Report

Contrast Invariance in the Human Lateral Occipital Complex Depends on Attention

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Summary

The human visual system has a remarkable ability to successfully operate under a variety of challenging viewing conditions. For example, our object-recognition capabilities are largely unaffected by low-contrast (e.g., foggy) environments. The basis for this ability appears to be reflected in the neural responses in higher cortical visual areas that have been characterized as being invariant to changes in luminance contrast: neurons in these areas respond nearly equally to low-contrast as compared to high-contrast stimuli [1, 2]. This response pattern is fundamentally different than that observed in earlier visual areas such as primary visual cortex (V1), which is highly dependent on contrast [3–5]. How this invariance is achieved in higher visual areas is largely unknown. We hypothesized that directed spatial attention is an important prerequisite of the contrast-invariant responses in higher visual areas and tested this with functional MRI (fMRI) while subjects directed their attention either toward or away from contrast-varying shape stimuli. We found that in the lateral occipital complex (LOC), a visual area important for processing shape information [6–10], attention changes the form of the contrast response function (CRF). By directing attention away from the shape stimuli, the CRF in the LOC was similar to that measured in V1. We describe a number of mechanisms that could account for this important function of attention.

Results and Discussion

We tested the hypothesis that attention plays a critical role in the contrast-invariant responses in higher visual areas by presenting contrast-varying shape stimuli under two different attention conditions. Each trial comprised a brief (200 ms) presentation of a pair of shapes of equal contrast on both sides of a central fixation point. In the attended condition, subjects directed their attention to the two shapes and judged whether they were the same or different. Performance varied as a function of contrast but reached asymptotic levels (95% correct) at very low contrast (3%) (Figure 1B). In the unattended condition, subjects directed their attention away from

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the shape stimuli by performing a difficult luminance discrimination task at the central fixation point (mean accuracy = 68%). Importantly, there was not a significant difference in performance in the fixation task as a function of contrast of the shape stimuli (Figure 1D), suggesting that the higher-contrast shapes were not capturing attention during the fixation task. Details of the spatial configuration of the stimuli and fixation task are shown in Figure 1. Contrast was defined as the percent change of a luminance decrement of the shape silhouettes with respect to a constant background luminance. Previous studies [2] and our own pilot results showed that fMRI responses in shape-processing areas can reach asymptotic levels at relatively low-contrast values. Therefore, to better characterize any potential differences due to attention, we presented contrast values in a restricted range from 0% to 30%.

Event-related fMRI averages were calculated for each attention condition at each contrast level for four separate observers. The LOC was predefined for each subject with a standard localizer scan that identified an area in the lateral occipital-temporal region with a larger fMRI signal to objects versus block-scrambled objects. An example of the single-subject event-related responses measured in the LOC is shown in Figure 2A. Note that the differences in the time to reach peak were not systematic across different subjects. The peak of the event-related averages in a window from 3 to 7 s (to account for the hemodynamic delay) was used as an estimate of the magnitude of the response and averaged across observers. The averaged peak responses in the LOC for the attended and unattended conditions are shown in Figure 2B. When attention was directed to the shape stimuli, the measured responses in the LOC were nearly invariant. That is, once the contrast was high enough for the shapes to be reliably detected ($\geq 1.5\%$), there was only a slight change in the fMRI magnitude across the range of contrast values. This is unlike the responses measured in the unattended condition, which monotonically increases with higher contrast values. Figure 2C shows the "attentional gain" or the percent difference in the fMRI signal between the two attention conditions as a function of contrast for the region of the CRF with a significant difference due to attention. There is a strong contrast-dependent effect on the degree of attentional modulation; attentional gain was much larger for low-contrast than for high-contrast stimuli.

The effect of attention on the CRFs that was observed in the LOC was not evident in earlier retinotopic areas. In particular, Figure 3A shows the response in the stimulus-restricted portion of V1 for the attended and unattended conditions. Though the silhouette stimuli (with only a single luminance boundary that varies in position across the visual field) might not be expected to evoke strong responses in V1, the fMRI signal nonetheless monotonically increases with increasing contrast. Similar response patterns in V1 have been measured in previous studies that used contrast-varying gratings [5].
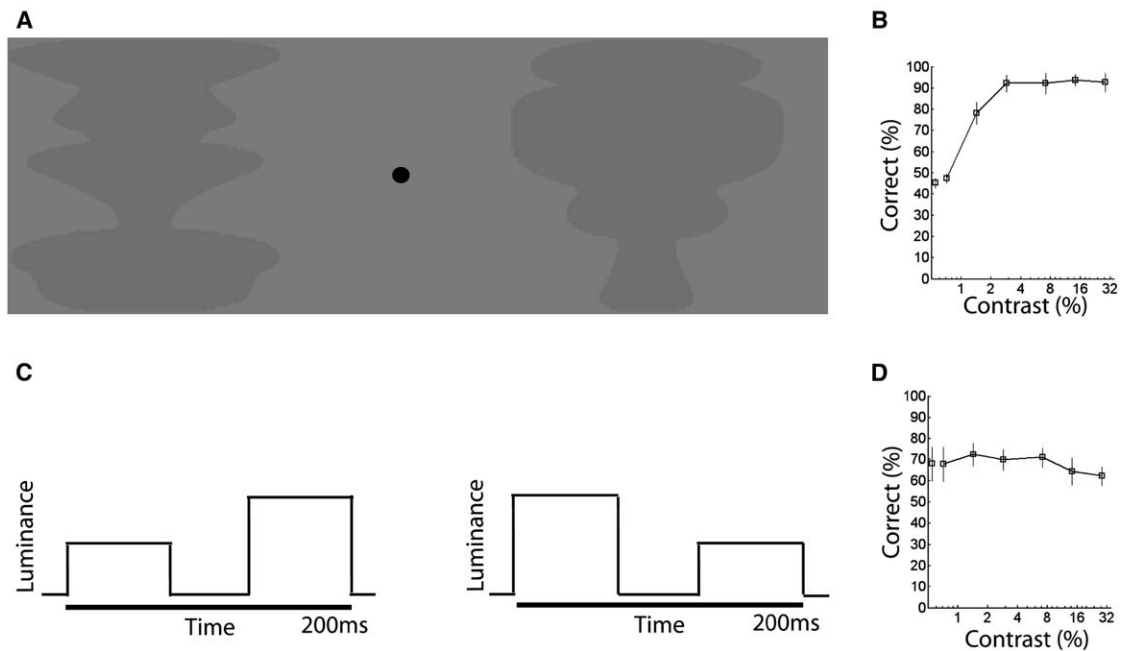
Figure 1. Stimuli and Behavioral Performance

(A) On each trial, a pair of shape silhouettes was presented for 200 ms. The maximum diameter of each shape was 5.5° and they were centered 5° from a central fixation mark. A 2800 ms delay separated each trial. Trials of varying contrast levels (0% to 30%) were presented in pseudo-random, fully counterbalanced order.

(B) Performance in the shape-matching task reached asymptotic levels at low-contrast values (the left-most unconnected point shows the zero-contrast condition).

(C) The luminance profile of the central fixation task designed to remove attention from the shape silhouettes. Subjects were instructed to determine the direction of change of the luminance—"dark-to-light" (left) or "light-to-dark" (right)—of the central fixation dot.

(D) Behavioral performance in the fixation task was not dependent on the contrast of the shapes. Error bars equal SEM.

Notably, in the current experiment, there was not a systematic difference between the two attention conditions in V1. Though this is inconsistent with earlier fMRI studies showing an attention effect in V1 [11–14], there are a number of methodological differences that could account for this. In particular, our stimuli were located relatively close to fixation (closest edge of the shapes was 2.5° from fixation) to allow subjects to accurately perform the shape-matching task while still maintaining central eye fixation. This separation may have been insufficient to isolate V1 attention effects, since it is not clear from previous studies how spatially precise attention effects are in V1. In addition, given the relatively small spatial separation, at least a portion of the central visual field was likely included in the V1 ROI (though more "restricted" ROI definitions were used in separate analyses with no change in the overall pattern of results). Finally, previous studies have found that attention effects in V1 depend on the type of stimulus being attended [14]. It is possible that a higher-order visual property such as complex shape does not differentially engage V1 under different attention conditions.

To directly compare the shapes of the CRFs, the fMRI signal magnitudes were baseline corrected and normalized with respect to the maximum value for each condition. Figure 3B shows the normalized curves for each of the attention conditions in the LOC, as well as the response in V1 averaged across attention conditions. Across the "invariant" (contrast > 2%) portion of the CRF within the LOC, there was a significant interaction

between the attended and unattended curves ($F_{4, 256} = 2.89$, $p < 0.02$). Also, note the similarity between the LOC response in the unattend condition and V1.

One possible explanation for the relatively invariant contrast response in the LOC measured in the attention condition is that the fMRI signal may be approaching a saturating nonlinearity or a "ceiling effect." In other words, the apparent neural invariance may simply be due to an artifact of a limited dynamic range at higher fMRI signal values. However, because of our choice in stimuli, this possibility is extremely unlikely. While the LOC is known to respond to shapes, two-dimensional stimuli consistently result in only moderate fMRI signal values as compared to other object stimuli [15–18]. We tested this directly in a control experiment with two of the four subjects by comparing the fMRI signal of the highest contrast 2D silhouettes used in the attention experiment with 3D versions of the stimuli (Figure 4A). The presentation parameters were identical to the attention experiment and subjects performed the same shape-matching task. Figure 4B plots the event-related responses for the two stimulus types from the same ROIs and shows a significantly larger signal in response to the 3D shapes versus 2D silhouettes. By showing that the fMRI signal in the LOC can be easily increased above the condition with the maximum value in the attention experiment, these results strongly suggest that the contrast-invariance response in LOC was not due to fMRI signal saturation.

Previous neurophysiological [1] and fMRI [2] studies have shown insensitivity to luminance contrast in
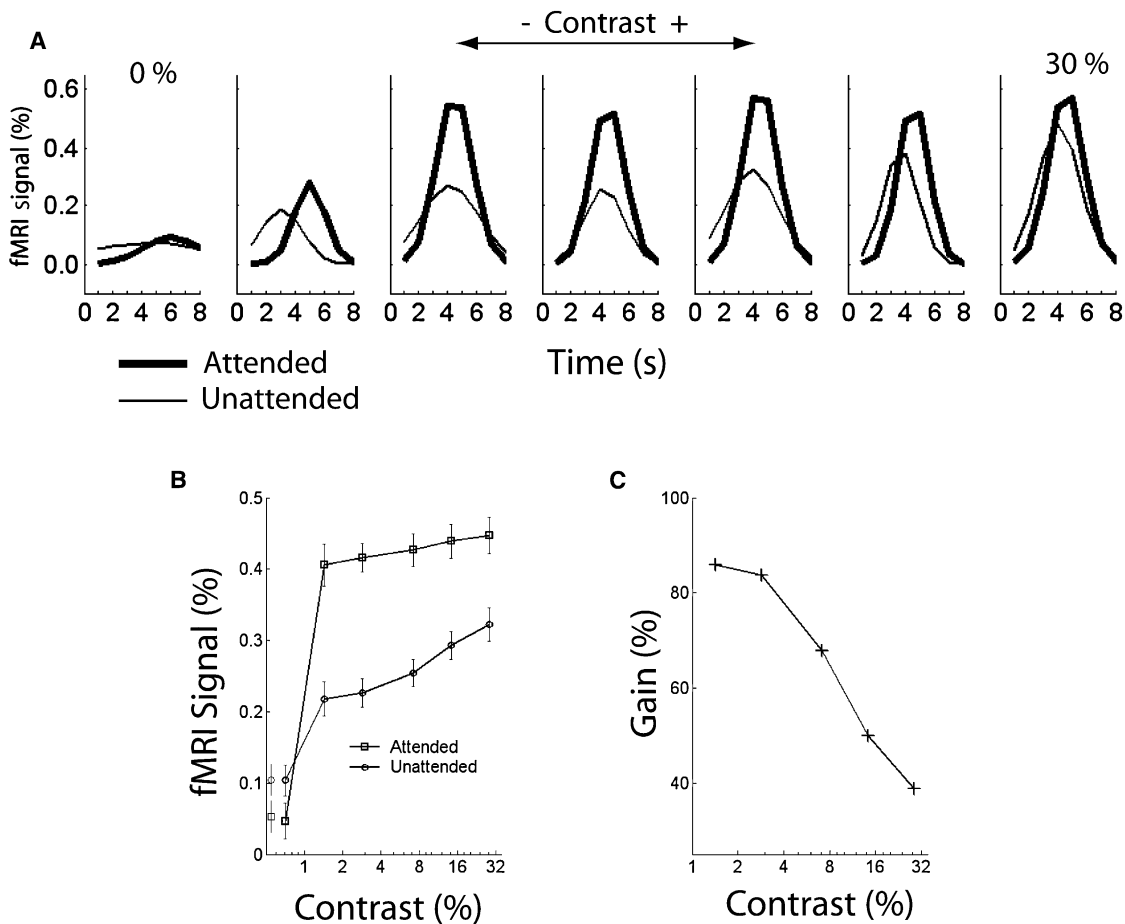
Figure 2. Attention Results in the LOC

(A) Event-related averages in the LOC from a single subject for each attention condition at each of the contrast levels.
(B) The peak of the fMRI signal averaged across all subjects for both attention conditions.
(C) The percent difference in fMRI signal between the attended and unattended peak responses across the range where there was a significant difference (the five highest contrast values). Error bars equal SEM.

higher-level visual areas. Consistent with these previous studies, our data show that when shape stimuli are attended, the magnitude of the fMRI signal in the LOC has little variation across a range of contrast values. However, when attention is removed from the stimuli, the fMRI response in the LOC becomes sensitive to contrast in a manner similar to V1. Our results were specific to the LOC—no other area that we examined showed the same modulating effect of attention (see Figure S1 in the Supplemental Data available with this article online for results from additional visual areas). Our results are unlike those of a previous fMRI study that varied contrast and attention and claimed that the CRF did not change under different attention conditions [2]. However, in the earlier study, only two relatively high-contrast values (10% and 100%) were used in the attention manipulation, which makes it difficult to characterize any systematic effects of attention. This is especially important considering that we observed the largest effect of attention at low (<10%) contrast values. Also, the previous study used a "blocked" experimental design, which has the disadvantage in attention experiments of allowing subjects to adjust their effort based on stimulus conditions for relatively long time periods. Though subjects may

have adjusted their effort in our event-related study, it could have only happened retrospectively, since the various contrast levels were unpredictable on each trial. Finally, though the previous study also used a central fixation task to remove attention, it was superimposed on the stimuli and was not as demanding as our task. Thus, our manipulation likely resulted in greater removal of attention from the stimuli.

There are a number of potential mechanisms that could account for our observed pattern of results. For example, there may be populations of contrast-sensitive and contrast-invariant neurons within the LOC, and attention may be required to engage the contrast-invariant population. Though infero-temporal cortex (IT) is often characterized as being shape selective, there are significant numbers of neurons, particularly in posterior IT subregions, that are selective for "simple" features such as oriented gratings [19]. Assuming these neurons are more sensitive to contrast variations (and that human cortex is similarly organized), a testable prediction is that contrast invariance would not exist, even with attention, in the LOC for simpler stimuli such as orientated gratings. That attention can operate to change the population of neurons coding a particular stimulus is consistent with
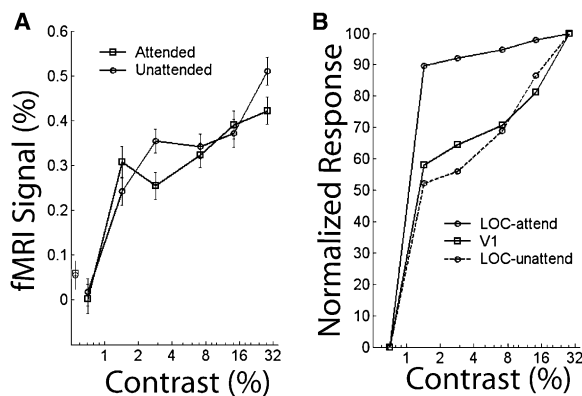
Figure 3. Comparison with V1

(A) The peak response averaged across subjects in V1 for the attended and unattended condition.

(B) The normalized peak responses for the six above-zero contrast values in LOC for both attention conditions and from V1 averaged across attention conditions. Error bars equal SEM.

a previous fMRI observation showing that attention can increase population selectivity in the LOC [20]. Specifically, fMRI adaptation was used to infer the amount of overlap in neural populations under different attention conditions, with the results suggesting that attention increases the specificity of or "sharpens" the population response. This previous finding of an increase in population selectivity with attention and the current results showing an increase in invariance with attention are not necessarily in conflict. The current study does not make statements about which population of neurons are responding to a given stimulus, only that the magnitude of the response does not differentiate between contrast levels. Attention may be serving multiple functions—both to increase the selectivity of the population of neurons responding to a shape or object stimulus and to normalize the response to varying contrast levels. In fact, normalizing the contrast response can be viewed as a form of selectivity sharpening in the shape dimension. Without contrast invariance, a preferred shape at low contrast could result in the same response as (i.e., not distinguished from) a nonpreferred shape at high contrast. However, with contrast invariance, response variation is devoted to coding shape features, thus allowing for higher selectivity in the shape dimension.

A second possible mechanism is that attention could simply shift the CRF horizontally so that low-contrast input becomes more effective—an effect that has been observed in neurophysiological studies of individual neurons [21–23] and behaviorally [24], sometimes referred to as "contrast gain." Similar to what we observed in our experiment, these studies showed that attention caused the greatest increase in neural firing rates and changes in detection threshold at low-intermediate contrast values. However, whether or not contrast invariance is achieved with a contrast-gain mechanism depends on the shape of the CRF without attention. A contrast-shift mechanism would only result in contrast invariance appearing at lower contrast values than that observed in the unattended curve. Since we did not observe contrast invariance in our unattended condition, it is difficult to conclude whether such a mechanism is occurring. However, over the range that we did characterize, it does not appear that a simple horizontal shift in the CRF is occurring in our LOC data.

Another possible mechanism is that the formation of contrast-invariant neural responses is an active process of the visual system and depends on the task demands of the observer. Specifically, attention may act to adaptively adjust the gain, perhaps to achieve behaviorally optimal signal-to-noise levels (i.e., to enable desired behavioral performance, low-contrast stimuli require more while high-contrast stimuli require less enhancement). Alternatively, attention may simply be maximizing the stimulus-specific response. Either case is a dynamic interpretation of attention since the gain is dependent on the stimulus conditions. However, such a mechanism would potentially offer a behaviorally optimal and efficient gain-control mechanism. Further studies manipulating both the task demands and stimulus properties will be required to assess whether such a mechanism occurs in the visual system.

In summary, our results demonstrate that attention is an important prerequisite for contrast-invariant responses in the LOC—a previously unknown function of attention with a number of potential underlying neural mechanisms. Future studies will be needed to isolate the relative contributions of these potential mechanism(s). In particular, future experiments manipulating other aspects of stimulus strength (e.g., additive noise) and/or different stimulus features (e.g., motion) would further contribute to the emerging picture of attention as a flexible mechanism for selectively adjusting neural responses.
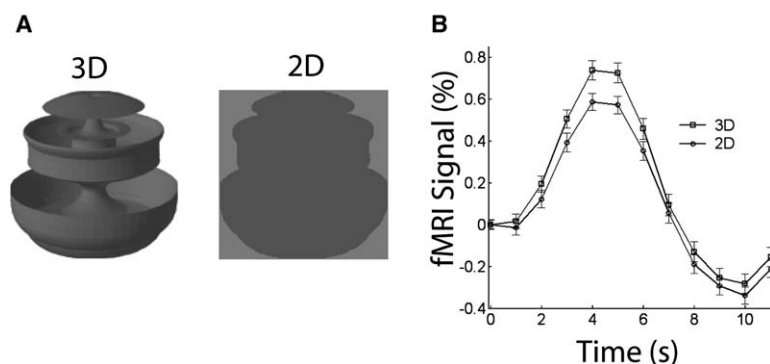

Figure 4. Control Experiment

(A) Examples of the stimuli used to test whether the fMRI signal was saturating in the attention experiment. Three-dimensional objects were compared to the highest contrast (30%) 2D silhouettes used in the attention experiment.

(B) Event-related averages for each stimulus condition showing a significantly larger signal for the 3D versus 2D shape silhouettes. Error bars equal SEM.

Experimental Procedures

Subjects

The four subjects ranged in age between 22 and 33 years and all had normal or corrected-to-normal vision and were experienced psychophysical observers. One of the subjects was an author (S.O.M.) and the other subjects were naive to the purpose of the experiment. Two of the four subjects participated in the control experiment comparing the responses to the 2D and 3D shapes. Informed consent was obtained from all subjects. The experiment was performed in compliance with the institutional guidelines of the University of Minnesota. All subjects received extensive training (approximately 60 min of practice) in both behavioral tasks before being scanned. The fixation task was designed to remove attention as much as possible from the shape stimuli and was therefore made to be difficult. The criteria for participating in the fMRI scans was 75% correct performance in two consecutive practice runs performed in the laboratory. Additional training on both tasks was performed before fMRI data collection while subjects were positioned in the scanner.

Visual Stimulus

Visual stimuli were presented via a PC running Presentation software (http://www.neurobs.com) and synchronized to fMRI data acquisition. An LCD projector was used to project the images onto a translucent back-projection screen located behind the subject's head inside the magnet bore. The subjects viewed the screen by looking at an angled mirror. Contrast values were calculated with photometer-calibrated luminance measurements.

Experimental Design

One experimental run consisted of 128 trials of 8 different trial conditions. Seven of these conditions were different contrast values. The eighth was a "fixation" condition where no stimulus (or fixation change) was presented and served as a baseline measurement. A given run presented each of the 8 trial types 16 times. Trial ordering was determined by pseudo-random m-sequences [25]. Each subject participated in 4 runs of each attention condition for a total of 64 trials per condition. The different attention runs were intermixed and counterbalanced across subjects.

Imaging Parameters and Data Analysis

MRI data were collected on a 3T Siemens Trio outfitted with an 8-channel phase-array coil. Echoplanar data were acquired with standard parameters (14.5 mm thick axial slices; field of view, 220 mm; matrix, 64 × 64; repetition time, TR, 1.0 s; echo time, TE, 30 ms; flip angle, 70º). The first four volumes were discarded to allow for magnetization equilibration. The bottom of the 14 functional slices was positioned at the bottom of the temporal lobes. This ensured coverage of most of visual cortex but did not include superior portions of the brain. A T1 weighted anatomical volume (3D MPRAGE; $1 \times 1 \times 1$ mm^3 resolution) was acquired for localization and visualization of the functional data.

After motion correction (SPM99, http://www.fil.ion.ucl.ac.uk/spm), the functional data were coregistered with the anatomical scan with BrainVoyager 2000. After regions of interest (ROIs) were defined (see below), time courses from each ROI were extracted and imported into Matlab for further analyses. For each scan, we averaged the signal intensity across the 16 trials in each condition at each of 12 time points. These event-related time courses of signal intensity were then converted to percent signal change by subtracting the corresponding value for the fixation condition and then dividing by that value. The resulting time course for each condition was then averaged across trials and subjects. The peak in the event-related averages served as the measured response for each condition.

Localizing Visual Areas

Two scans were used to localize object-processing areas in the occipital-temporal cortex. During these localizer scans, subjects viewed alternating 20 s blocks of shape silhouettes (100% contrast), scrambled shapes, and a blank fixation screen. The scrambled shapes were made by segmenting the object images into a 20 × 20 square grid and randomly rearranging the grid elements. BrainVoyager, via a boxcar response model smoothed with a hemodynamic response function, was used to identify voxels with a significantly

higher signal (p < .0001) in response to the object images compared to the scrambled images. Object-processing areas in the occipital-temporal cortex were defined based on previous studies (e.g., [7, 17]). Data were initially analyzed separately in each hemisphere and in separate LOC "subareas" including the lateral occipital area and posterior fusiform regions. Because no differences were observed between these areas, they were averaged together. To define primary visual cortex, a statistical contrast between the object and fixation epochs was used to define the stimulus-specific region in V1 in combination with separate retinotopic mapping data. The retinotopic data was collected in each subject during a separate session by standard procedures (e.g., [26, 27]).

Supplemental Data

The Supplemental Figure can be found with this article online at http://www.current-biology.com/cgi/content/full/16/6/606/DC1/.

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