Attention Extracts Signal in External Noise: A BOLD fMRI Study

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Abstract

■ On the basis of results from behavioral studies that spatial attention improves the exclusion of external noise in the target region, we predicted that attending to a spatial region would reduce the impact of external noise on the BOLD response in corresponding cortical areas, seen as *reduced* BOLD responses in conditions with large amounts of external noise but relatively low signal, and *increased* dynamic range of the BOLD response to variations in signal contrast. We found that, in the presence of external noise, covert attention reduced the trial-by-trial BOLD response by 15.5–18.9% in low signal contrast conditions in V1. It also increased the BOLD dynamic range in V1, V2, V3, V3A/B, and V4 by a factor of at least three. Overall, covert attention reduced the impact of external noise by about 73–85% in these early visual areas. It also increased the contrast gain by a factor of 2.6–3.8. ■

INTRODUCTION

The visual system has an amazing ability to separate "signal" from "noise" in its input and exclude irrelevant information. What counts as signal and noise is task dependent, so this filtering or external noise exclusion mechanism must be flexible and operate on demand. Our previous behavioral studies have focused on the role of spatial attention in filtering external noise for conditions in which target and external noise overlap in space and time (Lu, Lesmes, & Dosher, 2002; Dosher & Lu, 2000; Lu & Dosher, 2000). Through systematic manipulations of either the characteristics or the amount of the external noise superimposed on the signal stimuli and measurements of changes in perceptual discriminability, we developed an empirical paradigm and a theoretical framework to distinguish three classes of attention mechanisms—stimulus enhancement, external noise exclusion, and internal noise reduction, each with its signature performance patterns (Lu & Dosher, 1998). Behavioral studies have shown that, in the absence of decision uncertainty, one of the primary roles of spatial attention is to exclude external noise in the target region (Smith, Wolfgang, & Sinclair, 2004; Lu et al., 2002; Dosher & Lu, 2000; Lu & Dosher, 2000). Attention may also enhance stimulus in the target region in some circumstances (Morrone, Denti, & Spinelli, 2002; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Lu & Dosher, 1998, 2000; Lu, Liu, & Dosher, 2000).

These behavioral results suggest that attending to a spatial region would reduce the impact of external noise on the BOLD response in the corresponding cortical areas, with two specific predictions:

(1) Spatial attention would *reduce* the BOLD response to the target stimuli in conditions with large amounts of external noise but relatively low signal when the BOLD response is mainly driven by external noise. This prediction seems counterintuitive because most fMRI studies on attention have found increased BOLD responses to attended spatial regions (Li, Lu, Tjan, Dosher, & Chu, 2008; Buracas & Boynton, 2007; Kanwisher & Wojciulik, 2000; Brefczynski & DeYoe, 1999; Gandhi, Heeger, & Boynton, 1999; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Martinez et al., 1999; Posner & Gilbert, 1999; Somers, Dale, Seiffert, & Tootell, 1999; Watanabe et al., 1998). Consider the specific case in which a sinusoidal grating is embedded in white external noise. Neurons in V1 are each tuned to a relatively narrow band of spatial frequencies (De Valois & De Valois, 1988) such that some will respond to the spatial frequencies common to the grating and external noise whereas others will respond to other spatial frequencies that are present only in the external noise. By suppressing the responses of neurons tuned to those spatial frequencies that are only present in the external noise, attention would improve the signal-to-noise ratio and reduce the overall BOLD response when the input stimulus consists mostly of external noise. If most of the external noise is excluded in V1, this particular signature of external noise exclusion by attention will diminish as we move up the visual processing hierarchy. In the meantime, attention could also enhance the response of those neurons tuned to the grating

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and therefore increase the BOLD response when grating contrast is high.

(2) Spatial attention would increase the dynamic range of the BOLD response to variations in signal contrast. This is because both signal and external noise contribute to stimulus energy that drives the saturating BOLD response (Li et al., 2008; Buracas & Boynton, 2007; Murray & He, 2006; Gardner et al., 2005; Olman, Ugurbil, Schrater, & Kersten, 2004; Boynton, Demb, Glover, & Heeger, 1999). Excluding external noise would decrease the contribution of external noise to the BOLD response, increase the relative contribution of the signal to stimulus energy, and therefore enhance the impact of signal contrast on the BOLD response.

We tested both predictions in this study. We measured and compared the BOLD contrast response functions (CRF) between the attended and the unattended conditions in several retinotopically defined early visual areas in the presence of high levels of external noise (Figure 1A). The signal was a sinusoidal pattern of one of two orientations. The attention conditions were blocked while the different signal contrast conditions were intermixed in each block. Although most of the behavioral studies on spatial attention have used trial-by-trial manipulations of attention, it is not practical to simultaneously intermix both attention and stimulus contrast conditions because of the large number of trials required to counterbalance the trial types in estimating the BOLD hemodynamic functions.

Using a combination of event-related and mixed designs, we estimated two types of spatial attention effects: (1) the transient trial-by-trial effects of attention through extraction of the BOLD hemodynamic response functions (HRFs) in the attended and unattended conditions and (2) the block effects of attention by comparing the BOLD responses in the attended blocks with those in the unattended blocks. This was done using a mixed design (Experiments 1A and 2A), in which both the attended and the unattended blocks were included in the same runs and normalized by the same mean BOLD amplitudes. Each block in the mixed-design experiment is a mini event-related design. We further augmented Experiments 1A and 2A with conventional event-related experiments (Experiments 1B and 2B) to increase the precision in estimating the BOLD HRFs and to test additional signal contrast conditions (Experiment 2B).

To quantify the effects of covert attention, we fit the BOLD CRF in each cortical region and attention condition with a modified Naka–Rushton equation (Li et al., 2008; Boynton et al., 1999; Naka & Rushton, 1966):

$$R(c) = b + \frac{A_R R_{\max} E(c)}{A_a^2 c_{50}^2 + E(c)}, \tag{1}$$

where the total stimulus energy is defined as $E(c) = A_f^2 g_N^2 E_N + E_S c^2$, c is the contrast of the signal grating, $E_S = 0.25$ is the signal energy at maximum signal contrast, E_N is the expected energy of external noise, and g_N is the gain of external noise relative to that of the signal stimulus. The value b represents baseline activity, and c_{50} denotes the contrast at which the response reaches half of its maximum dynamic range in the unattended condition. $R_{\max}$ is the maximum response above the baseline. Effects of attention are modeled with three modulators: an A_a that reflects contrast gain in the attended condition, an A_f that quantifies external noise exclusion in the attended

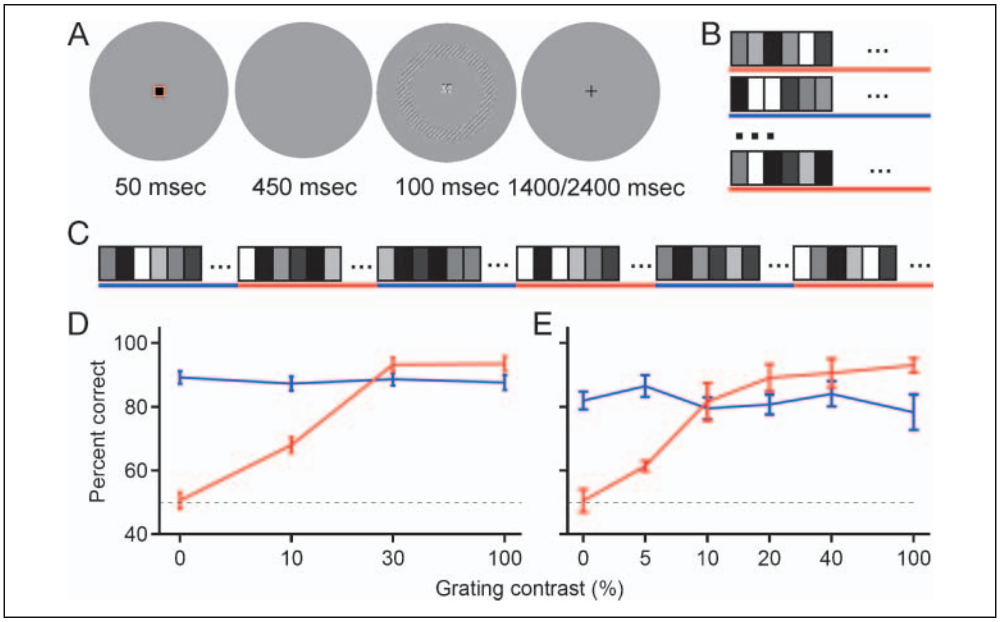

Figure 1. (A) Display sequence of a typical trial. (B) Three runs of an event-related design (Experiments 1B and 2B). Subjects performed the central (blue) and peripheral (red) tasks in separate runs. Within each run, a counterbalanced random trial sequence of five (Experiment 1B) and seven (Experiment 2B) conditions was used. (C) A single run of a mixed-design (Experiments 1A and 2A) includes three peripheral and three central task blocks. Each block contains an event-related design. (D) Performance accuracy in Experiment 1. (E) Performance accuracy in Experiment 2. Blue symbols and lines: central task; red symbols and lines: peripheral task. Dashed line indicates the chance level. Error bars: standard error.

condition, and an A_R that reflects response gain in the attended condition. All three attention modulators are set to 1 in the unattended condition. A reduction of c_{50} by A_a (<1.0) is mathematically equivalent to a contrast gain of $1/A_a$, corresponding to a leftward shift of the CRF. External noise exclusion ($A_f < 1.0$) increases the relative contribution of signal contrast to the total stimulus energy ($E(c)$) and therefore the dynamic range of the BOLD response to signal contrast (the difference between the BOLD responses in 0% and 100% signal contrast conditions).

METHODS

With attention as a block factor, an idealized design of the experiment would be a mixed design with many signal contrast conditions [e.g., 6 signal contrasts + fixation] in each block. However, the idealized design would require an impractical duration of fMRI scans, which would lead to subject fatigue and instability of BOLD baseline (Huettel, Song, & McCarthy, 2008). Truncating the design would destroy the counterbalancing scheme and increase estimation error. Our solution was to use a slightly more complicate design, essentially breaking a single experiment into two parts. Part A of Experiments 1 and 2 used a mixed design with four signal contrast conditions to measure both trial-by-trial and block effects of attention; Part B of Experiments 1 and 2 used an event-related design (with six contrast conditions in Experiment 2B) to measure trial-by-trial effects of attention. Combining the mixed and event-related designs allowed us to sample more signal contrast conditions and to improve estimates of the block effects of attention and the HRFs. In Experiment 1, the BOLD CRF was sampled at four signal contrast levels with signals embedded in a fixed high level of static external noise. In Experiment 2, the CRF was sampled at six signal contrast levels with signals embedded in dynamic external noise at a different fixed level. The two forms of external noise at two different contrast levels were used to test the repeatability of our findings. The goal is to understand how attention differentially affects signal and external noise in visual images. A third experiment was run to quantify the effect of general task difficulty on the BOLD response.

Subjects

Five male and three female subjects (age = 26–39 years) participated in Experiment 1. Three male and two female subjects (age = 28–41 years) participated in Experiment 2. Three of the eight subjects from Experiment 1 participated in Experiment 3. All subjects had normal or corrected-to-normal vision via MRI compatible glasses and provided informed consent. The experimental protocol was approved by the institutional review board of the University of Southern California.

Stimuli

Visual stimuli were generated on a Windows PC computer running Matlab programs based on Psychtoolbox extensions (Brainard, 1997) and displayed on a rear projection screen. A mirror system delivered the displays to the eyes of the subject, who viewed them binocularly at a distance of 75 cm. The signal stimuli were windowed sinusoidal luminance gratings at 2 cycles/degree and oriented at $45° \pm \alpha°$, where α was 5 in Experiments 1 and 2 and ranged between 1 and 10 in Experiment 3. The annular window, centered at the fixation point, extended from 5° to 7° eccentricity with 0.2° linear ramps on both the inner and the outer edges (Figure 1A). Four peak grating contrasts, 0%, 10%, 30%, and 100%, were used in Experiment 1. Four peak grating contrasts, 0%, 10%, 20%, and 100%, were used in Experiment 2A. Six peak grating contrasts, 0%, 5%, 10%, 20%, 40%, and 100%, were used in Experiment 2B. A single grating contrast, 20%, was used in Experiment 3.

External noise images were constructed from 0.071×0.071 deg^2 pixels, with each pixel's contrast independently sampled from a binary distribution, with equal probability of being $+0.5$ or -0.5 in Experiments 1 and 3, and $+1.0$ or -1.0 in Experiment 2. The external noise images were windowed with an annulus that extended from 4.5° to 7.5° eccentricity and combined with the signal stimuli via spatial and temporal integration (Figure 1A)—in each display frame, a checkerboard pattern was used to sample pixels from the signal and external noise images with equal probability; across display frames, the noise checks were shuffled randomly. In Experiments 1 and 3, a single "static" external noise image was used in each trial; signal and noise checks were shuffled only once. In Experiment 2, "dynamic" external noise was used—six independent external noise images were generated for each trial; signal and noise checks were shuffled every 16.7 msec.

A fixation "+," a square cue, all 0.3° × 0.3° in size, and letters "T" and "L" (both 0.29° × 0.48°) served as display items in the center of the display.

MRI Data Acquisition

MRI recording was performed using a standard birdcage head coil on a Siemens 3T Trio Magnetic Resonance Imaging System with TIM, housed in the Dana and David Dornsife Cognitive Neuroscience Imaging Center at the University of Southern California. BOLD functional activations were measured with a T2*-weighted EPI sequence (repetition time = 1000 msec, echo time = 30 msec, flip angle = 65°, field of view = 224 × 224 mm, in-plane resolution = 64 × 64 pixels or 3.5 × 3.5 mm, slice thickness = 4 mm). Fifteen interlaced slices (no gap) were acquired. The slice orientation was perpendicular to the calcarine sulcus of each subject. In addition, a T1-weighted volume (three-dimensional MPRAGE; $1 \times 1 \times 1$ mm^3 resolution, inversion time = 1100 msec, repetition time = 2070 msec, echo time = 4.14 msec, flip angle = 12°, water excitation on) was acquired in each scanning session.

Retinotopy and ROIs

Each subject completed a separate retinotopy and ROI session prior to the main experiments. Standard retinotopy stimuli, wedges and rings made of flickering radial checkerboard patterns, and analysis procedures (Li et al., 2008; Sereno et al., 1995) were used to demarcate retinotopically defined V1, V2, V3, V3A/B, and V4 regions of the visual cortex based on the standard convention (Figure 2A). Full hemifields were included in V4 and V3A/B (Wandell, Dumoulin, & Brewer, 2007).

The ROIs—subregions of the retinotopically defined cortical areas corresponding to the signal annulus—were then defined by the data from a block design experiment that compared blocks with the grating stimulus at 100% contrast to those with the grating stimulus at 0% contrast. Voxels on the retinotopic map that were also activated by the annulus defined the ROIs (Figure 2B) and were used for all the subsequent ROI analysis.

Procedure

In Experiments 1 and 2, there were two types of experimental trials and one type of fixation trial. Each experimental trial began with a 50-msec cue and a 450-msec blank screen, followed by a 100-msec simultaneous presentation of signal and external noise stimuli in the annulus and either a masked "T" or a masked "L" at the center of the display. A fixation display (a "+" at the center of a blank screen) was then shown until the end of the trial. There were two kinds of cues: a small red square in the center of a slightly larger dark square that signaled a central task trial and a small dark square on a slightly larger red square that signaled a peripheral task trial. In the central (or "unattended") task, subjects were asked to identify whether the letter at the center of the display was a "T" or an "L." In the peripheral ("attended") task, subjects were asked to identify whether the orientation of the grating in the peripheral was + or −5° from 45°. Auditory feedback was provided immediately after each response. In a fixation trial, the fixation display was presented for the entire duration of a trial; no response was necessary. Eye movements were monitored using an infrared eye tracker with remote optics (ASL 504 LRO).

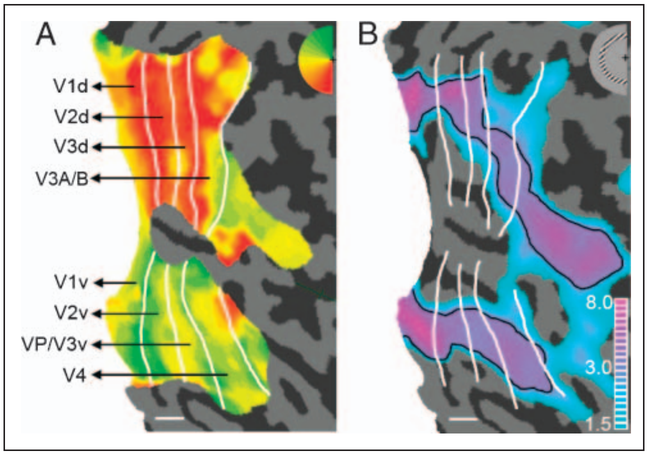

Figure 2. (A) The retinotopy of a typical subject. The colors denote significant activations by the wedge stimulus in the different sectors of the visual field, as illustrated by the half disk at the upper right corner. (B) ROIs, demarcated by the black lines ($t \geq 3, p < .003$), and boundaries of visual areas (the white lines). Different t values are illustrated using different colors. The scale bars denote 1 cm on the flattened cortical surface.

Design

A mixed design was used in Experiments 1A and 2A to isolate the long-lasting block effects of attention between the central and the peripheral blocks as well as the trial-by-trial effects of attention. In both experiments, each run consisted of six alternating blocks of central and peripheral task trials. Within each block, subjects only performed one task as indicated by the fixation mark. A rapid event-related design with 3-sec trial duration and a counterbalanced trial sequence was used to present the four signal contrast conditions and fixation condition within each block. Each block consisted of 26 trials, 5 trials for each of the five conditions and one extra trial at the beginning of each block (Kourtzi & Kanwisher, 2001). The six consecutive blocks were preceded and followed by 20-sec fixation displays. Each scanning session consisted of six functional runs (8.5 min each) and one structural run and lasted about 1 hour.

A conventional event-related design was used in Experiments 1B and 2B to replicate results on trial-by-trial effects of attention obtained in Experiments 1A and 2A and to provide more samples along the BOLD CRFs. In these experiments, the BOLD fMRI responses to the central and peripheral tasks were collected in separate runs. Within each run, subjects only performed one task. In Experiment 1B, a rapid event-related design with a 2-sec trial duration and a counterbalanced random trial sequence of five stimulus conditions, four signal contrast conditions plus fixation, was used. Each run consisted of a total of 127 trials, 25 trials for each condition, and 2 extra trials in the beginning of the run. These trials were preceded and followed by an 8-sec fixation display. Each scanning session, consisting of eight functional runs (4.5 min each) and one structural run, lasted about an hour. In Experiment 2B, a rapid event-related design with a 3-sec trial duration and a counterbalanced random trial sequence of seven stimulus conditions, six signal contrast conditions plus fixation, was used. Each run consisted of a total of 149 trials, 21 trials for each condition, and 2 extra trials in the beginning of the run. These trials were preceded and followed by a 20-sec fixation display. Each scanning session, consisting of eight functional runs (8 min each) and one structural run, lasted about 1.5 hours. In both experiments, the order of the two task runs was counterbalanced within each session. Seven subjects participated in Experiment 1B. Five subjects participated in Experiment 2B.

Experiment 3 was conducted to investigate the potential impact of general task difficulty on the BOLD response. It used a design that is identical to that of Experiment 1B, with the following modifications: (1) grating contrast was held constant at 20%; (2) instead of manipulating grating contrast, we manipulated the angular difference of the test grating relative to the implicit standard of 45° to generate four task "difficulty" levels: 45° ± 1°, 45° ± 2°, 45° ± 5°, and 45° ± 10°; and (3) subjects only performed the peripheral task, which was identical to the periphery task in Experiments 1 and 2. Three subjects participated in the control experiment.

Data Analysis

MRI- and fMRI-related data analyses were performed using BrainVoyager QX 1.8 (Brain Innovation, Maastricht, The Netherlands) on a Dell computer. All the fMRI data were first preprocessed to correct for slice timing and head movements, followed by high-pass temporal filtering (cutoff: 3 cycles/run) and removal of linear drift. The two-dimensional functional images were aligned to the three-dimensional structural images in the same session. Additional curve fitting and statistical analyses were performed in Matlab.

The BOLD responses in the five ROIs were estimated in each task and contrast condition. Specifically, the averaged T2*-weighed intensity signal within each ROI from each run was normalized by a percent signal-change transformation [(value − mean) / mean × 100]. After dividing the time series in the mixed design (Experiments 1A and 2A) by blocks, the normalized data (Y) from both the mixed-design and the event-related design (Experiments 1 and 2) of all subjects in each ROI were submitted to a multisession general linear model (GLM) event-related analysis (Boynton et al., 1999; Dale & Buckner, 1997)

$$Y = X\beta + \varepsilon \qquad (2)$$

where the design matrix X has $20 \times 4 \times 2 + 4 = 164$ columns in Experiment 1, including 20 columns for each of the four contrast conditions in each of the two attention conditions, two columns representing the run factors for attended and unattended event-related design runs, and two for the unattended and attended blocks of the mixed-design runs. The 20 βs in each contrast and attention condition were used to construct the HRF of that condition in each ROI. The difference between the β values in the attended and unattended blocks in the mixed design was used to estimate the block effect of attention. The design matrix has $20 \times 6 \times 2 + 4 = 244$ columns in Experiment 2, reflecting six (instead of four) contrast conditions. The design matrix has $20 \times 4 + 1 = 81$ columns in Experiment 3, reflecting four orientation conditions.

We then fit the difference of Gamma functions (DOGM) (Friston et al., 1998)

$$\begin{aligned} h(t) = g\Bigg[\left(\frac{t}{d_1}\right)^{a_1} \exp\left(\frac{-(t-d_1)}{b_1}\right) \\ - c\left(\frac{t}{d_2}\right)^{a_2} \exp\left(\frac{-(t-d_2)}{b_2}\right)\Bigg] \end{aligned} \qquad (3)$$

to the estimated HRFs using a least squares procedure with three constraints: (1) $d_1 = a_1 b_1$, (2) $d_2 = a_2 b_2$, and (3) all the HRFs in each ROI have the same shape and differ only in peak amplitude. The best-fitting DOGM function accounted for 97.4%, 96.2%, 97.6%, 97.0%, and 98.8% of the variance of the GLM-estimated HRFs in the five ROIs in Experiment 1 and 94.3%, 94.4%, 94.0%, 95.9%, and 95.9% of the variances in the five ROIs in Experiment 2, suggesting that DOGM is a good low-dimensional approximation of the free-form HRF estimated using GLM. For both experiments, constraining the shapes of the HRFs in each ROI did not significantly change the quality of the fits (all $p > .20$). The HRF shapes are also very similar to those of the same five ROIs in a previous publication (Li et al., 2008). The peak amplitudes of the best-fitting DOGM functions were used to construct the average BOLD CRF.

To estimate the variability of the BOLD CRF and to examine the data pattern from individual subjects, we used the best-fitting DOGM functions as the template HRFs to extract the amplitude of the BOLD response in all the experimental conditions using the GLM model for each subject. Again, the time series in Experiments 1A and 2A were divided into blocks and treated as separate event-related runs. These BOLD response amplitudes were also used to compute the standard error of the BOLD responses in each experimental condition with a bootstrap procedure.

All the model-fitting procedures were implemented in Matlab using a nonlinear least-square method that minimized $\Sigma(y_i^{\text{predicted}} - y_i^{\text{measured}})^2$, where y_i^{measured} and $y_i^{\text{predicted}}$ denote measured values and the corresponding model predictions, respectively. The goodness of fit was evaluated by the r^2 statistic:

$$r^2 = 1.0 - \frac{\sum\left(y_i^{\text{predicted}} - y_i^{\text{measured}}\right)^2}{\sum\left[y_i^{\text{measured}} - \text{mean}\left(y_i^{\text{measured}}\right)\right]^2}. \qquad (4)$$

An F test for nested models was used to statistically compare the models. For two nested models with k_{full} and k_{reduced} parameters, the F statistic is defined as:

$$F(df_1, df_2) = \frac{\left(r^2_{\text{full}} - r^2_{\text{reduced}}\right)/df_1}{\left(1 - r^2_{\text{full}}\right)/df_2}, \qquad (5)$$

where $df_1 = k_{\text{full}} - k_{\text{reduced}}$ and $df_2 = N - k_{\text{full}}$; N is the number of predicted data points.

To gauge the variability of the observed attention effects, the standard deviations of the parameters of the modified Naka–Rushton model were estimated using a resampling procedure (Maloney, 1990): The BOLD amplitude in a given experimental condition was treated as a Gaussian random variable with mean and standard deviation generated from the bootstrap procedure. We sampled from these distributions 2000 pairs of CRFs for the two attention conditions in each ROI. The Naka–Rushton model was fitted to the CRFs to generate 2000 sets of parameters, from which the standard deviations of the model parameters were computed.

RESULTS

Experiments 1 and 2: Effects of Attention in High External Noise

The behavioral data from the A and B versions of each experiment were virtually identical. In the unattended condition, subjects correctly identified the letter in the center of the display with 88.2 ± 2.0% and 81.8 ± 2.5% accuracy in Experiment 1 (Figure 1D) and Experiment 2 (Figure 1E), respectively, independent of the contrast level of the peripheral target, $F(3, 36) = 1.3, p > .2$ and $F(5, 20) = 1.76, p > .15$. In the attended condition, as the contrast of the signal grating increased from 0% to 100%, subjects' performance in the peripheral task increased from 50.6 ± 2.5% to 93.4 ± 2.4% correct in Experiment 1 and from 50.5 ± 3.3% to 93.0 ± 1.2% correct in Experiment 2. The patterns of eye fixation were virtually the same across all the experimental conditions along several dimensions: horizontal and vertical eye position during fixation, fixation duration, number of blinks per trial, number of saccades per trial, and saccade amplitude (all $p > .10$).

We found that spatial attention increased the BOLD responses over an entire attended block by 0.12 ± 0.02, 0.13 ± 0.01, 0.11 ± 0.01, 0.14 ± 0.01, and 0.09 ± 0.01 in units of percent signal change in V1, V2, V3, V3A/B, and V4 in Experiment 1A and by 0.12 ± 0.03, 0.11 ± 0.02, 0.14 ± 0.02, 0.09 ± 0.01, and 0.11 ± 0.02 in units of percent signal change in these areas in Experiment 2A. For the four observers who participated in both Experiments 1A and 1B and all the observers in Experiments 2A and 2B, the trial-by-trial BOLD CRF estimated from the two data sets were virtually identical, $F(1, 3) = 0.006, p > .50$ and $F(1, 4) = 0.02, p > .50$. This result is important because it not only controls for the BOLD baseline issue but also represents a replication of the pattern of results in two different experimental designs. We combined data from the A and B versions of each experiment in the subsequent analyses.

The average trial-by-trial HRFs in the highest and the lowest signal contrast conditions in Experiments 1 and 2 are plotted in Figures 3A and B and Figures 4A and B, respectively. The peak amplitudes of the HRFs in all the signal contrast conditions of Experiments 1 and 2 are shown as CRFs in Figures 3C and 4C, respectively. The BOLD response reflects the combined effect of grating contrast and external noise in the region of the grating. It is remarkable that, in V1, increasing the grating contrast from 0 to 100% had very little impact on the BOLD response in the central task condition when the grating was unattended: The trial-by-trial BOLD response is virtually the same in all the signal contrast conditions in both Experiments 1 and 2. This suggests that, absent attention, the BOLD response in V1 is mostly determined by the constant external noise inputs. Attending to the grating stimulus greatly increased the effect of grating signal contrast in V1: The BOLD amplitude was significantly reduced relative to the unattended condition in the two lowest signal contrast conditions in Experiment 1 (15.5%), $t(15) = 2.953$, $p < .01$, and in the three lowest signal contrast conditions in Experiment 2 (18.9%), $t(14) = 3.041, p < .01$); it then increased to a greater level compared with the unattended condition when the signal contrast was high. The pattern of results is consistent across subjects (Figure 5A).

The trial-by-trial dynamic range of the BOLD response—the difference between the BOLD responses in the highest and lowest signal contrast conditions—increased from 0.00 ± 0.01 in the unattended condition to 0.06 ± 0.02 in the attended condition in V1 in Experiment 1 and from −0.02 ± 0.02 to 0.05 ± 0.03 in Experiment 2. Both increases are significant ($p < .01$). In V2, V3, V3A/B, and V4, we did not observe significant decrease of the BOLD response in the lowest signal contrast conditions in the attended condition; however, the dynamic range of the BOLD response increased from 0.00 ± 0.02 to 0.05 ± 0.01, from 0.02 ± 0.02 to 0.07 ± 0.01, from 0.02 ± 0.02 to 0.07 ± 0.02, and from 0.03 ± 0.02 to 0.09 ± 0.02 between the unattended and the attended conditions in Experiment 1 (all $p < .01$) and from 0.00 ± 0.03 to 0.06 ± 0.02, from 0.01 ± 0.04 to 0.10 ± 0.03, from 0.01 ± 0.05 to 0.11 ± 0.03, and from 0.02 ± 0.03 to 0.12 ± 0.03 in Experiment 2 (all $p < .01$). The pattern of results is quite consistent across subjects (Figure 5B). Covert attention increases the dynamic range of the BOLD response to signal contrast variation by a factor of at least three in these cortical areas.

In both Experiments 1 and 2, we found relatively long-lasting block effects of attention that increased the BOLD response for the entire block of attended trials, including the fixation trials. This is consistent with many previous fMRI attention studies (Li et al., 2008; Buracas & Boynton, 2007; Murray & He, 2006; Olman et al., 2004). At the trial-by-trial level, attention responded differentially to the signal and external noise in visual images. In low signal contrast conditions, the energy in the stimulus was dominated by external noise. A reduction of the BOLD response in the low signal contrast conditions directly demonstrates external noise exclusion by covert attention. In mid to high signal contrast conditions, both signal and external noise contributed to the stimulus energy. By excluding external noise, attention increased the weight of signal contribution

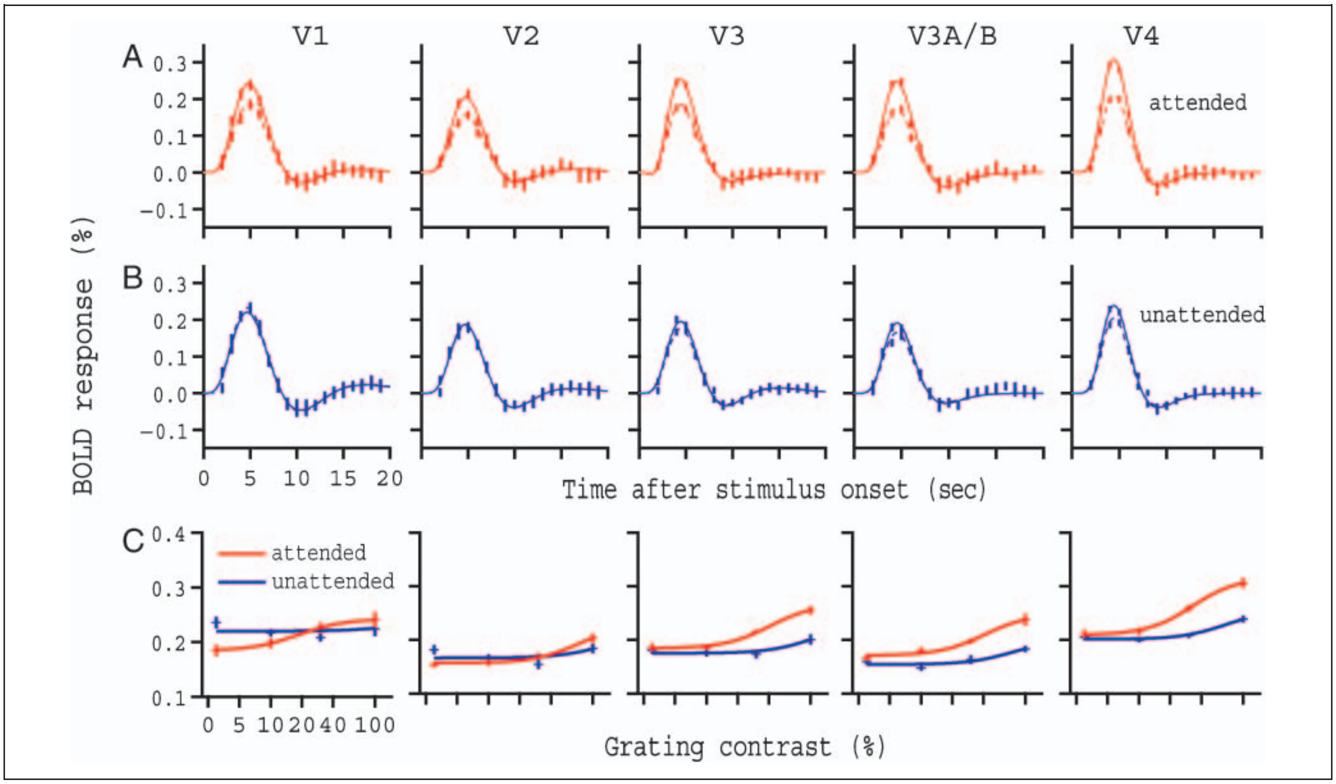

Figure 3. (A, B) Estimated HRFs from Experiment 1 (A: attended; B: unattended). The two curves in each panel represent HRFs in the lowest (0%, dashed) and highest (100%, solid) signal contrast conditions. HRFs of the intermediate contrast conditions are not shown. Smooth curves represent predictions of the best-fitting DOGM. (C) Trial-by-trial BOLD CRFs from Experiment 1. Smooth curves represent predictions of the best-fitting Naka–Rushton model. Red dots and lines: attended condition. Blue dots and lines: unattended condition. Error bars are generated from a bootstrap procedure.

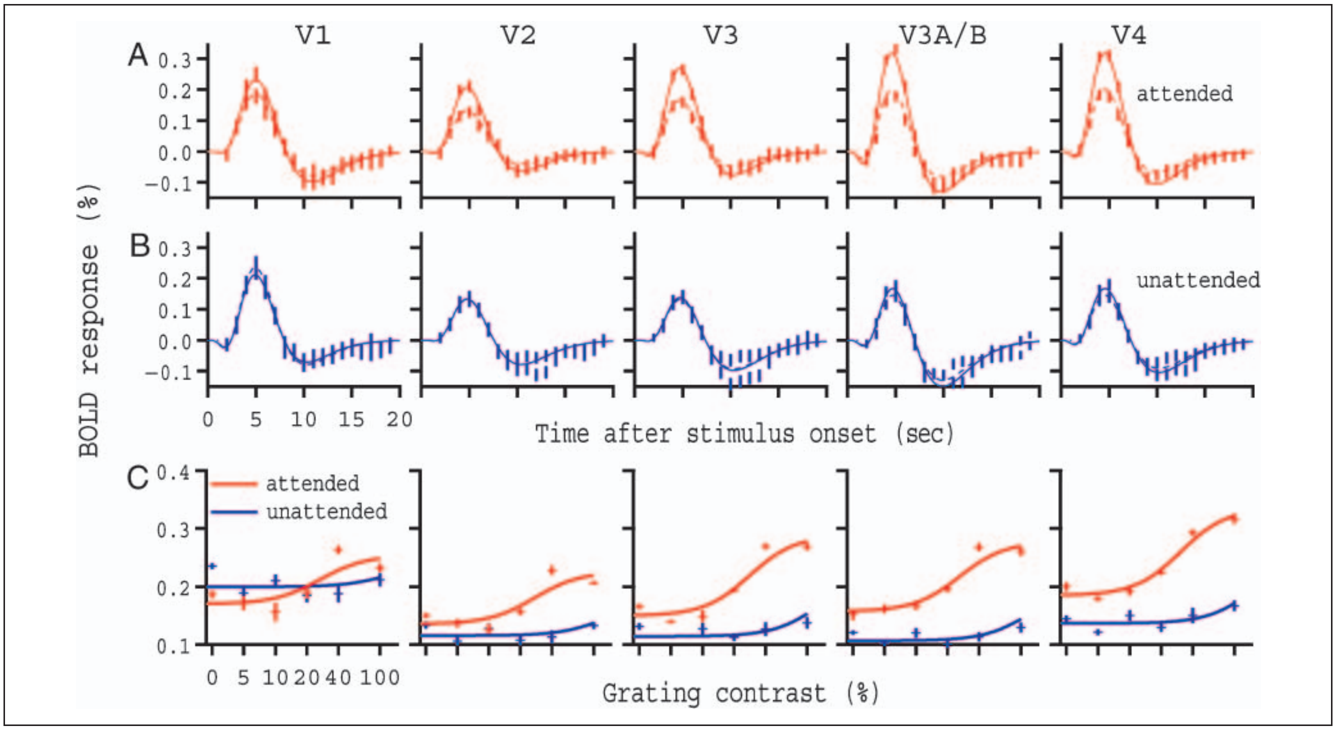

Figure 4. HRFs (A and B) and CRFs (C) from Experiment 2. The arrangement is the same as that for Figure 3.

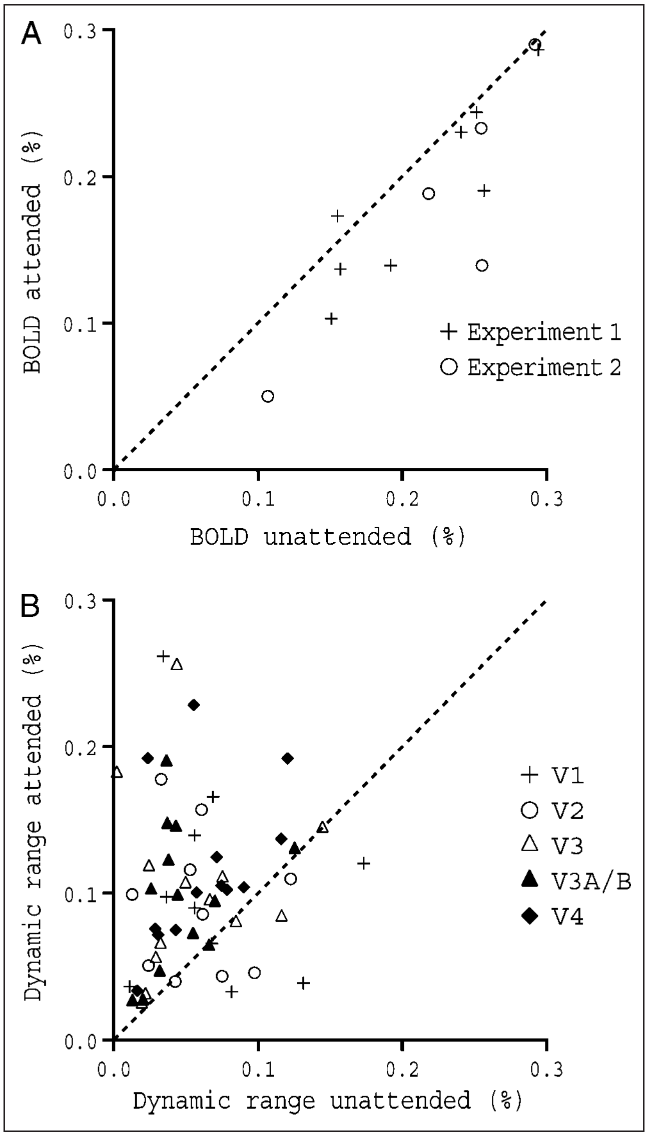

Figure 5. (A) Scatter plot of individual subjects' BOLD responses in V1 in the lowest two (Experiment 1) or three (Experiment 2) signal contrast conditions in the unattended condition versus the attended condition for individual subjects in Experiments 1 and 2, showing a reduction of the BOLD response with covert attention at low signal contrast. (B) Scatter plot of individual subjects' BOLD dynamic range (across the full 0–100% contrast range) in the unattended versus attended conditions in Experiments 1 and 2, showing an increase in the dynamic range of the BOLD response with covert attention. Each symbol represents one subject.

to the stimulus energy and therefore enhanced the impact of signal contrast and increased the dynamic range of the BOLD responses.

To quantify the effects of covert attention, we fit the trial-by-trial BOLD CRF in each cortical region and attention condition using Equation 1 with $E_N = 0.125$ and 0.50 in Experiments 1 and 2, respectively. A model lattice, with all eight possible combinations of A_a, A_f, and A_R, was constructed to test several versions of the modified Naka–Rushton model. This included three models that contain one of the attention modulators (A_a, A_f, or A_R), three models that contain pairs of the three attention modulators, one full model that contains all three attention modulators, and one most reduced model that contains no attention modulator. We first tested if A_a and A_f can be constrained to be the same across cortical regions. We then tested if adding A_R would improve the fits of the $A_a + A_f$ model and compared the $A_R + A_f$ model with the most saturated $A_a + A_f + A_R$ model.

The model that has the same contrast gain (A_a) and magnitude of external noise exclusion (A_f) in all the cortical regions provided the best fit to the data in both Experiments 1 and 2. The model is statistically equivalent to the model that contains independent contrast gain and magnitude of external noise exclusion in different cortical regions, Experiment 1, $F(8, 5) = 0.0445$, $p > .9$, and Experiment 2, $F(8, 25) = 0.288$, $p > .9$, and also superior to the reduced models in which attention does not change contrast gain, $F(5, 13) = 6.89$, $p < .01$ and $F(5, 33) = 8.48$, $p < .001$, exclude external noise, $F(5, 13) = 3.21$, $p < .05$ and $F(5, 33) = 7.30$, $p < .01$, or both, $F(10, 13) = 4.76$, $p < .01$ and $F(10, 33) = 5.85$, $p < .001$. Adding A_R did not significantly improve the fits of the $A_a + A_f$ model: Experiment 1, $F(9, 4) = 0.0370$, $p > .9$; Experiment 2, $F(9, 24) = 0.197$, $p > .9$. On the other hand, the $A_R + A_f$ model produced significantly worse fits than the most saturated $A_a + A_f + A_R$ model: Experiment 1, $F(1, 28) = 25.3$, $p < .0001$; Experiment 2, $F(1, 48) = 8.28$, $p < .01$.

The best-fitting model accounted for 97.6% and 92.7% of the variance in Experiments 1 and 2, respectively. The parameters of this model are listed in Table 1. We conclude that attention reduced the impact of external noise by 73 ± 3% and 85 ± 1% across all the cortical areas in Experiments 1 and 2, respectively. It also increased the contrast gain by 2.6 ± 0.1 and 3.8 ± 0.2 in these cortical regions in the two experiments, consistent with our recent findings in a related set of experiments without external noise (Li et al., 2008).

It is known that the repetition of stimuli leads to adaptation, and some have suggested that the effect of adaptation can be enhanced by attention (Boynton, 2004; Murray & Wojciulik, 2004). The use of very brief stimuli (100 msec), long ISI (1.9 and 2.9 sec), and pseudorandom stimulus sequences with counterbalanced event history in the current study greatly reduced potential effects of adaptation. The brief stimulus duration and long ISI also greatly reduced potential effects of brightness filling-in that predominantly takes place in V1 and interactions of negative afterimages and attention, both associated with long stimulus presentations (Dale & Buckner, 1997).

Experiment 3: Effects of Task Difficulty on the BOLD Response

In Experiments 1 and 2, the attended periphery task was performed with a constant discrimination precision (45° ±

Table 1. Parameters of the Best-fitting Naka–Rushton Equation to the Average BOLD CRFs

			Unattended			*Attended*		
Experiment	*Visual Area*	R_{max}	b	C_{50}	g_N	b	$A\alpha$	A_f
1	V1	.17 ± .02	.06 ± .02	.09 ± .07	.87 ± .12	.07 ± .03	.39 ± .01	.27 ± .03
	V2	.07 ± .02	.15 ± .01	.53 ± .07	.77 ± .07	.15 ± .01		
	V3	.10 ± .02	.12 ± .02	.27 ± .10	.85 ± .10	.16 ± .02		
	V3A/B	.09 ± .02	.12 ± .02	.27 ± .12	.64 ± .13	.16 ± .01		
	V4	.14 ± .03	.12 ± .03	.24 ± .07	.83 ± .12	.18 ± .02		
2	V1	.16 ± .04	.09 ± .04	.38 ± .11	.83 ± .18	.09 ± .03	.26 ± .06	.15 ± .01
	V2	.12 ± .01	.05 ± .01	.47 ± .07	.66 ± .11	.10 ± .01		
	V3	.17 ± .02	.05 ± .01	.51 ± .08	.55 ± .12	.12 ± .01		
	V3A/B	.15 ± .02	.05 ± .01	.47 ± .11	.52 ± .18	.13 ± .01		
	V4	.19 ± .02	.05 ± .02	.54 ± .11	.64 ± .17	.15 ± .02		

The standard errors are from a bootstrap procedure.

5°), leading to behavioral accuracies ranging from chance level to about 93% correct across the contrast range as signal contrast varied from 0% to 100%. Because a number of fMRI studies have suggested that task difficulty might change the BOLD response (Ress & Heeger, 2003; Backus, Fleet, Parker, & Heeger, 2001; Huk & Heeger, 2000; Ress, Backus, & Heeger, 2000), one natural question is whether general task difficulty had any impact on the observed BOLD CRFs in this study. To directly investigate this issue, we manipulated the precision of orientation discrimination from 45° ± 1° to 45° ± 10° while keeping the contrast of the stimulus constant at 20%. The task is otherwise the same as that in Experiments 1 and 2. We found that although performance accuracy depended on the required precision in orientation discrimination (ranging from 59.3% to 99.3% correct with increasing angular difference), there was no detectable change in the BOLD response in any of the five tested visual areas when the target contrast was kept constant, $F(3, 6) = 0.58$, $p > .50$ (Figure 6).

These results show that the BOLD contrast responses in early visual areas depend only on stimulus contrast and are invariant to general task difficulty. This is in complete agreement with what we found in the absence of external noise (Li et al., 2008). The results are also consistent with Buracas, Fine, and Boynton (2005), who found that the fMRI responses in V1–V3 and MT+ did not depend significantly on task (speed discrimination vs. contrast discrimination). These results are not incompatible with studies that observed correlations between behavioral performance and the amplitude of the BOLD response because they used stimulus contrast as the independent variable so an elevated BOLD response to an increase in physical or perceived contrast covaried with improved performance (Ress & Heeger, 2003; Backus et al., 2001; Huk & Heeger, 2000; Ress et al., 2000).

DISCUSSION

There is converging evidence from neurophysiology (Reynolds, Chelazzi, & Desimone, 1999; Luck, Chelazzi, Hillyard, & Desimone, 1997; Treue & Andersen, 1996; Haenny, Maunsell, & Schiller, 1988; Spitzer, Desimone, & Moran, 1988; Moran & Desimone, 1985), functional

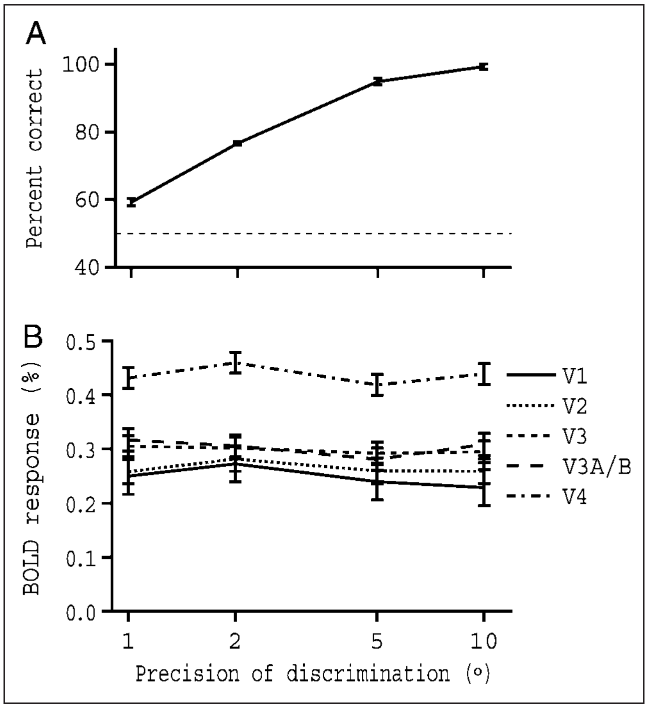

Figure 6. (A) Average performance accuracy at four orientation difference conditions (Experiment 3). The dashed line indicates chance level. (B) BOLD responses in the five cortical regions, shown as functions of orientation difference. Subjects only performed the peripheral task in this experiment. Error bars indicate standard error.

imaging (Kastner, De Weerd, Desimone, & Ungerleider, 1998), and psychophysical studies (Lu & Dosher, 2004; Smith et al., 2004; Lu et al., 2002; Dosher & Lu, 2000; Lu & Dosher, 2000; Enns & Di Lollo, 1997; Shiu & Pashler, 1994) that covert attention can improve performance by excluding unwanted, task-irrelevant information (for a review, see Desimone & Duncan, 1995). However, most of the previous neurophysiological and functional imaging studies have focused on the effects of attention in the presence of distractors that are spatially separated from the target(s). When the target and external noise overlap in space and time, as in a noise masking experiment, an attention mechanism must do more than spatially selecting the target to have any useful effect on performance. Our behavioral studies have concluded that in the absence of decision uncertainty, one of the primary roles of spatial attention is to exclude external noise in the target region (Smith et al., 2004; Lu et al., 2002; Dosher & Lu, 2000; Lu & Dosher, 2000), although attention may also enhance stimulus in the target region in some circumstances (Morrone et al., 2002; Carrasco et al., 2000; Lu & Dosher, 1998, 2000; Lu et al., 2000).

These psychophysical findings suggest that attending to a spatial region would reduce the impact of external noise on the BOLD response when the target stimulus is embedded in high levels of external noise, with two specific predictions: (1) Spatial attention would reduce the BOLD response to the target stimuli in conditions with large amount of external noise but relatively low signal, where the BOLD response is mainly driven by the external noise; and (2) spatial attention would increase the dynamic range of the BOLD response to signal contrast variations. Both of these predictions are clearly supported by the results of the current study, when the signal was embedded in either static (Experiment 1) or dynamic external noise (Experiment 2). Although attention generally increased the BOLD response in attended blocks, at a trial-by-trial level, attention acted differentially on the signal and external noise in visual images. In area V1, the measured BOLD response to target signal embedded in high levels of external noise was reduced by 15.5–18.9% in the attended condition relative to the unattended condition when the signal contrast was low. In all five cortical areas, V1, V2, V3, V3A/B, and V4, external noise exclusion was demonstrated by the significantly increased dynamic range of the BOLD response to signal contrast variations. On the basis of the Naka–Rushton model, we found that covert attention excluded 73–85% of the external noise in V1, V2, V3, V3A/B, and V4, comparable to estimates of the magnitude of external noise exclusion in behavioral studies.

It is worth noting that, in this study, a single coefficient of external noise exclusion could account for the impact of covert attention across all the cortical areas, be it a reduction in the BOLD response when the target contrast is low or an increase in the dynamic range of the BOLD response. Because the particular type of external noise, white pixel noise, provided better stimulation for neurons in V1 than neurons in higher visual areas with larger receptive fields, V1 may have been tuned to the spatial frequency of the target in the attended condition and thus reduced the impact of the broadband noise. Once the external noise is excluded in V1 by selecting the target spatial frequency, the elevated signal-to-noise ratio passes on to higher cortical areas. The use of broadband white noise may have also highlighted the impact of external noise exclusion in V1 such that both effects of external noise exclusion—reduced BOLD response in low signal conditions and increased BOLD dynamic range—are observable. In several behavioral studies, we varied the characteristics (e.g., spatial frequency, orientation, spatial and temporal window) of external noise to investigate the nature of external noise exclusion (Lu & Dosher, 2004). Application of these behavioral paradigms in fMRI research may allow us to gain further insights into the nature of external noise exclusion in extrastriate cortical areas. One possibility is to use bandpass filtered external noise with spatial frequency content similar to that of the signal stimuli, which is known to generate increasingly stronger BOLD responses along the visual-processing hierarchy (Tjan, Lestou, & Kourtzi, 2006). This type of external noise, in contrast to white external noise used in the current study, may reveal reduced BOLD response in low signal contrast conditions in extrastriate cortical areas in the attended condition.

Covert attention increases the dynamic range of the BOLD response to signal contrast variation by a factor of at least 3 when the signal stimulus is embedded in external noise. It is important to note that the increased dynamic range of the BOLD response by covert attention is achieved through external noise exclusion rather than response gain—according to the Naka–Rushton model (Equation 1), both the signal and the external noise contribute to the BOLD response; excluding external noise reduces the denominator (gain control) and therefore increases the response's dependence on signal contrast. Similar modeling results on the basis of contrast normalization in visual cortex have been discussed (Reynolds & Heeger, 2009; Boynton, 2005). Because the maximum BOLD response in each cortical region in the attended condition was greater than that in the unattended condition, when including block as well as trial-by-trial effects of attention, the small dynamic range in the unattended condition cannot be attributed to the ceiling effect on the BOLD response. Rather, the impact of target signal on the BOLD response was much smaller even in the highest signal contrast condition because lack of attention to the target region made the noisy target "invisible" to the visual system. With covert attention to the target region, the target signal was "extracted" from external noise and had a significantly stronger impact on the BOLD responses. This observation is consistent with Olman et al. (2004), who found that both perceived contrast and BOLD fMRI response are higher for natural images than pink noise and whitened noise images because the visual system excludes energy from the less interesting noise images.

In addition to external noise exclusion, we also found that covert attention increased the contrast gain in the cortical areas corresponding to the attended spatial locations by a factor of about 2.6 to 3.8, seen as an apparent leftward shift of the CRF to lower contrast values. This finding goes beyond the previous psychophysical observations, which focused on "pure" external noise exclusion by covert attention in the presence of high external noise (Smith et al., 2004; Lu et al., 2002; Dosher & Lu, 2000; Lu & Dosher, 2000). However, this apparent difference may nonetheless be compatible with the psychophysical results, which assess the total signal-to-noise ratio in the perceptual system. In the presence of large amounts of external noise, increasing contrast gain does not change the signal-to-noise ratio in perceptual decision and therefore is not directly observable in psychophysical measures, although increasing contrast gain enhances performance in zero or low external noise conditions (Lu & Dosher, 1998). The magnitude of contrast gain in this experiment is consistent with that found in a related fMRI study that did not superimpose any external noise on the target signal (Li et al., 2008) and that found in neurophysiology (Reynolds, Pasternak, & Desimone, 2000).

In summary, we found physiological evidence for the external noise exclusion mechanism in spatial attention. External noise exclusion leads to improved signal-to-noise ratio in perceptual processes and better detection or discrimination of perceptual targets. Covert attention extracts signal from external noise.

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