Duration-Dependent fMRI Adaptation and Distributed Viewer-Centered Face Representation in Human Visual Cortex

Two functional magnetic resonance imaging (fMRI) face viewpoint adaptation experiments were conducted to investigate whether fMRI adaptation in high-level visual cortex depends on the duration of adaptation and how different views of a face are represented in the human visual system. We found adaptation effects in multiple face-selective areas, which suggest a distributed, viewer-centered representation of faces in the human visual system. However, the nature of the adaptation effects was dependent on the length of adaptation. With long adaptation durations, face-selective areas along the hierarchy of the visual system gradually exhibited viewpointtuned adaptation. As the angular difference between the adapter and test stimulus increased, the blood oxygen level-dependent (BOLD) signal evoked by the test stimulus gradually increased as a function of the amount of 3-dimensional (3D) rotation. With short adaptation durations, however, face-selective areas in the ventral pathway, including the lateral occipital cortex and right fusiform area, exhibited viewpoint-sensitive adaptation. These areas showed an increase in the BOLD signal with a 3D rotation, but this signal increase was independent of the amount of rotation. Further, the right superior temporal sulcus showed little or very weak viewpoint adaptation with short adaptation durations. Our findings suggest that long- and short-term fMRI adaptations may reflect selective properties of different neuronal mechanisms.

Keywords: adaptation, face, fMRI, viewpoint, visual cortex

Introduction

A hallmark feature of the human visual system is its ability to recognize most objects from different viewing angles. Two competing theories of object recognition propose different explanations. The viewer-centered theory (e.g., Ullman 1989; Poggio and Edelman 1990) suggests that recognition is based on matching specific views to a set of templates, which requires explicit viewer-specific object representations. The objectcentered theory (e.g., Biederman 1987) suggests that it is based on constructing a structural description of simple parts, which does not require explicit representations of objects from specific views. Very recently, a viewpoint aftereffect was found to strongly support the existence of viewer-centered object representations in the human high-level visual system (Fang and He 2005). Specifically, after visual adaptation to an object viewed 30° from one side, when the same object was subsequently presented near the front view, the perceived viewing directions were biased in a direction opposite to that of the adapted viewpoint.

Although our previous behavioral adaptation experiment supported the idea that objects and faces are represented by populations of viewpoint-tuned neurons, how these representations are implemented in the visual cortex is still unknown. In

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the current study, we focus on how different views of a face are represented in the human visual cortex. For example, what are the viewpoint-tuning properties of the various face-selective occipital-temporal areas? How are these properties established along the hierarchy of the visual system? Are there cortical areas in the visual system that respond to faces in a viewpointindependent fashion? We used functional magnetic resonance imaging (fMRI) adaptation experiments to address these questions. Previous functional magnetic resonance adaptation experiments (Grill-Spector and others 1999; Andrews and Ewbank 2004) have given partial answers to the above questions. However, these studies provided limited information about specific viewpoint-tuning properties. In addition, a blocked adaptation design may have confounded adaptation with attention (Kanwisher and Yovel 2006).

Adaptation has served as a powerful psychophysical tool for demonstrating selective neural sensitivities to various stimulus dimensions, from low-level stimulus features (Kohler and Wallach 1944; Blakemore and Campbell 1969; Anstis and Moulden 1970) to high-level object and face properties (Webster and Maclin 1999; Leopold and others 2001; Zhao and Chubb 2001; Suzuki and Grabowecky 2002; Rhodes and others 2003; Watson and Clifford 2003; Webster and others 2004; Fang and He 2005). In these studies, subjects were typically exposed to adapting stimuli for long durations (tens of seconds preadaptation and several seconds topping-up adaptation, here called "long-term adaptation"), and the subsequently perceived visual distortions in the test stimuli were used to infer how visual properties are represented in the human visual system. More recently, there has been an explosion of fMRI studies using adaptation as an experimental tool to make inferences about subvoxel level neural selectivity in specific cortical regions (Grill-Spector and others 2006; Krekelberg and others 2006).

Unlike the long-term adaptation designs traditionally used in psychophysical and single-unit studies, most of the fMRI adaptation studies, especially those related to object representations in occipital-temporal cortical visual areas, have used brief (e.g., 300 ms) adaptation times (Kourtzi and Kanwisher 2000, 2001; here called "short-term adaptation"). Though the pattern of results in these fMRI studies is often consistent with the adaptation logic, there has been little validation of the technique, and we know little about its underlying mechanism. For example, orientation-selective fMRI adaptation in V1 can be easily demonstrated using long-term adaptation (Fang and others 2005; Larsson and others 2006) but not using shortterm adaptation (Boynton and Finney 2003; Murray and others 2006). It has been recognized that the duration of adaptation has a strong in uence on the susceptibility of an area to adaptation, especially in the early visual cortex (Krekelberg and others 2006). Importantly, there is evidence to suggest that the temporal dynamics of high-level behavioral adaptation are similar to those of traditional low-level adaptation effects (Leopold and others 2005). For example, just as with low-level adaptations, the face identity aftereffect grows logarithmically stronger as a function of adaptation time and exponentially weaker as a function of test duration. Similarly, in our recent



Figure 2. Schematic descriptions of the long-term adaptation, short-term adaptation, and no adaptation experiments. In the long-term adaptation experiment, test stimuli were preceded by 25-s preadaptation and 5-s topping-up adaptation. In the short-term adaptation experiment, test stimuli were preceded by only 0.3-s adaptation.

The short-term and no adaptation experiments (Fig. 2) each consisted of eight 210-s scans, and each scan consisted of 64 continuous trials. Like the long-term adaptation experiment, there were 4 types of trials—Test0, Test30, Test90, and Fixation trials. For the short-term adaptation experiment, in the TEST0, Test30, and Test90 trials, after 0.3-s adaptation and 0.4-s blank interval, a test stimulus was presented for 0.3 s, followed by 2-s blank interval. For the no adaptation experiment, in the Test0, Test30, and Test90 trials, a test stimulus was presented for 0.3 s, followed by 2.7-s blank interval. For both of these 2 experiments, in the Fixation trials, there was only a blank interval lasting 3 s. The positions of test stimuli (and the adapters in the short-term adaptation experiment) were randomly distributed within that $9.4^{\circ} \times 9.4^{\circ}$ area.

For each of the 3 event-related experiments, there were a total of 64×8 trials, 128 for each type of trial. The order of the 4 types of trials (Test0, Test30, Test90, and Fixation) was counterbalanced across 8 adaptation scans using M-sequences (Buracas and Boynton 2002). These are pseudorandom sequences that have the advantage of being perfectly counterbalanced *n* trials back (we tested up to 10 trials back), so that each type of trials was preceded and followed equally often by all types of trials, including itself.

Before the subjects were scanned, subjects were given 128 practice trials. In addition, each subject participated in a psychophysical view-point adaptation experiment (Fang and He 2005); all exhibited a strong viewpoint aftereffect.

Magnetic Resonance Imaging Data Acquisition

In the scanner, the stimuli were back projected via a video projector (60 Hz) onto a translucent screen placed inside the scanner bore.

Subjects viewed the stimuli through a mirror located above their eyes. The fMRI data were collected using a 3-T Siemens Trio scanner with a high-resolution 8-channel head array coil. Blood oxygen leveldependent (BOLD) signals were measured with an echo planar-imaging sequence (time echo: 30 ms, time repetition: 1000 ms, field of view: 22×22 cm², matrix: 64×64 , ip angle: 60° , slice thickness: 5 mm, gap: 1 mm, number of slices: 14, slice orientation: axial). The bottom slice was positioned at the bottom of the temporal lobes. T₂-weighted structural images at the same slice locations and a high-resolution 3D structural data set (3D magnetization-prepared rapid gradient echo; $1 \times 1 \times 1$ mm³ resolution) were collected in the same session before the functional runs. Each subject participated in 4 fMRI sessions. One session was conducted to define retinotopic areas, and the other 3 were dedicated to the long-term, short-term, and no adaptation experiments, respectively. These 4 sessions were conducted on different days. The temporal order of the long-term and short-term adaptation experiments was randomized across subjects, and the no adaptation experiment was run last. The block-design ROI scan was conducted in all the long-term, short-term, and no adaptation sessions.

Magnetic Resonance Imaging Data Processing and Analysis

The anatomical volume for each subject in the retinotopic mapping session was transformed into a brain space that was common for all subjects (Talairach and Tournoux 1988) and then in ated using BrainVoyager 2000. Functional volumes in all the sessions for each subject were preprocessed that included 3D motion correction using SPM99, linear trend removal, and high-pass (0.015 Hz) (Smith and others 1999) filtering using BrainVoyager 2000. The images were then aligned

to the anatomical volume in the retinotopic mapping session and transformed into Talairach space. The first 10 s of BOLD signals were discarded to minimize transient magnetic saturation effects.

A general linear model procedure was used for ROI analysis. Faceselective areas were defined as areas that respond more strongly to faces than nonface objects ($P < 10^{-4}$, uncorrected). Nonface-selective areas were defined as voxels that passed the opposite contrast. The ROI in V1 was defined as area that responds more strongly to texture patterns (scrambled faces) than blank screen ($P < 10^{-4}$, uncorrected) and confined by the V1/V2 boundaries defined by the retinotopic mapping experiment.

The event-related BOLD signals were calculated separately for each subject and each experiment, following the method used by Kourtzi and Kanwisher (2000). For each event-related scan, the time course of magnetic resonance signal intensity was first extracted by averaging the data from all the voxels within the predefined ROI. The average eventrelated time course was then calculated for each type of trial by selective averaging to stimulus onset and using the average signal intensity during the Fixation trials as a baseline to calculate percent signal change. Specifically, in each scan, we averaged the signal intensity across the 16 trials for each type of trial at each of 13 corresponding time points (seconds) starting from the stimulus onset. These eventrelated time courses of signal intensity were then converted to time courses of percent signal change for each type of trial by subtracting the corresponding value for the Fixation trial and then dividing by that value. Because M-sequences have the advantage that each type of trials was preceded and followed equally often by all types of trials, the overlapping BOLD responses due to the short interstimulus interval are removed by this averaging procedure. The resulting time course for each type of trial was then averaged across scans for each subject and then across subjects.

To more directly compare the effect of adaptation duration on the rotation-dependent responses, we calculated an index of adaptation strength by removing potential scaling effects. Following the method used by Murray and Wojciulik (2004), we normalized the peak responses to re ect the proportional increase with respect to the Test0 condition: $[(P_{\theta}/P0)-1]$, where P_{θ} are the peaks for the different rotations (Test0, Test30, or Test90) and P0 is the peak for the 0° rotation (Test0).

Eye Movement Recording

Eye movements of 5 subjects in the long-term, short-term, and no adaptation experiments were recorded with a long-distance optics module of ASL eyetracker (Applied Science Laboratories, Bedford, MA) in the 3-T magnet.

Results

Behavioral Responses to Test Stimuli

In the long-term, short-term, and no adaptation experiments, subjects' responses to the test stimuli were both accurate and fast. The correct rates for the 3 types of test stimuli in all experiments were above 98%. The reaction times (Mean \pm standard error) were as follows: 436 ± 21 ms (Test0), 452 ± 22 ms (Test30), and 443 ± 20 ms (Test90) for the long-term adaptation experiment, 440 ± 33 ms (Test0), 460 ± 30 ms (Test30), and 458 ± 28 ms (Test90) for the short-term adaptation experiment, and 486 ± 18 ms (Test0), 493 ± 20 ms (Test30), and 500 ± 19 ms (Test90) for the no adaptation experiment. For all the experiments, there were no significant performance (both reaction time and correct rate) differences between the trial types and no significant correlation between performance and the peak values of the event-related BOLD signals.

Eye Movements

The measurements indicated that eye movements were small and gaze distributions were not systematically different across trial types. Further statistical analyses showed no significant difference across trial types in the mean eye position (long-term adaptation—*x* position: $F_{2,10} = 0.677$, P = 0.535; *y* position: $F_{2,10} = 0.093$, P = 0.913; short-term adaptation—*x* position: $F_{2,10} = 0.76$, P = 0.499; *y* position: $F_{2,10} = 0.179$, P = 0.84; no adaptation—*x* position: $F_{2,10} = 0.688$, P = 0.53; *y* position: $F_{2,10} = 0.277$, P = 0.765), the mean saccade amplitude (long-term adaptation—*x* position: $F_{2,10} = 1.047$, P = 0.395; *y* position: $F_{2,10} = 0.431$, P = 0.664; short-term adaptation—*x* position: $F_{2,10} = 0.431$, P = 0.664; short-term adaptation—*x* position: $F_{2,10} = 0.398$, P = 0.684; *y* position: $F_{2,10} = 0.706$, P = 0.522; no adaptation—*x* position: $F_{2,10} = 1.072$, P = 0.387; *y* position: $F_{2,10} = 1.254$, P = 0.336), and the number of saccades (long-term adaptation: $F_{2,10} = 0.135$, P = 0.876; short-term adaptation: $F_{2,10} = 1.65$, P = 0.251; no adaptation: $F_{2,10} = 0.958$, P = 0.424). These results suggest that it is unlikely that our results could be significantly confounded by eye movements.

Region of Interest

A block-design scan (Fig. 3) was used to define ROIs, including face-selective areas and nonface-selective areas. Subjects passively viewed images of faces, nonface objects, and texture patterns (scrambled faces). Face-selective areas were defined as areas that responded more strongly to faces than nonface objects ($P < 10^{-4}$, uncorrected). Three areas were consistently found in all subjects, including the right fusiform face area



Figure 3. ROI in a representative inflated brain. The experimental procedure for ROI localization is shown at the top. Face-selective areas (red/yellow) were defined as areas that respond more strongly to faces than nonface objects ($P < 10^{-4}$, uncorrected). Blue/green areas indicate voxels that passed the opposite contrast. Face-selective ROIs consistently found in all subject include 1) rFFA (right: $33 \pm 1, -40 \pm 2, -14 \pm 1$), 2) rSTS (right: $44 \pm 2, -40 \pm 3, 12 \pm 2$), and 3) face-selective area in the LO (right: $37 \pm 2, -68 \pm 3, -4 \pm 2$; left: $-41 \pm 1, -65 \pm 2, 2 \pm 3$). Nonface-selective ROIs include 1) PHC (right: $24 \pm 1, -35 \pm 2, -10 \pm 2$) rendered in blue and green and 2) primary visual cortex (V1, $0 \pm 1, -84 \pm 1, -2 \pm 2$) defined by texture stimuli and retinotopic mapping. The white lines in the bottom row are boundaries of early visual areas obtained from retinotopic mapping. The inner pair separate V1 and V2, and the outer pair separate V2 and V3.

(rFFA), the right superior temporal sulcus (rSTS), and a faceselective area in the lateral occipital cortex (LO) in both hemispheres. The face-selective LO area is also referred to as LOa (Grill-Spector and others 1999), PF (Avidan and others 2002), or OFA (Gauthier and others 2000). In addition to these face-selective areas, left superior temporal sulcus and left fusiform face area (IFFA) were found in 3 and 5 (out of 7) subjects, respectively, according to the above criterion. Nonface-selective ROIs include a region in the parahippocampal cortex (PHC) that responded more strongly to nonface objects than faces ($P < 10^{-4}$, uncorrected) and primary visual cortex (V1) defined by texture patterns and retinotopic mapping (see Materials and Methods). The PHC defined here is likely the same parahippocampal place area defined by Epstein and Kanwisher (1998), a cortical area that has been demonstrated to respond more strongly to houses and places than to other kinds of objects. For the long-term, short-term, and no adaptation experiments, this localization scan was run at the beginning of each session (total of 3 times), and the ROI locations were very similar across sessions. For fMRI data analyses, because there was no qualitative difference between the ROI locations defined in different sessions, the fMRI data presented below are from the ROIs defined in the first event-related fMRI session.

The fMRI Long-Term Adaptation Effect

After adapting to one view of a face, a cortical area that contains a collection of neural populations tuned to different views should exhibit viewpoint-tuned adaptation effect. By "tuning," we mean that, as the angular difference between the adapter and test stimulus increases, the peak amplitude of the BOLD signal evoked by the test stimulus should gradually increase as a function of the amount of 3D rotation and saturate at some angle.

A repeated-measures analysis of variance (ANOVA) of the peak amplitude revealed a significant main effect of angular difference between adapter and test stimulus in rFFA ($F_{2,14}$ = 14.581, P = 0.001), rSTS ($F_{2,14} = 16.028$, P < 0.001), and LO ($F_{2,14} = 5.822$, P = 0.017). In rFFA and rSTS, the BOLD signals evoked by the Test0, Test30, and Test90 showed a monotonic increase (Test90 > Test30 > Test0). This response pattern (viewpoint-tuned adaptation) was consistently observed in all 7 subjects and was confirmed by post hoc least significant difference (LSD) tests (all t > 2.6 and P < 0.04). In LO, the Test90 evoked a stronger signal than the Test30 (t = 3.022, P = 0.023). But there was no significant difference between the signals evoked by the Test0 and Test30. The nonface-selective areas V1 and right parahippocampal cortex (rPHC) did not exhibit any adaptation effect (Fig. 5).

The fMRI Short-Term Adaptation Effect

A repeated-measures ANOVA of the peak amplitude revealed a significant main effect of angular difference between adapter and test stimulus in rFFA ($F_{2,14} = 8.244$, P = 0.006) and LO ($F_{2,14} =$ 5.934, P = 0.016) but not in rSTS ($F_{2,14} = 1.986$, P = 0.18). We further used post hoc LSD tests to examine if there was also a monotonic increase of the peak amplitudes in rFFA and LO. It was found that the BOLD signal evoked by the Test30 was significantly stronger than that by the Test0 (both *t* > 2.513 and P < 0.046), but there was no significant difference between the signals evoked by the Test30 and Test90. We call this effect (Test90 = Test30 > Test0) viewpoint-sensitive adaptation effect. By "sensitive," we mean that these areas showed an increase in the fMRI signal with a 3D rotation, but this signal increase was independent of the amount of rotation. The nonface-selective areas V1 and rPHC again did not exhibit any adaptation effect (Fig. 5).

The fMRI Responses to Test Stimuli without Adaptation

The BOLD signals in the face-selective and nonface-selective areas to different test stimuli without adaptation can be used to examine if there was any cortical response bias to a specific view of face. Repeated-measures ANOVAs showed there was no significant main effect of angular difference between adapter and test stimulus in both the face-selective areas (Fig. 4) and the nonface-selective areas (Fig. 5). We referred to the test stimuli as Test0, Test30, and Test90 here for consistency, but they essentially were faces turned 60° , 30° , and -30° from the front view. These results demonstrate that different BOLD responses to different test stimuli after adaptation are not due to a cortical response bias to a particular view of face.

Comparison between Long-Term and Sbort-Term Adaptation

We found viewpoint-tuned adaptation with the long-term adaptation paradigm and viewpoint-sensitive adaptation with the short-term adaptation paradigm. In order to test the effect of adaptation duration directly, we performed 2-way ANOVAs (adaptation duration [long vs. short] × test view [Test0 vs. Test30 vs. Test90]). The interaction of adaptation duration and test view was significant in rFFA ($F_{2,35} = 5.021$, P = 0.026), rSTS ($F_{2,35} = 7.986$, P = 0.006), and LO ($F_{2,35} = 9.473$, P = 0.003) but not in V1 and rPHC.

To more directly compare the effect of adaptation duration between the 2 paradigms, we plotted the index of adaptation strength in Figure 6. Consistent with the statistics on the peak values, the indices were higher in the long-term adaptation experiment than that in the short-term one at the Test90 condition (at rFFA and rSTS, both t > 2.4 and P < 0.05), and there were interaction effects between adaptation duration and test view (at rFFA, rSTS, and LO, all F > 4.753 and P < 0.03).

Discussion

We found fMRI face viewpoint adaptation in multiple faceselective areas but not in the nonface-selective areas, which suggests a distributed but confined viewer-centered representation in the human visual system. This is in line with the results of Grill-Spector and others (1999) and Andrews and Ewbank (2004). More importantly, the adaptation effects were different with the long-term and short-term adaptation paradigms. Specifically, with long-term adaptation, the face-selective areas along the hierarchy of visual system gradually exhibited viewpoint-tuned adaptation. With short-term adaptation, however, face-selective areas in the ventral pathway, including LO and rFFA, exhibited viewpoint-sensitive adaptation. Another difference was that rSTS showed little adaptation effect with short adaptation durations. These differences cannot be explained simply by suggesting that longer adaptation durations lead to a stronger adaptation effect, which has been used to explain our orientation adaptation data in V1 (Fang and others 2005). Although the adaptation effect is generally stronger in rFFA and rSTS with the long-term adaptation paradigm, in LO, the short-term adaptation paradigm was even more sensitive than the long-term adaptation paradigm. Specifically, there was



Figure 4. Time courses of event-related BOLD signals averaged across 7 subjects from the face-selective areas (rFFA, rSTS, and LO) in the long-term adaptation, short-term adaptation, and no adaptation experiments. Error bars denote 1 standard error of mean across subjects and scans at each time point.

a larger difference between the fMRI signals evoked by the Test0 and Test30 after short-term adaptation. These differences suggest that the neural mechanisms underlying the short-term and long-term adaptations may be qualitatively different—a possibility that is described in more detail below.

The no adaptation experiment was important; without it, one could argue that the observed changes in fMRI signals to different test stimuli after adaptation were due to a neural response bias to particular face views. However, in this study, there was no difference in the fMRI signal to different face views, ruling out this potential confound. In any of these 3 experiments, there was no significant performance (both reaction time and correct rate) difference between the trial types and no significant correlation between performance and the peak values of the event-related BOLD signals. Together with the null adaptation effect in the nonface-selective areas (V1 and rPHC), the overall pattern of results can be best explained by adaptation mechanisms.

Long-Term Adaptation

Neural fatigue is often suggested as a simple mechanism for adaptation effects. According to the fatigue model, all neurons initially responsive to a stimulus show a reduction in their response after adapting to a stimulus. The reduction in a neuron's activity is proportional to its response to the adapting stimulus before adaptation. Thus, if we carefully select the test stimuli based on tuning curve properties measured in singleunit studies, we should observe viewpoint-tuned fMRI adaptation according the fatigue model. This is exactly what we found in the rSTS and rFFA in the long-term viewpoint adaptation experiment. In a previous neurophysiological study, it was found that the majority of neurons in the superior temporal sulcus (STS) (110 out of a sample of 119 responsive to the head) exhibited view selectivity, and most of them showed a unimodal tuning property (Perrett and others 1991). On average, the maximal response of these neurons was reduced by half after the head was rotated in-depth by 60° away from the optimal view. The same population of neurons was found to maintain their viewpoint selectivity irrespective of image position, size, orientation, and different lighting conditions (Perrett and others 1982, 1984, 1989). The finding of viewpoint-tuned face-selective neurons in STS has been confirmed by other groups (Desimone and others 1984; Hasselmo and others 1989; De Souza and others 2005). Such neurons were also found in the inferior temporal cortex (IT) (Desimone and others 1984). In the behavioral adaptation experiment (Fang and He 2005), we found the strength of face viewpoint adaptation effect in human

stimuli, requiring a much larger rotation (90°) to evoke a differential response.

The viewpoint-tuned fMRI adaptation in rSTS and rFFA in the long-term adaptation experiment suggests a position-invariant viewer-centered face representation in these 2 areas (the positions of adapting and test stimuli were different and the adapting stimulus was slowly drifting, See Materials and Methods). The viewpoint-tuned property of rSTS and rFFA at the population level revealed with the current fMRI technique neither excludes the possibility that there are some neurons sensitive to 3D face structure in these areas (Hasselmo and others

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	clear that potent	ially different mechanisms may su	ipport long-				
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