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Attention increases neural selectivity in the human lateral occipital complex

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It is well established that attention increases the efficiency of information processing, but the neural mechanisms underlying this improvement are not fully understood. Evidence indicates that neural firing rates increase for attended stimuli, but another possibility is that attention could increase the selectivity of the neural population representing an attended stimulus. We tested this latter hypothesis by using functional magnetic resonance imaging (fMRI) to measure population selectivity for object views under different attention conditions in the human lateral occipital complex (LOC). Our data not only show increased neural activity (or 'gain') with attention, consistent with existing models, but also increased population selectivity that cannot be accounted for by gain mechanisms alone. Our results suggest that attention increases the specificity of the neural population representing an attended object.

Our experience of a visual scene is powerfully determined by the focus of attention[1,2]. What are the neural mechanisms underlying visual attention? Previous studies have shown that attention may reduce the size of receptive fields[3,4] as well as increase neural firing rate in restricted cortical areas when attention is directed to particular locations or features[5,6]. Here we address a more controversial possibility: that attention increases the selectivity of the neural population coding for features of an attended stimulus. Although earlier studies that investigated selectivity at the single-neuron level indicate sharper tuning with attention[7,8], more recent investigations have not confirmed this finding, showing only a multiplicative gain of the sensory response[9–11].

Unlike previous studies, which examined tuning of individual neurons, the present study examines selectivity at the population level by asking whether attention determines which neurons are active for a given stimulus. The population-level response is particularly relevant in light of recent studies demonstrating that complex shapes are represented by a distributed population code where a specific shape recruits a unique, parts-based population of neurons[12]. Thus, a previously unexplored role of attention may be to increase the specificity of this population code by restricting activity to the most relevant neurons for a particular stimulus. We examined this possibility by measuring selectivity for object views under different attention conditions in the human LOC, a cortical area previously shown to be important for processing object shape[13–16]. Our fMRI data show reduced overlap (greater selectivity) in the neural populations representing attended versus unattended objects.

RESULTS

Our experiments make use of the 'adaptation effect,' whereby repetition of the same stimulus elicits a smaller fMRI signal than the presentation of two different stimuli[16–20]. This decrease in signal, which is thought to arise from neural adaptation, provides a method for probing the extent to which the same population of neurons represents a given stimulus as it undergoes various changes[16,19,20]. Thus, recovery from adaptation for a given stimulus change indicates the recruitment of a new population of neurons to represent the changed stimulus (for review, see ref. 21).

Using an event-related fMRI adaptation design[16,20], we measured the response in the human LOC (**Fig. 1**) to different views of the same object by parametrically changing the degree of image-plane rotation between pairs of objects (**Fig. 2**; see **Supplementary Fig. 1** online for examples of all the objects). Using a manipulation that was both easily parameterized and known to recruit different neural populations[19,22–27], we were able to measure selectivity to different views of an object; we reasoned that if distinct neural populations respond to objects across changes in rotation, then the degree of adaptation would vary as a function of object rotation, with larger responses occurring for larger rotation changes.

To evaluate the effects of attention on selectivity, subjects viewed the displays under two different conditions. In the unattended condition, subjects detected slight changes in color of the fixation dot that occurred during the presentation of the two objects. In the attended condition, subjects reported whether the second object was rotated to the left or right (or not at all) relative to its first presentation. Of critical importance was the effect of attention on the amount of adaptation across object rotations. If attention increases selectivity, we should observe larger rotation-dependent responses when subjects attend to object shape compared to when they attend away. In other words, if attending to the objects increases selectivity, then only a restricted population of neurons will represent a particular object view. Consequently, when the adapting and test stimulus are of differ-

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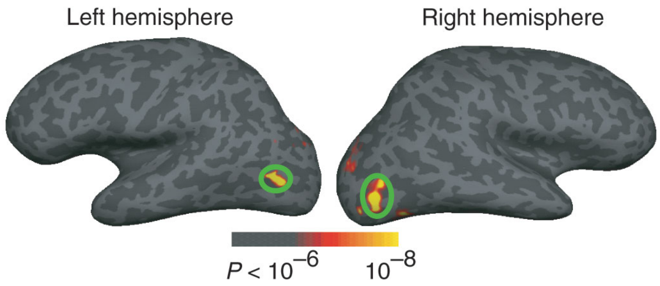

Figure 1 Region of interest. The inflated cortex of one subject showing areas responding significantly more to images of novel, grayscale objects (see **Supplementary Fig. 1** online) than to scrambled images. The color-scale represents statistical values comparing the fMRI signal while subjects viewed the objects versus the scrambled images. The LOC, identified by the green circles above for this subject, served as the ROI for analyzing the event-related data.

ent orientations we expect minimal overlap in the neural populations representing each object and therefore little adaptation (*i.e.*, larger rotation-dependent responses). If, on the other hand, attention does not changing selectivity but only the gain of the sensory response, then we should observe an overall increase in signal strength when attention is directed to the objects, but the amount of adaptation across views should be the same when the objects are attended and when they are not.

Event-related averages of the summed response to the object pairs (stimulus 1, ISI, stimulus 2) in the LOC for the different trial types are shown in **Figure 3a**,**b**. To allow for the hemodynamic delay, the peak in MR signal occurring 5 s after stimulus presentation from each hemisphere in each subject served as the measured response for each condition (see **Supplementary Fig. 2** online for a comparison of left and right hemispheres). A rotation (0°/15°/45°) by task (attended/unattended) repeated-measures ANOVA was performed on the peak responses. We observed a significant effect of rotation ($F_{2,17}$ = 33.9, $P < 0.0001$), with larger responses to larger rotation changes, indicating that different views of the same object are represented by different populations of neurons in the LOC. This finding is consistent with a previous neuroimaging study that used adaptation to investigate viewpoint invariance[19]. No significant effects were observed in early visual areas (**Supplementary Fig. 3** online), possibly due to non-optimal stimuli or timing parameters for lower-level areas[28]. There was an overall significant increase in the LOC response when subjects performed the rotation task compared to the color-fixation task ($F_{1,17} = 33.1, P < 0.0001$). This finding is in agreement with other studies showing enhanced activity with attention to a given attribute specifically in the cortical areas that process that attribute[29–31].

More importantly, we also observed a significant task-by-rotation interaction ($F_{2,34} = 9.2$ $P < 0.001$). That is, there was greater recovery from adaptation when subjects attended to the objects compared to when they attended away. To more directly compare the effect of attention on the rotation-dependent responses, we removed any potential scaling effects by normalizing the peak responses to reflect the proportional increase with respect to the 0° condition: $[(P_\theta/P_0) - 1]$, where P_θ are the peaks for the different rotations, and P_0 is the peak for the 0° rotation. The adaptation functions (**Fig. 3c**) using the normalized index represent the degree to which a new population of neurons is recruited as a function of rotation. Comparing the normalized values, there was a significant increase in the rotation-dependent response for the attended condition ($F_{1,17} = 42.8, P < 0.0001$), reflecting increased population selectivity. Although the gain model can easily account for the overall signal increase we observed in the LOC when objects are attended, it cannot account for the additional effect of attention on the rotation-dependent responses. Instead, our finding indicates that attention acts to reduce overlap in the populations of neurons representing attended objects.

The normalization procedure used to compare the rotation-dependent responses, however, does not take into account the fact that the amount of adaptation can depend on the overall response level of the initial adapting stimulus. **Figure 4** shows how the normalized response curves could diverge as a function of different gain values due to attention (see Methods for equations and further details). A large enough gain change due to attention could result in the observed difference between the attended and unattended adaptation functions (**Fig. 3c**). However, our estimated gain change of 1.30 (the gain between the 45° attended versus 45° unattended conditions) contributes little to the divergence. The large difference in gain that would be required to obtain our results (a gain factor of 2.20) is very unlikely. It is, for example, substantially larger than any gain differences due to attention previously observed in extrastriate areas.

Recall that in this experiment, subjects performed a rotation task. To test whether the effects were due to attention to object shape or attention to the orientation of the symmetry axis of the objects, we conducted a second experiment in which subjects performed a same/different shape-matching task. The design was the same as the first experiment except that the second object of the image pair could either be the same or different shape as the first image. Here, subjects attended to object identity and were told to ignore any changes in rotation between the image pairs. We observed a significant rotation-dependent response ($F_{2,11} = 6.68, P < 0.005$) with a magnitude similar to that of the rotation task of experiment 1 (**Fig. 5**, right), suggesting

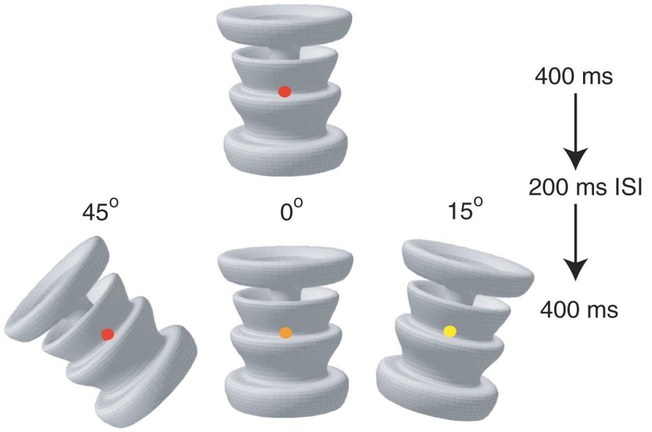

Figure 2 Schematic of the event-related design. Each trial contained a pair of object images each shown for 400 ms and separated by a 200-ms interstimulus interval (ISI). The second stimulus was in one of three orientations with respect to the first stimulus: rotated 0, ±15 or ±45°. Subjects either attended to the fixation dot and performed a same/different color-matching task (color-fixation task) or attended to the shape and reported if it had been rotated to the left, right or not rotated (rotation task). Experiment 2 used the same design except that on half the trials, the second object could be the same or different shape than the first, and subjects performed a shape-matching task.

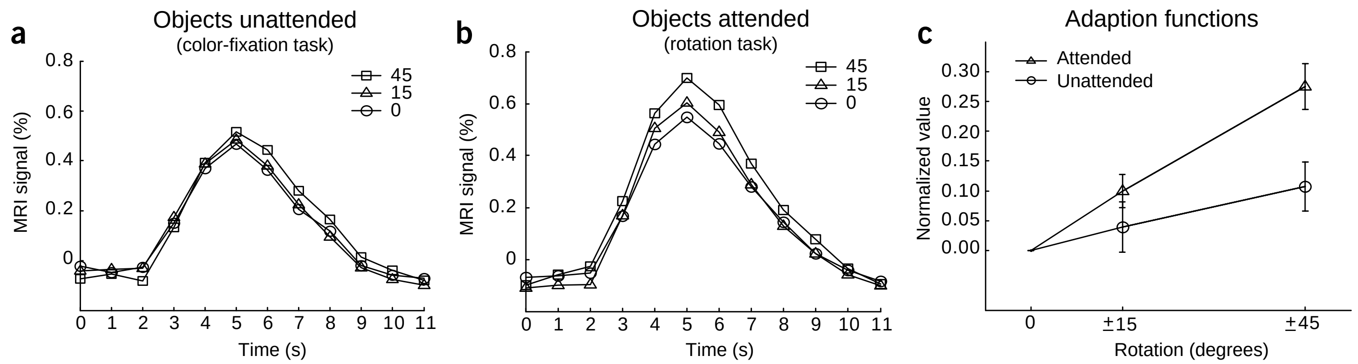

Figure 3 LOC results for experiment 1. Average time course of percent signal change from a fixation baseline for the three different rotation conditions are shown for the unattended (**a**) and attended (**b**) conditions. Trials start at time = 0 s. During both conditions, there was a significant rotation-dependent effect. That is, there was a progressive signal increase as a function of rotation. However, the rotation-dependent effect was significantly increased for the attended condition. (**c**) Adaptation functions were calculated by normalizing the peak responses to the peak in the 0° condition (see text for details). The functions represent the extent to which a new population of neurons was activated as a function of the angular relationship between the pairs of objects. The function is significantly higher for the attended as compared to the unattended condition, indicating greater population selectivity. Error bars are standard error measured across hemispheres and subjects.

that any task requiring attention to the objects would enhance rotation-dependent population selectivity. Experiment 2 also allowed us to compare the responses when the object pairs were of different shape. There was no effect of rotation on the different-shape response ($F_{2,11} = 0.59$, $P = 0.593$). In addition, with the restricted image set we used, a 45° image-plane rotation seemed to be equivalent to a change in object shape (**Fig. 5**, right).

DISCUSSION

It is generally accepted that attention serves to increase the firing rate of neurons within restricted visual areas. Although the details of gain models differ in whether the increase is better characterized as multiplicative[9–11] or as an increase in the effective strength of the stimulus[32], gain models predict increasing responses both to preferred and non-preferred stimuli. Because the LOC is an area that is important for processing object shape, a gain model predicts that when attention is directed to the objects, there should be an increase in the response of all neurons within the LOC that respond to objects. At first glance, our data seem to be consistent with this idea because we observed a significant signal increase in the LOC when subjects attended to the objects versus when attention was directed to the fixation dot. However, the gain model does not explain the most important aspect of our findings: that the focus of attention determined the magnitude of adaptation to different views of the same object.

There are a number of possible of mechanisms that could be occurring at the single-neuron level that could account for our observed findings at the population level. One possibility is that when attention is focused on the objects, the gain of specific neurons within the LOC may be increased relative to other neurons, thereby increasing population selectivity for the attended object. Although this idea is similar to a gain model, it requires an additional mechanism to restrict the gain increase to a select population of neurons, such as a gain increase in neurons that are above an activity threshold.

A second and very different possibility is that attention changes the tuning properties of individual neurons. For example, if attention served to narrow the tuning functions of individual neurons in the LOC, only a select number of neurons would participate in the representation of a particular attended object. Although earlier reports suggested sharpened tuning of individual neurons with attention[7,8], recent data have not confirmed this finding[9–11]. For example, one monkey neurophysiology study examined orientation tuning of individual V4 neurons with and without attention[9]. The authors emphasized that the predominant effect of attention was a change in gain in the neural response with no change in tuning width. However, a considerable number of neurons (16%) had no identifiable tuning and low overall response without attention, yet showed normal tuning functions with attention. If a similar phenomenon occurs in the human LOC, it could account for our findings. The existence of neurons with such a response pattern would result in both an increase in overall activity and an increase in population selectivity, both of which we observed in our data.

No matter which of these mechanisms is occurring at the individual neuron level, our results indicate that attention reduces the overlap in the neural populations representing attended objects.

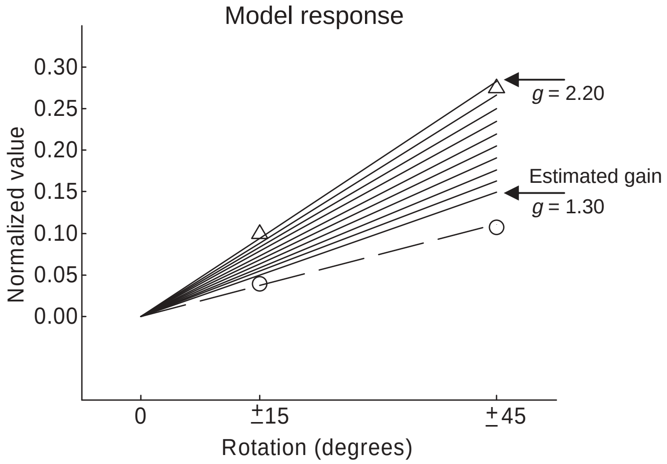

Figure 4 Adaptation model. Model responses for the unattended pair (dashed line) and the attended pair (solid lines) with different gain factors ranging from 1.30 to 2.20 in steps of 0.10. Symbols are actual data from **Figure 3c**. Equations are described in Methods. The graph shows that a very large (2.20) multiplicative gain could account for the divergence observed in our measured data in **Figure 3c**. However, our best estimate of the gain (1.30) contributes little to the observed effect.

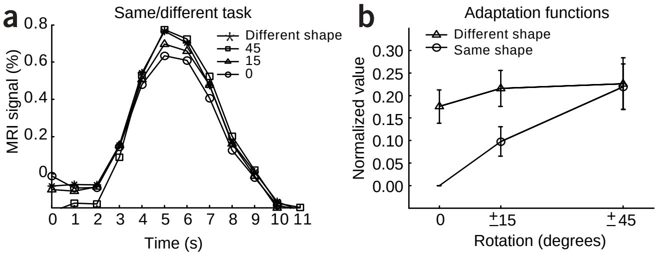

Figure 5 LOC results for experiment 2. (**a**) Rotation-dependent effects were similar in magnitude to the rotation task of experiment 1, indicating that increased selectivity results whenever attention is focused on the objects. (**b**) The functions for the same objects and different objects showing that a 45° image plane rotation is equivalent to a change in object shape.

The increase in resolution afforded by attention[33,34] may be achieved by restricting which neurons code a particular object view or shape—a strategy particularly useful for a distributed, parts-based population code[12]. The current results show that visual attention is not only accompanied by an amplification of neural responses but also that attention may act to sharpen the population-level response to attended objects, thereby increasing the efficiency of the population code.

METHODS

fMRI acquisition. Scanning was done on a 1.5T GE Signa scanner at the University of California, Davis Research Imaging Center in Sacramento, California. An echo planar sequence was used (TR = 1 s, TE = 40 ms). Twelve axial slices (64 × 64 matrix, 220 mm FOV, 5 mm thick), where the bottom slice was positioned at the bottom of the temporal lobes, were acquired using a standard 5-inch diameter GE circular surface coil positioned at the back of head. The functional data were corrected for slice acquisition timing differences and head motion using SPM99 (http://www.fil.ion.ucl.ac.uk/spm).

A total of ten subjects participated in experiment 1. One subject's data were not used because of excessive head motion. Six subjects participated in experiment 2. The experiments were undertaken with each subject's written consent, and procedures were approved in advance by the Institutional Review Board on Human Subjects Research at the University of California, Davis. Visual stimuli were displayed with a PC running Presentation software (Neurobehavioral Systems; http://nbs.neuro-bs.com/) through a LCD projector onto a rear projection screen located at the feet of the subjects and viewed with angled mirrors. The stimuli subtended, on average, 6° of visual angle. A total of 40 novel, grayscale images of objects were used that appeared to be three-dimensional using shading cues (**Supplementary Fig. 1** online).

Experimental design and protocol. For each experiment, subjects were run on a total of ten scans, each lasting 6 min, 44 s. Two of the runs were used to localize the LOC. During these localizer scans, subjects viewed alternating 20-s blocks of intact objects, scrambled objects and a blank fixation screen. The scrambled objects were made by segmenting the object images into a 20 × 20 square grid and randomly rearranging the grid elements. We used SPM99, with a boxcar response model smoothed with a hemodynamic response function, to compare the fMRI signal while subjects viewed the intact versus scrambled objects. The 10 ± 4 contiguous voxels with the highest statistical values in this comparison and located near the ventral occipital-temporal cortex were chosen for each subject. When the event-related analysis was extended to include less significantly active voxels and/or regions slightly more anterior (*e.g.*, activation anterior to the LOC in right hemisphere of **Fig. 1**), the pattern of responses was very similar. Early visual areas were identified by locating voxels with a higher fMRI signal when subjects viewed the scrambled objects versus the fixation epochs and located near the calcarine sulcus. To aid in visualization, the results were projected onto inflated and flattened visual cortices[35,36] in a subset of the subjects to ensure correct identification. In general, it is difficult to differentiate the border between V1 and V2 with foveal stimuli, so we considered our definition to include both areas.

There were eight event-related scans in experiment 1. In four of these, subjects performed a same/different color-matching task of the fixation dot, and in the other four scans, subjects performed the rotation task. The order of tasks was counterbalanced across subjects. The color-fixation task was made more difficult (87% correct; s.d. = 4%) than the rotation task (99% correct; s.d. = 1%) to ensure that overall effort or 'engagement' in the stimuli could not account for the increased rotation-dependent effects or the magnitude increases that were expected for the rotation-task condition. There was no significant difference in accuracy for the different rotation conditions for either the color-fixation task (mean % correct ± s.d.: 0°, 85 ± 5%; 15°, 87 ± 5%; 45°, 87 ± 4%) or the rotation task (0°, 15°, 45°: all 99 ± 1% correct). Reaction times also did not significantly differ as a function of rotation angle for either task: color-fixation (mean ± s.d.: 0°, 806 ± 93 ms; 15°, 798 ± 88 ms; 45°, 800 ± 95 ms), rotation task (0°, 609 ± 76 ms; 15°, 626 ± 70 ms; 45°, 605 ± 68 ms).

Each trial in the event-related experiments lasted one second. The object images were presented for 400 ms with a 200-ms interstimulus interval (ISI). In experiment 1, the pairs of objects were always the same shape and the only difference was the image-plane angular relationship (0°, ±15° or ±45°), giving a total of three stimulus conditions plus the fixation condition. The first object was always presented 'vertically', as each object had an identifiable vertical orientation. Each trial was separated by 2 s, and the order of conditions was determined using m-sequences[37]. These are pseudo-random sequences that have the advantage of being perfectly counterbalanced *n*-trials back (we tested up to 10 trials back), so that trials from each condition, including the fixation condition, were preceded equally often by trials for each of the other conditions. Each scan consisted of 32 trials per rotation condition and there were four scans for each attention condition, yielding a total of 128 trials per condition per subject.

The design of experiment 2 was the same except that the second image of the pair could be a different shape, and subjects performed a same-different shape-matching task on the image pairs. Thus, there were a total of six stimulus conditions (three rotations with either same or different image pairs) plus the fixation condition. There were a total of 16 trials per rotation condition per scan and 8 total scans, yielding again 128 trials per condition per subject. Subjects performed the shape-matching task equally well for each of the three rotation conditions (mean % correct ± s.d.: 0°, 98 ± 2%; 15°, 98 ± 1%; 45°, 97 ± 2%). Similarly, reaction times did not differ for the three rotation conditions (0°, 686 ± 56 ms; 15°, 686 ± 55 ms; 45°, 685 ± 59 ms).

fMRI data analysis. The analysis of the event-related data was done using a similar design to previous studies[16,20]. The time course of MR signal intensity was extracted by averaging the data from all the voxels within the independently defined ROIs identified with the localizer scans. For each scan, we averaged the signal intensity across the 32 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 runs and then across subjects. The peak in activity for the time courses occurring 5 s after stimulus presentation served as the measured response for each condition and were used in repeated-measures ANOVAs.

Adaptation model. In the attended condition, assuming a multiplicative gain mechanism of attention, the response to the first stimulus should produce more adaptation than in the unattended condition, simply because the response is greater. We examined how different response levels due to a multiplicative gain mechanism could result in a divergence in the normalized adaptation functions. Let x be the stimulus orientation of the second presented stimulus with respect to the first, and $s(x)$ be the shape of the tuning function of object-selective neurons with a maximum of 1 at $x = 0$. The response to the second stimulus should increase as a function of $s(x)$. The function f describes this 'release from adaptation'. It follows that the response to the second stimulus is $f(s(x))$, and the response to the unattended pair is $1 + f(s(x))$. For the attended conditions, we included a multiplicative gain factor, g. The response to the image pair with attention is $g + gf(gs(x))$. The

g inside the function f accounts for the greater adaptation due to the response increase of the first stimulus. The g outside the function f is the multiplicative gain applied to the second stimulus.

For the model responses in **Figure 4**, we let $s(x) = 1 - (x/45)$. This is likely a very good approximation. In preliminary studies, we tried 90° and 135° rotations and did not observe responses any larger than the 45° condition. Also, experiment 2 showed that a 45° rotation is equivalent to a change in shape. However, we did try other functions and the results did not significantly differ. Once $s(x)$ was chosen, we let the observed unattended data constrain the function f. For the curves in **Figure 4**, $f(s) = 1 - (s/5)$. We then applied gain factors ranging from 1.30 (our estimate of the gain in our experiment based on the increase in the attended versus unattended 45° conditions) to 2.20 (the multiplicative increase needed to explain our observed data with purely a gain mechanism) and normalized the output with respect to the 0° condition.

Note: Supplementary information is available on the Nature Neuroscience website.

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COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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