

Blood oxygenation level-dependent contrast response functions identify mechanisms of covert attention in early visual areas

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Covert attention can lead to improved performance in perceptual tasks. The neural and functional mechanisms of covert attention are still under investigation. Using both rapid event-related and mixed designs, we measured the blood oxygenation level-dependent functional MRI contrast response functions over the full range of contrast (0–100%) in the retinotopically defined early visual areas (V1, V2, V3, V3A, and V4) in humans. Covert attention increased both the baseline activities and contrast gains in the five cortical areas. The effect on baseline can be decomposed into a transient trial-by-trial component and a component across an entire attention block. On average, increase in contrast gain accounted for $\approx 88.0\%$, 28.5% , 12.7% , 35.9% , and 25.2% of the trial-by-trial effects of attention in the five areas, respectively, and 22.2% , 12.8% , 7.4% , 19.7% , and 17.3% of the total effects of attention in those areas, consistent with single-unit findings in V4 and MT. The results provide strong evidence for a stimulus enhancement mechanism of attention as demonstrated in various behavioral studies.

contrast gain | increased baseline | response gain | stimulus enhancement

Covert attention can lead to improved performance accuracy and response time (1, 2). Since the initial discovery that attention increases the blood oxygenation level-dependent (BOLD) responses in early visual areas (3–9), a large number of new studies have further documented many interesting effects of attention in the visual pathway, including attentional modulation of the BOLD responses in the lateral geniculate nucleus (10), increased BOLD activities in the visual cortical areas corresponding to the attended spatial location in the absence of visual stimulation (6, 11, 12), different effects of endogenous and exogenous attention (13, 14), and topographic maps of visual spatial attention in parietal cortex (15). How attention enhances visual stimuli in early visual cortical areas, however, remains unclear. We attempt to address this fundamental question in this study.

There are three potential mechanisms underlying the increased BOLD responses in early visual areas (Fig. 1): increased contrast gain, increased response gain, and increased baseline activity. Formulated in terms of the impact of attention on contrast response functions (CRFs), these three mechanisms have distinct behavioral and functional significance. In the behavioral domain, a theoretical framework based on analyses of human observers distinguishes three mechanisms of attention: stimulus enhancement, external noise exclusion, and nonlinearity change (16, 17). Whereas an increase in baseline activity need not contribute to improved discrimination and cannot be observed in psychophysical studies (18), increased contrast gain (18, 19) is related to behaviorally identified stimulus enhancement in a discrimination task, and response gain corresponds to nonlinearity changes observed behaviorally (20). Because most of the functional MRI (fMRI) attention studies used a single stimulus contrast, the observed increases of the BOLD response are compatible with any of the three potential modulations of

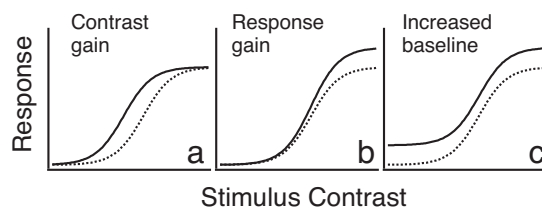


Fig. 1. Three potential mechanisms of covert attention. (a) Contrast gain. (b) Response gain. (c) Increased baseline activity.

CRFs. To understand the mechanism underlying the increased BOLD responses, it is necessary to study the impact of covert attention over a wide range of stimulus contrasts.

CRFs—mean firing rate versus signal stimulus contrast—characterize one of the most fundamental properties of visual neurons (21). In fMRI research, a number of retinotopy techniques have been developed to demarcate individual early visual areas in humans (22, 23). BOLD CRFs can then be obtained by manipulating stimulus contrast and observing the summed BOLD responses in individual visual cortical areas (24–28). In this study, we investigated attentional modulation of the BOLD CRFs in five early visual areas of the human brain.

Attentional modulation of CRFs has been examined in single-unit recordings, human psychophysics, and fMRI. Martinez-Trujillo and Treue (29) found that attention increased contrast gain in monkey MT. Recording from monkey V4, Reynolds *et al.* (19) and Williford and Maunsell (18) both found that attention increased baseline spontaneous activity but disagreed on whether attention also increased the effective contrast (19) or response gain (18). In psychophysical studies, several findings have also been reported, supporting response gain (30), contrast gain at an early stage followed by response gain at a later stage for endogenous attention (31), or contrast gain for endogenous attention and a mixture of response gain and contrast gain for exogenous attention (32). Finally, using both contrast and speed discrimination in an fMRI study, Buracas and Boynton (25) found that the modulation of the BOLD responses in early visual areas (V1, V2, V3, and MT+) by spatial attention was similar across stimulus contrasts, consistent with an increased baseline mechanism.

The current study complements that of Buracas and Boynton (25). After obtaining the retinotopies of the observers, BOLD

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Table 1. Parameters of the best fitting Naka–Rushton model

Visual area	R_{max}	Unattended		Attended	
		c_{50}	b	c_{50}	b
V1	0.13 ± 0.02	11.60 ± 3.90	0.16 ± 0.03	2.18 ± 0.52	0.16 ± 0.03
V2	0.14 ± 0.01	7.04 ± 1.20	0.08 ± 0.02	2.52 ± 0.36	0.13 ± 0.02
V3	0.17 ± 0.01	6.16 ± 0.92	0.03 ± 0.01	2.55 ± 0.33	0.14 ± 0.02
V3A	0.15 ± 0.01	8.06 ± 1.35	0.11 ± 0.03	2.43 ± 0.34	0.17 ± 0.02
V4	0.18 ± 0.01	6.40 ± 1.41	0.12 ± 0.02	2.27 ± 0.24	0.19 ± 0.03

maximum dynamic range, and R_{max} is the maximum response above the baseline.

The mechanisms of attention in the early visual areas were tested with a nested model lattice of eight models (SI Text). In the most saturated model, all parameters of the Naka–Rushton equation (b , c_{50} , and R_{max}) are changed between the attended and unattended conditions. In the most reduced model, the attention conditions do not differ and share all parameters of the Naka–Rushton equation. Intermediate models sharing some but not all parameters were also considered. Statistical tests of nested models identify the simplest model that accounts for the data: an increase of b in the attended condition signifies increased baseline activity; a decrease of c_{50} signifies contrast gain; and an increase of R_{max} indicates response gain.

In all of the five cortical areas, the best fitting Naka–Rushton model included both contrast gain and increased baseline activity. The model, shown as smooth curves in Fig. 3*b*, accounted for 96.3% of the variance in the data. This model is statistically as good as the most saturated model [$F(5,30) = 1.14, P > 0.30$] and superior to all of its reduced versions ($P < 0.005$). In comparison, the response-gain-only model is significantly inferior to the full model [83.9% of variance, $F(10,30) = 12.70, P < 0.00001$], as were all of the intermediate models that included response gain but not at least one of the other two mechanisms ($P < 0.005$). A bootstrap procedure with 1,000,000 iterations was used to evaluate the effect of individual differences on model selection (SI Text). The contrast-gain-plus-increased-baseline model was the best fitting model 85.3% of the time, the baseline-alone model was the best 6.26% of the time, and the contrast-gain-alone model was the best 0.42% of the time. Importantly, the pure response-gain model was never the best fitting model. These results convincingly support the contrast-gain-plus-increased-baseline model as the best account of our data.

The parameters of the best fitting contrast-gain-plus-increased-baseline model and their standard deviations are listed in Table 1. Attention increased the baseline activity by 0.004, 0.057, 0.112, 0.059, and 0.078 in units of percent signal change in V1, V2, V3, V3A, and V4, respectively. These baseline increases occur within the trial duration and are over and above the block effects of attention. The contrast-gain effects [$c_{50}(un)/c_{50}(att)$] in these regions were 5.31, 2.79, 2.42, 3.32, and 2.81, respectively.

Fig. 3*c* plots the difference between the BOLD contrast responses with and without attention. All of the difference functions exhibit a bump in the intermediate contrast conditions, characteristic of the contrast-gain mechanism of attention. An estimated 88.0%, 28.5%, 12.7%, 35.9%, and 25.2% (mean = 38.1%) of the attention effects in areas V1, V2, V3, V3A, and V4, respectively, were accounted for by contrast gain, and the rest were accounted for by increased baseline activities. It is remarkable that V1, unlike other area, has within-trial attention effects dominated by contrast gain.

If we combine trial-by-trial and block effects of attention, then 77.8%, 87.2%, 92.6%, 80.3%, and 82.7% of the total attention effects are accounted for by increased baseline activities; 22.2%, 12.8%, 7.4%, 19.7%, and 17.3% (mean = 15.9%) are accounted

for by contrast gain. In previous fMRI studies based on block designs (25), trial-by-trial and block effects of attention were not separately estimated. The observed effects of attention de facto combined trial-by-trial and block factors of covert attention and so estimated mostly baseline differences.

Effects of attention at other eccentricities are also estimated (SI Text). In general, attending to the grating reduced the BOLD response in foveal regions and increased the BOLD responses in cortical areas near the regions of interest (ROIs) corresponding to the signal gratings used in this study.

Experiment 2: Effect of Task Difficulty on the BOLD Response. Characterizing CRF requires measurements of the BOLD responses over a wide range of signal contrast, corresponding to a wide range of performance accuracies. Several fMRI studies have suggested that task difficulty could change the BOLD responses (12, 35–37). Buracas and Boynton (25) approached the issue by adjusting task precision in distinct contrast conditions to equate task difficulty (accuracy), thus covarying the variable of interest, contrast, with other stimulus properties, such as speed or contrast increments. Instead, we chose to explicitly investigate the effects of task difficulty on the BOLD responses by manipulating the precision of orientation discrimination from $45 \pm 1^\circ$ to $45 \pm 10^\circ$ while keeping the contrast of the stimulus constant; 1.9% and 19% contrast were tested separately.

Fig. 4 shows the BOLD response amplitude as functions of the discrimination precision. The BOLD response was unchanged by task precision in all five early visual areas, for both grating contrast levels in both attention conditions (all $P > 0.50$), although behavioral accuracy ranged from 50.8% to 72.0% at 1.9% contrast and 65.2% to 98.6% correct at 19% contrast. Different accuracy levels resulted in different proportions of the “correct” vs. “incorrect” feedback, so the results also rule out feedback as an explanation for the observed effects of attention in Experiment 1.

Summary and Discussion

By measuring attentional modulation of the BOLD CRFs, we found that attention both amplifies the effective stimulus contrast and increases baseline activity. The results provide converging evidence for a stimulus enhancement mechanism of attention observed in behavioral studies and a mixture of

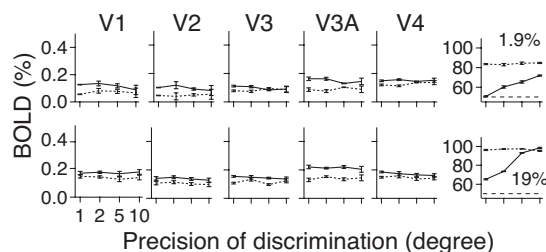


Fig. 4. Results of Experiment 2. The BOLD responses and performance accuracies are plotted in separate rows for the two grating contrast conditions.

retinotopy, 14 3.5-mm-thick interlaced slices (no gap) were acquired. In Experiments 1 and 2, 12 4-mm interlaced slices (no gap) were acquired. In both cases, all of the slices were oriented perpendicular to the calcarine sulcus of the observer.

Displays and Visual Stimuli. All visual stimuli were generated by a Dell PC computer running Matlab programs based on the Psychtoolbox extensions and displayed on a 32- × 24-cm rear-projection screen mounted perpendicularly to the toe-head axis in the bore of the magnet, directly above the observer's head. The video projection system consisted of a Christie DLV1280-DX three-chip DLP projector (1,024 × 768, 60 Hz), located outside of the magnet room, a lens, an iris, a wave guide, and a mirror system that delivered the images from the projector to the screen at a right angle. The background luminance of the display was set at 156 cd/m², with the maximum luminance at 312 cd/m². The projection system has a built-in linear gamma, verified with both psychophysical procedures and photometric measurements. Virtually identical psychometric thresholds were obtained from the projection system and a calibrated CRT display. Observers viewed the displays binocularly at a viewing distance of 75 cm, a full image on the screen subtended 24° (width) × 18° (height).

Wedges and rings made of flickering radial color checkerboard patterns were used to identify retinotopic visual areas of each observer (*SI Text*). Windowed, contrast-reversing (7.5 Hz) sinusoidal luminance gratings at 2 cycles per degree and oriented at 45 ± θ° from the vertical served as stimuli in the experiments. The window was a 5–7° annulus, centered around the fixation point, with 0.2° linear ramps on both the inner and outer edges (*Fig. S1a*). A fixation “+,” a square cue, 0.3° × 0.3° in size, and the letters T and L (both 0.29° × 0.48°) also served as display items in the center of the display.

Procedure. In both experiments, each trial started with a 50-ms cue and a 450-ms blank screen (*Fig. S1*). A small red cue square in the center of a slightly larger dark gray square signaled a central task trial, and a small dark gray cue square on a slightly larger red square signaled a peripheral task trial. In a fixation trial, the fixation display (a “+” at the center of a blank screen) was presented throughout the whole trial; no response was made. The task cue was followed by simultaneous presentations (100 ms) of a grating stimulus in the annulus and either a masked T or L at the center of the display and then a 2.4-s fixation screen in Experiment 1 and a 1.4-s fixation screen in Experiment 2. Auditory feedback followed each response. We also monitored eye movements in the scanner using an infrared eye tracker with remote optics (ASL 504 LRO).

Design. We used a block design and an annulus display, identical to that for the main experiments, to localize the ROIs. Each block consisted of 6 s of windowed gratings at 100% contrast followed by 6 s of a blank screen at mean luminance (*SI Text*).

Experiment 1A used a mixed design in which each run consisted of six blocks of alternating central (T or L) and peripheral (±5° from 45°) task conditions, with 26 trials of 3 s each per block (*SI Text*). The task cue was the same in every block. Within each block, 25 trials were evenly divided across four stimulus contrasts (0%, 3%, 30%, and 100%) and one fixation condition; one extra trial in the beginning of each block was included for counterbalancing purposes. There were a total of 156 trials, preceded and followed by a 20-s fixation display. The order of the blocks and all of the contrast conditions within each block were counterbalanced (45). Each scan session consisted of one structural MRI and six functional runs. Each observer participated in one session of data collection. A session lasted ≈ 1 h.

In Experiment 1A, the desire to have enough blocks in each run and counterbalancing of conditions within each block limited the number of contrast conditions. In Experiment 1B, a rapid event-related design was used to sample CRFs in more contrast conditions. Unlike Experiment 1A, the central and peripheral tasks occurred in separate runs. Six grating contrast conditions, 0%, 1%, 3%, 10%, 30%, and 100%, and one fixation condition were included in each event-related run. Each run consisted of a total of 148 trials. Excluding the first filler trial, there were 21 trials for each condition. Each trial lasted 3 s. These trials were preceded and followed by a 20-s fixation display. The order of the conditions was coun-

terbalanced. Each scan session consisted of one structural MRI and five functional runs of a single (central letter or peripheral grating) task. The order of the two tasks was counterbalanced across observers. Each observer participated in two sessions of data collection. A session lasted ≈ 1 h.

The event-related design was used in Experiment 2. There were two types of runs with identical stimuli but different task instructions: In the central task runs, observers were asked to identify the letter at the center of the display; in the peripheral task runs, observers were asked to identify whether the orientation of the grating in the periphery was ±θ° from 45°. While the grating contrast was kept constant, four θ conditions, 1°, 2°, 5°, and 10°, and one fixation condition were included in each event-related run. Each run consisted of a total of 127 trials of 2 s each, 25 trials for each condition preceded by two filler trials. These trials were preceded and followed by an 8-s fixation display. The order of the conditions was counterbalanced. Each session consisted of one structural MRI and eight functional runs. The order of the two tasks (the central letter task and the peripheral orientation task) was counterbalanced within each session. Each observer participated in two sessions of data collection, each with a constant grating contrast (1.9% and 19%). In the 19% condition, no mask was used in the central task. A session lasted ≈ 1 h.

Data Analyses. All MRI- and fMRI-related data analyses were performed by using a combination of BrainVoyager QX (Brain Innovation) and in-house Matlab programs. All of the fMRI data were first preprocessed to correct for slice timing and head movement, followed by high-pass temporal filtering (cutoff: 3 cycles per run) and removal of linear drift. The 2D functional images were aligned to the 3D structural images in the same session and transformed into the Talairach space. Data from multiple sessions were coregistered through alignment of the structural images from those sessions. Additional curve-fitting and statistical analyses were performed in Matlab.

The BOLD responses to the gratings were obtained in five visual areas, V1, V2, V3, V3A, and V4, in both the central letter (“unattended”) and the peripheral grating (“attended”) conditions. The BOLD signal in each run was normalized by a percent-signal-change transform. The normalized BOLD time series for each subject in each ROI were modeled with a general linear model using the best fitting difference of gamma function as the shape of the HRF with the constraints that $d_1 = a_1 b_1$ and $d_2 = a_2 b_2$ (46):

$$h(t|contrast,attention) = \beta(contrast,attention)h_0(t)$$

$$h_0(t) = \frac{1}{\max(h_0(t))} \left[\left(\frac{t}{d_1} \right)^{a_1} \exp\left(-\frac{(t-d_1)}{b_1} \right) - g \left(\frac{t}{d_2} \right)^{a_2} \exp\left(-\frac{(t-d_2)}{b_2} \right) \right]. \quad [2]$$

The shape of the HRF in an ROI was constrained to be the same in all of the contrast and attention conditions for each subject; the amplitude $\beta(contrast,attention)$ was estimated for each contrast and attention condition. To model the mixed design data from Experiment 1A, a block factor was included in the attended block in the general linear model in addition to the trial-by-trial HRF predictors. The procedure combines deconvolution and HRF curve fitting into one single step. Data from Experiment 1A and 1B were first analyzed separately and had virtually identical trial-by-trial CRFs. They were then combined in a joint analysis. The shapes of the HRFs obtained from Experiment 1 were used to estimate the amplitude of the BOLD responses in Experiment 2 with a deconvolution procedure. The aggregate CRFs in each attention condition in each ROI are the average of the amplitudes of the HRFs across subjects.

All the fitting procedures were implemented in Matlab using a nonlinear least-square method. The goodness of fit was evaluated by the r^2 statistic. Different variants of the models were compared by using an F test for nested models (*SI Text*).

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