseline shifts are small in absolute terms, they are large in relative terms. For example, Luck et al. (1997) reported a baseline shift of only 4 spikes/s in a population of V4 neurons when attention was directed inside the receptive field versus outside. However, this shift was from approximately 10 to 14 spikes/s, which corresponds to a 40% increase in firing rate. V2 showed a similar 44% increase in baseline firing rate, increasing from approximately 8 to 12 spikes/s. Because fMRI is averaging over many thousands of neurons, a small increase in absolute spike rate across a large population

of neurons could easily manifest in a large difference measured with fMRI.

Our results, in combination with previous electrophysiology studies, raise the fundamental theoretical question of whether baseline shifts have functional value—do they contribute to the perceptual benefits that are associated with spatial attention? While any increase in firing rate increases an individual neuron's signal-to-noise (assuming a Poisson process), it is not clear what the signal-to-noise benefits are at the population level. For example, if a relatively small population of neurons respond to a particular stimulus in the unattended condition (i.e., those that are selective for that stimulus), it is not clear what signal-to-noise benefits are obtained with attention by adding a constant increase in firing rate to all neurons—whether they are stimulus-selective or not. In addition, baseline shifts are not consistent with psychophysical (Carrasco, Ling, & Read, 2004; Huang & Dobkins, 2005; Rezec, Krekelberg, & Dobkins, 2004) and electrophysiological findings (Martínez-Trujillo & Treue, 2002; Reynolds et al., 2000) of increased contrast gain with attention. The hallmark of a contrast gain change is a differential effect of attention on the CRFs with the largest increase in gain occurring at intermediate contrast levels. The lack of such a differential effect of attention on the CRFs in the current experiment suggests that the neural mechanisms of attention-based increases in contrast gain are mediated by higher stages of the visual system.

Our results suggest that most signal increases measured in previous fMRI studies of attention in early visual cortex are the result of baseline shifts and raise the question of whether stimulus-evoked increases are even measurable with fMRI. Based on the findings from electrophysiology, it would appear that stimulus-evoked increases would only be apparent in later visual stages like V4 and beyond. We were not able to consistently localize retinotopic areas beyond V3 in this experiment. However, in a previous experiment (Murray & He, 2006) that focused on lateral occipital shape-processing regions, we did observe significant stimulus-evoked changes with attention. That experiment was similar to our Experiment 2 described here in that attention was directed to a specific location for an entire scan. Specifically, in different scans, attention was directed either to fixation or to peripheral locations where shape stimuli of different luminance contrast appeared. Thus, all of the differences measured in response to the stimuli as a function of attention were related to stimulus-evoked increases. Interestingly, significant stimulus-evoked changes were observed only in the LOC and not in early visual cortex—a finding consistent with the idea that stimulus-evoked differences with attention may only exist in higher stages of the visual system.

Overall, the common notion that spatial attention increases the fMRI-measured stimulus response in early visual cortex appears to be wrong, at least within the confines of our specific experimental and stimulus design.

Instead, attention appears to increase overall baseline activity and operate independently of the stimulus. Future studies—focusing on different visual areas, stimulus configuration, and task demands—which include separate measurements of baseline-shifts and stimulus-evoked changes are necessary to more accurately characterize the effects of attention in visual cortex.

Acknowledgments

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