studies, the absolute level of IL-2 varied between donors. For each of the cell populations from four donors (Fig. 4A), mutation of the *nef* gene resulted in diminished T cell sensitization. There remained a varied viral-mediated sensitization with the Nef-negative virus, presumably because of Tat. Both HIV infection and either Tat or Nef expression in primary cells result in increased T cell activity as defined by IL-2 (*12*, *14*, *15*), and these enhancements have been shown to vary with the donor by yet-unidentified mechanisms.

The ability of HIV to promote an active state in quiescent T cells would be expected to also positively influence viral replication from infected resting cells. Compared to the wt HIV, the Nef-negative virus had a similar infectivity in preactivated T cells for single-cycle viral production (Fig. 4B). However, the infection of quiescent cells, followed by a 5-day resting state before activation, resulted in an increase in viral replication when a functional *nef* gene was present (Fig. 4C). This increase in viral synthesis is due to Nef alone, and unlike the IL-2 study above, the comparison does not include the effect of Tat expression on viral replication from resting T cells. It also differs from the IL-2 study in that the generated data do not include the activity of uninfected cells. We also found that if the 5-day preactivation incubation, during which the viral gene products are synthesized, is eliminated, the enhancement is lost, with wt and Nef-negative virions yielding similar viral production (Fig. 4D).

This Nef-mediated effect is in addition to the previously characterized increase in virion infectivity (*25*–*27*). Whereas the increase in infectivity is manifest before viral gene expression in the newly infected cell (*20*, *28*, *29*), the positive effect on viral output from quiescent T cells is dependent on viral gene activity in the newly infected cell.

Our ability to detect two of the multiply spliced transcripts, *nef* and *tat*, but not the third, *rev*, suggests that the demonstrated singly spliced transcript for *env* in resting T cells (Fig. 2D) is not likely to become transported to the cytosol (*30*). About 80% of the singly spliced *env* message is spliced at the *nef* site (*22*), and in our system this *env* transcript may be a precursor to the doubly spliced *nef* transcript. Our findings are in part corroborated by previous work, in which reverse-transcribed DNA or gene transcription by integrase mutants has been indicated (*3*, *5*, *24*, *31*). Because cell-cycle progression of primary T cells past the G_{1a} stage is essential for HIV reverse transcription (*32*), we presume that our population, although not supportive of viral replication, includes cells at various stages as found in vivo.

Beyond the potential to alter resting T cells in vivo, the capacity of preintegration transcription by HIV raises other issues. HIV may be able to affect cell function in the absence of productive infection, such as in nonlymphatic cells where binding and entry (but not integration) can occur. Moreover, the extensive presence of unintegrated HIV DNA in T cells of infected individuals may have an underappreciated bioactivity. Last, with the ability to transcribe in the absence of proviral formation, HIV could induce cytotoxic T lymphocyte recognition and destruction of a cell that is not replicating virus particles.

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34. We thank T. Trischmann of the Blood Services Section, Department of Transfusion Medicine, NIH, for providing elutriated lymphocytes; E. Major for use of his BL3 facility; C. Spina, J. Guatelli, A. Engelman, and M. Martin for HIV plasmids; and E. Major, S. Hoare, M. Eiden, and B. Moss for their comments and criticisms concerning this manuscript.

12 April 2001; accepted 2 July 2001

Representation of Perceived Object Shape by the Human Lateral Occipital Complex

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The human lateral occipital complex (LOC) has been implicated in object recognition, but it is unknown whether this region represents low-level image features or perceived object shape. We used an event-related functional magnetic resonance imaging adaptation paradigm in which the response to pairs of successively presented stimuli is lower when they are identical than when they are different. Adaptation across a change between the two stimuli in a pair provides evidence for a common neural representation invariant to that change. We found adaptation in the LOC when perceived shape was identical but contours differed, but not when contours were identical but perceived shape differed. These data indicate that the LOC represents not simple image features, but rather higher level shape information.

A central goal for any theory of human visual object recognition is to characterize the internal representations we extract from visually presented objects. Recent findings from neuroimaging in humans suggest that the LOC (Fig. 1) plays a critical role in object recognition. These studies (*1*–*6*) further suggest that the LOC may represent object shape independent of the particular visual features (e.g. luminance, motion, texture, or stereoscopic depth cues) that define that shape. However, previous results are also consistent with the possibility that the LOC instead represents low-level information about visual contours. The two hypotheses are difficult to distinguish because contours are always present in images of objects. However, contour and shape information are not the same thing: A given shape can be represented by more than one set of local contours (Fig. 2A), and a given set of contours can represent more than one shape (Fig. 2B). The present

study used these two contrasting cases to test whether the LOC represents low-level contour information, or higher level information about object shape.

Our experiments make use of a neural adaptation effect in which responses are lower for stimuli that have been viewed recently than for stimuli that have not (*7*, *8*). Because adaptation depends critically on the sameness of two stimuli, it provides a technique for asking what counts as the same to a particular neural population—that is, what information is included in the representation and what information is not (*8*, *9*). For example, it has been shown that adaptation occurs in the LOC even when objects are presented in different locations or sizes, indicating that the representations in this region are largely invariant to changes in size and location (*9*).

We used an event-related (*7*, *10*) adaptation paradigm in which each trial consisted of a pair of images presented sequentially (*11*). If neural populations in the LOC represent object shape but not the contours defining the shape, then we should observe adaptation when the two stimuli in a trial have the same perceived shape even if they have different contours (Fig. 2A). Conversely, if neural populations in the LOC represent information about contours but not perceived shape, then we should observe adaptation when the two stimuli have identical contours even if they have different perceived shapes (Fig. 2B).

A region of interest (ROI) comprising the LOC was identified individually for each subject as the set of all contiguous voxels in the ventral occipitotemporal cortex that were activated more strongly ($P < 10^{-3}$) by intact than by scrambled images of objects presented in two localizer scans, as described previously (*6*) (Fig. 1). The magnitude of the response in this ROI was then measured for each subject in each condition in two main experiments.

Each of the main experiments included an Identical condition (in which the two stimuli in a pair were identical in all respects) and a Completely Different condition (in which the two stimuli differed in perceived shape, contours, and depth relations). These two conditions provided upper and lower reference points to which we could compare the response for the critical condition in each experiment: in experiment 1, the Same Shape condition (in which the two stimuli had different contours and different depth relations as shown in Fig. 2A), and in experiment 2, the Same Contours condition (in which the two stimuli had different perceived shapes and different depth relations as shown in Fig. 2B). A fourth Same Depth condition in each experiment (in which the two stimuli had different contours and different perceived shape, but the same depth relations) enabled us to measure any adaptation for sameness in depth relations alone. We computed the time course of percent signal change from the fixation baseline separately for each of the four stimulus conditions in each of the 10 subjects in each experiment, as described previously (*6*). The average across subjects of these time courses of response for each condition are shown in Fig. 3 (experiment 1) and Fig. 4 (experiment 2). The response was significantly lower for the Identical than for the Completely Different conditions in both experiments at time points 4, 5, and 6 (*12*), replicating our previously reported event-related adaptation effect (*6*).

The goal of experiment 1 was to investigate whether sameness of perceived shape is sufficient for adaptation in the LOC by testing responses to stimuli that had the same

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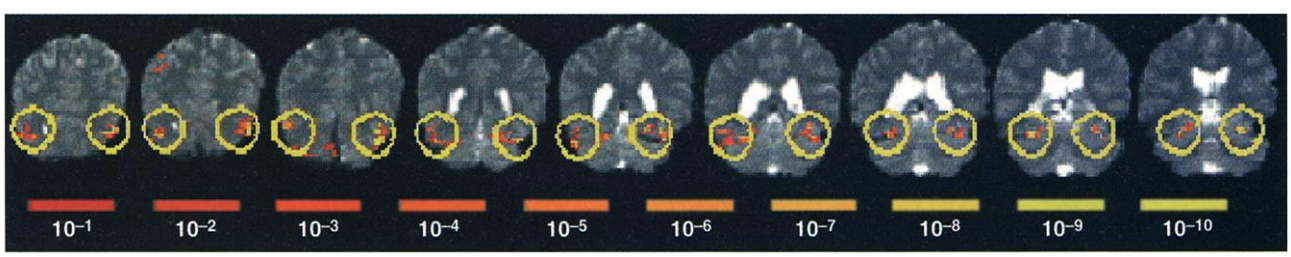

Fig. 1. Nine consecutive slices from one subject showing regions responding significantly more strongly to intact images of objects (300 pixel by 300 pixel gray-scale images and line drawings of familiar and novel objects) than to control images in which the images of objects have been divided into squares with a 20 by 20 grid and the component squares have been randomly rearranged within three concentric rings around the fixation point. Significance maps reflect the results of linear regression ($r \geq 0.3$) of the fMRI signal intensity to the stimulus protocol for viewing of intact objects versus scrambled objects. The right hemisphere appears on the left. For each subject the LOC was identified as the set of all voxels that produced a significantly higher response to intact than to scrambled objects in the ventral occipitotemporal cortex. These voxels, marked by the yellow circles, served as the ROI for analyzing the data from the event-related adaptation scans in this subject. Note that despite the name "Lateral Occipital Complex" this region extends well into ventral and temporal regions. When the analyses reported here were carried out separately for the more anterior regions and the more posterior regions, the pattern of responses was very similar, indicating that the functions described here were found throughout this rather large region of cortex.

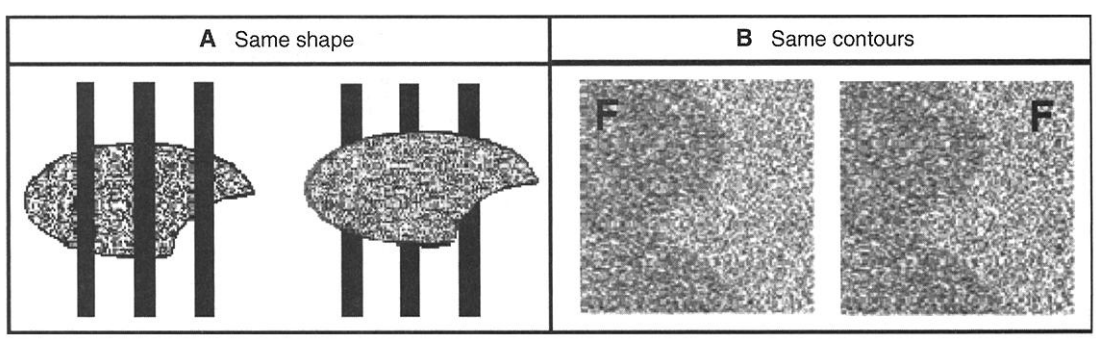

Fig. 2. Displays illustrating the critical conditions in experiments 1 and 2. (**A**) Same Shape condition in which the two stimuli in a trial depicted the same shape but had different local contours due to occlusion and stereoscopic depth cues. (**B**) Same Contours condition in which the two stimuli in a trial had the same contours but different shape due to stereoscopically induced figure-ground reversal (F indicates the figure for each stimulus). The disparity value was 0.2° in both experiments.

perceived shape but different contours (Same Shape condition) due to occlusion (Fig. 2A). As shown in Fig. 3, the mean signal at the peak of the hemodynamic response (4 to 6 s after trial onset) in the critical Same Shape condition was significantly lower [$F(1, 87) = 5.5$, $P < 0.05$] than that in the Completely Different condition, but not significantly different [$F(1, 87) < 1$, $P = 0.83$] from that in the Identical condition (Fig. 3). Thus, adaptation for pairs of stimuli with the same perceived shape but different contours was as strong as that for identical images. These results suggest that the LOC represents perceived shape, rather than image contours.

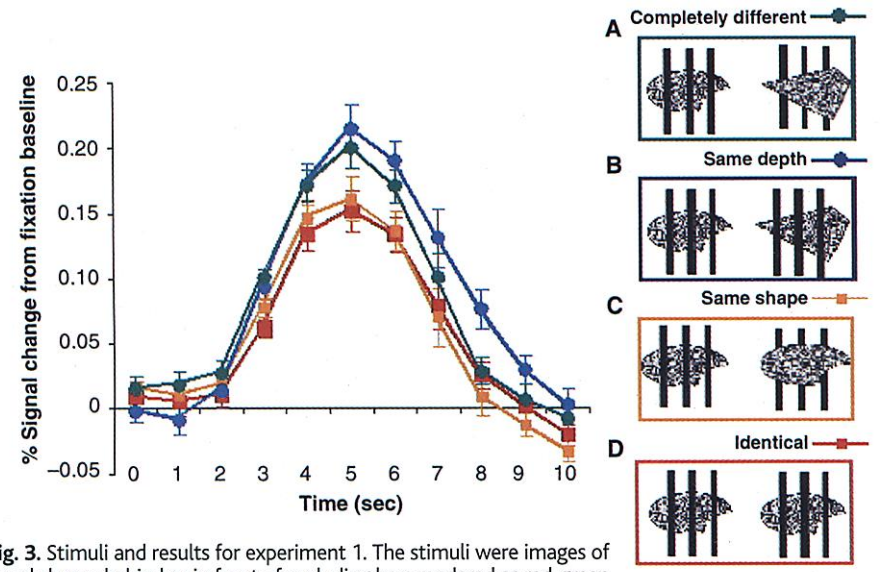

Fig. 3. Stimuli and results for experiment 1. The stimuli were images of novel shapes behind or in front of occluding bars rendered as red-green anaglyphs and presented stereoscopically to the subjects through red-green glasses. The critical condition was the Same Shape condition where the two objects in a trial had the same shape but different local contours. The results reported are average percent signal increases (from the fixation baseline trials) within the LOC for each condition. Trials start at time = 0 s. The error bars indicate standard errors of the percent signal change measured across all trials for each stimulus condition averaged across all scans and subjects. Early retinotopic regions bordering the calcarine sulcus did not show adaptation for any of the experimental conditions; that is, no main effect of Shape Condition [$F(3, 297) < 1$, $P = 0.42$] and no significant interactions between Shape Condition and Time [$F(30, 297) < 1$, $P = 0.57$] were observed.

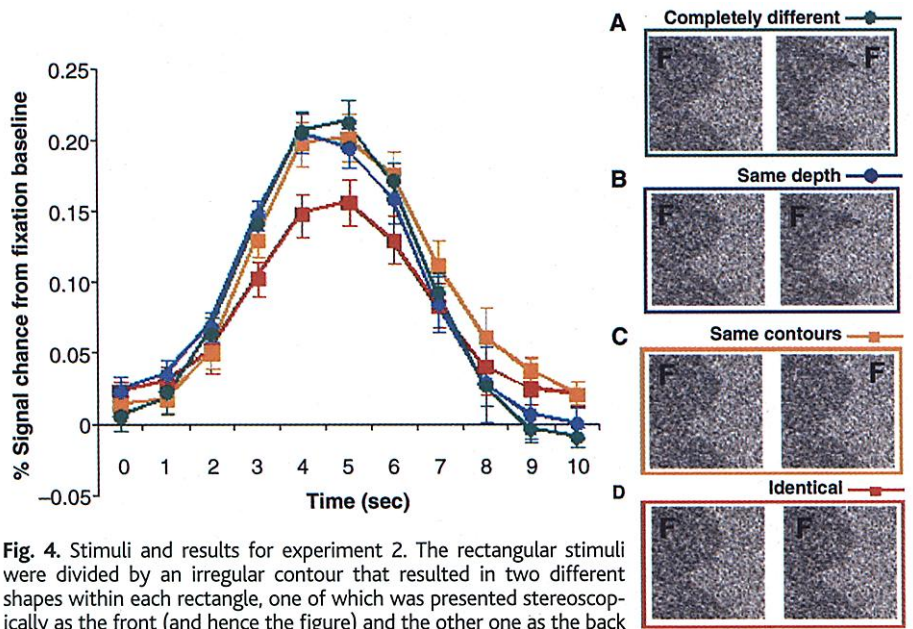

Fig. 4. Stimuli and results for experiment 2. The rectangular stimuli were divided by an irregular contour that resulted in two different shapes within each rectangle, one of which was presented stereoscopically as the front (and hence the figure) and the other one as the back (and hence the ground). To facilitate the segmentation between figure and ground, we used different contrasts for the two shapes in the rectangle. The letter F indicates which shape appeared in front in each image. The critical condition was the Same Contours condition where the two displays in a trial had the same contours but depicted different shapes. The results reported are average percent signal increases (from the fixation baseline trials) within the LOC for each condition. Trials start at time = 0 s. The error bars indicate standard errors of the percent signal change measured across all trials for each stimulus condition averaged across all scans and subjects. Early retinotopic regions bordering the calcarine sulcus did not show adaptation for any of the experimental conditions; that is, no main effect of Shape Condition [$F(3, 297) < 1$, $P = 0.86$] and no significant interactions between Shape Condition and time [$F(30, 297) < 1$, $P = 0.53$] were observed.

Beyond its implications for shape representations in the LOC, experiment 1 also provides some clues about what other information may be represented in the LOC. In particular, a reversal in depth relations between the two stimuli in a trial had no effect on responses in the LOC, compared with conditions in which depth relations were not reversed; that is, no differences were found in the peak responses in the Same Shape [$F(1, 87) < 1$, $P = 0.83$] versus Identical conditions, or the Completely Different versus Same Depth conditions [$F(1, 87) = 1.2$, $P = 0.27$]. These results are consistent with other evidence (*6*) suggesting that depth information may not be represented in the LOC.

In sum, experiment 1 demonstrates that sameness of perceived shape can be sufficient to cause maximal adaptation in the LOC, even when the two stimuli have substantially different low-level contours. Our second experiment tested whether sameness of perceived shape is necessary for adaptation in the LOC. If it is, no adaptation should be observed for the Same Contour condition, in which stimulus pairs share the same contours but depict different shapes because of a figure-ground reversal (Fig. 2B).

The time course of the response of the LOC to each of the conditions in experiment 2 is shown in Fig. 4. No adaptation was observed in the LOC for the Same Contour condition; that is, the response in the Same Contours condition was not significantly lower [$F(1, 87) = 3.3$, $P = 0.07$] than the response in the Completely Different condition, yet was significantly higher [$F(1, 87) = 12.1$, $P < 0.001$) than the response for the Identical condition. Evidently, sameness of contours was not sufficient to produce adaptation in the LOC.

Two lines of evidence argue against an account of our findings in terms of greater attentional engagement in the shape-change conditions. First, one would expect changes in depth relations to be at least as salient as changes in shape, yet they do not produce recovery from adaptation in the LOC (whereas shape changes do). Second, we ran four additional subjects on new versions of experiments 1 and 2 in which each stimulus moved very slightly vertically or diagonally (45°), and subjects indicated whether the two stimuli in a pair moved in the same or different direction. The sub-

jects' performance on this task was similar across conditions (identical, 68%; completely different, 71%; same depth, 69%; same shape, 68%; same contours, 72%). Despite the attention to each stimulus required by this task, the pattern of data from these four subjects closely matched the findings from the main experiments. Thus, our findings apparently reflect neural adaptation to shape repetitions rather than fluctuations in attentional engagement.

In summary, we found that sameness of perceived shape (but not of low-level contours) is necessary and sufficient for adaptation in the LOC. Evidently, neural populations in the LOC represent object shape rather than the low-level features defining the shape.

How abstract are these shape representations? The present results indicate that the LOC contains representations in which contours have been completed (experiment 1) and figure-ground borders have been assigned (experiment 2) (*13–16*). Evidence that object representations of this kind play a central role in visual cognition comes from developmental studies showing that infants only a few months old complete representations of objects behind occluders (*17*), and psychophysical experiments on adults suggesting that such completed representations determine the allocation of visual attention (*18*, *19*). Other functional magnetic resonance imaging (fMRI) studies have shown responses in the LOC for shapes defined by different form cues (texture, stereo, motion) (*4*, *5*) and adaptation across changes in size and position, but little adaptation across changes in viewpoint and illumination (*9*). Taken together, these results make important progress in situating the LOC on a continuum of possible shape computations: After contour completion, border ownership, and invariance to form cues, size and position have been attained, but before invariance to viewpoint and illumination has been achieved.

The shape representations in the LOC resemble those found in inferotemporal cortex in monkeys. In particular, in the monkey brain, contours are completed and borders are assigned in early visual areas (*20*, *21*), whereas shape-selective neurons invariant to form cues (*22*, *23*), as well as to location and size but not to viewpoint (*24*), are observed in inferotemporal cortex.

Important questions remain. Are the representations in the LOC more like representations of visual surfaces (*25*), structural descriptions of objects in which part structure is made explicit (*26*), sets of moderately complex features (*27*) or image fragments (*28*), or yet some other kind of shape representation? Does the cortical neighborhood of the LOC hold several qualitatively distinct representations that may constitute intermediate stages in the derivation of shape representations? The present study provides both an important first step and a powerful tool for answering these long-standing questions, which are at the very core of current theories of object recognition.

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11. For each experiment the subjects were run on four event-related scans. The event-related scans consisted of one epoch of experimental trials and two 8-s fixation epochs, one at the beginning and one at the end of the scan. Each scan contained 25 experimental trials for each of the four conditions plus 25 fixation trials, for a total of 125 trials per scan. A new trial began every 3 s and consisted of a pair of images presented sequentially. Each stimulus was presented for 300 ms with a blank interval of 400 ms between stimuli, and a blank interval of 2 s after the second stimulus. Previous human fMRI (*6*) and neurophysiological studies (*8*, *29*, *30*) have reported adaptation effects for short-stimulus presentations similar to the ones used in the current studies. Specific stimuli were counterbalanced across conditions such that each specific stimulus appeared equally often in each condition. Thus, differences in the response between conditions were due to the relation between the two images in a pair and not due to the stimuli used in each condition. As reported previously (*6*), the order of presentation was counterbalanced so that trials from each condition, including the fixation condition, were preceded equally often by trials from each of the other conditions for two trials back. Subjects were instructed to passively view the images while fixating. Twelve students from the University of Tuebingen participated in experiments 1 and 2 in the same session. The data from two subjects in experiment 2 were excluded owing to excessive head movement. For all the experiments, scanning was done on the 1.5-T Siemens scanner at the University Clinic in Tuebingen, Germany. A gradient echo pulse sequence [repetition time (TR) = 2 s for the scans used to localize medial temporal/medial, the LOC, and the early visual areas; TR = 1 s for the event-related scans, echo time (TE) = 40 ms] was used. Eleven near coronal slices (parallel to the brainstem, 5 mm thick with 3.00 mm by 3.00 mm in-plane resolution) were collected with a head coil. The data were analyzed with BrainVoyager 4.3 software.
12. Because of the hemodynamic lag in the blood oxygenation level–dependent (BOLD) fMRI response, differences between conditions (as well as the peak in overall response) are expected to occur at a lag of several seconds after stimulus onset (*31*). To find the latencies where any adaptation effects occurred, we performed an analysis of variance in each experiment with factors of Shape Condition and Time point (measurements made at latencies of 0 through 10 s after trial onset). A significant main effect of Shape Condition {experiment 1, [$F(3, 297) = 16.7$, $P < 0.001$]; experiment 2, [$F(3, 297) = 4.4$, $P < 0.01$]} and significant interactions between Shape Condition and Time (10 time points) for each experiment {experiment 1, [$F(30, 297) = 1.5$, $P < 0.05$]; experiment 2, [$F(30, 297) = 1.6$, $P < 0.05$]} verified that adaptation occurred and that it varied with latency. Follow-up contrast analyses performed separately on each time point tested for a significantly lower response for the Identical compared with the Completely Different conditions. This adaptation effect was found for each experiment only for time point 4 {experiment 1, [$F(1, 27) = 5.3$, $P < 0.05$]; experiment 2, [$F(1, 27) = 19.1$, $P < 0.001$]}, time point 5 {experiment 1, [$F(1, 27) = 5.3$, $P < 0.05$]; experiment 2, [$F(1, 27) = 10.3$, $P < 0.01$]}, and time point 6 {experiment 1, [$F(1, 27) = 4.5$, $P < 0.05$]; experiment 2, [$F(1, 27) = 4.3$, $P < 0.05$]}, but not for the onset of a trial, i.e., time point 0 {experiment 1, [$F(1, 27) < 1$, $P = 0.73$]; experiment 2, [$F(1, 27) = 1.1$, $P = 0.31$]}. The average of the response at time points 4, 5, and 6 was therefore taken as the measure of response magnitude for each condition in subsequent analyses. To exclude any possible baseline effects, we subtracted the responses at time point 0 from the mean peak response (across time points 4, 5, and 6) for the corresponding condition. The same statistical results were found when the response at time point 0 was not subtracted from the mean peak response. To determine whether the critical condition in each experiment showed any significant adaptation at all, we compared the mean peak response of the critical condition with that of the Completely Different condition in a planned contrast test. To determine whether adaptation effects in the critical condition were weaker than the maximal adaptation possible, we compared the mean peak response of the critical condition with that of the Identical condition in a second planned contrast in each experiment. Note that all of the effects reported in this paper also reached significance in an independent replication of both experiments 1 and 2 on an additional 10 subjects (*32*).
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33. We thank B. Anderson, P. Cavanagh, P. Downing, K. Grill-Spector, Y. Jiang, K. Nakayama, M. Potter, J. Rubin, and L. Spelke for comments on the manuscript. We also thank M. Shuman and members of the MGH-NMR Center and the University Clinics, Tübingen, for technical assistance and support. Supported by McDonnell-Pew grant 3944900 (Z.K.) and NEI grant EY13455 (N.K.).

28 March 2001; accepted 6 July 2001