Neural Correlates of High-Level Adaptation-Related Aftereffects

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Submitted 6 July 2009; accepted in final form 13 January 2010

Cziráki C, Greenlee MW, Kovács G. Neural correlates of high-level adaptation-related aftereffects. J Neurophysiol 103: 1410–1417, 2010. First published January 13, 2010; doi:10.1152/jn.00582.2009. Prolonged exposure to complex stimuli, such as faces, biases perceptual decisions toward nonadapted, dissimilar stimuli, leading to contrastive aftereffects. Here we tested the neural correlates of this perceptual bias using a functional magnetic resonance imaging adaptation (fMRIa) paradigm. Adaptation to a face or hand stimulus led to aftereffects by biasing the categorization of subsequent ambiguous face/hand composite stimuli away from the adaptor category. The simultaneously observed fMRIs in the face-sensitive fusiform area (FFA) and in the body-part–sensitive extrastriate body area (EBA) depended on the behavioral response of the subjects: adaptation to the preferred stimulus of the given area led to larger signal reduction during trials when it biased perception than during trials when it was less effective. Activity in two frontal areas correlated positively with the activity patterns in FFA and EBA. Based on our novel adaptation paradigm, the results suggest that the adaptation-induced aftereffects are mediated by the relative activity of category-sensitive areas of the human brain as demonstrated by fMRI.

INTRODUCTION

Prolonged exposure to complex stimuli, such as faces, biases perceptual judgments toward nonadapted, dissimilar stimuli, leading to contrastive aftereffects (Leopold et al. 2001; Webster et al. 2004). Such aftereffects suggest that adaptation is not a unique property of low- and midlevel neural processes, but also exists at higher-level cortical areas (Clifford et al. 2007; Watson and Clifford 2003). Previous studies of high-level adaptation, however, invariably used stimuli with continuously varying parameters such as a point-by-point face-morphing (Leopold et al. 2001; Rhodes et al. 2003; Webster et al. 2004), changes of viewpoint (Fang et al. 2005, 2007), or eye-gaze direction (Calder et al. 2007; Jenkins et al. 2006; Schweinberger et al. 2007). Unfortunately, such methods do not allow for the testing of adaptation-related aftereffects for object categories that are more distant in the object space, such as faces and hands, and for which identifying corresponding points and creating a continuous stimulus space are otherwise not possible (Op de Beeck et al. 2008). In our current functional magnetic resonance imaging adaptation (fMRIa) experiments we used ambiguous, noisy stimulus composites (AMB) as targets, which were constructed from overlapping human faces and hands with varying Fourier phase coherences. The choice of ambiguous stimuli was motivated by three facts. First, for such stimuli current theories of decision making suggest random discrimination performance (Gold and Shadlen 2007), making them ideal for testing the possible interactions of adaptation and decision-related processes. Second, previous fMRI studies invariably found that the body-selective regions of the human occipitotemporal cortex are spatially distinct from the face-selective regions (for a review, see Peelen and Downing 2007). This spatial division enables us to measure the adaptation effects on the fMRI signal individually for the two stimulus categories, making up our stimulus composites. Third, we know that for ambiguous stimuli (overlapping face–house composites; Furey et al. 2006; O’Craven et al. 1999) or the Rubin face/vase illusion (Hasson et al. 2001) the activity of face-selective areas is enhanced when selective attention is drawn to the face interpretation of the stimuli.

We hypothesized that if the occipitotemporal category-specific areas mediate the adaptation aftereffects, similar to the attentional modulation of the areas, then the observed fMRIs should reflect the behavioral choice of the subjects: adaptation to the preferred stimulus of the given area should lead to larger signal reduction during trials when it biases category decisions behaviorally than during trials when it is not strong enough to change perception.

Our results suggest that category decision biases are reflected in the relative activity change of the category-sensitive occipitotemporal areas. Adaptation leads to significant reductions in blood oxygenation level–dependent (BOLD) signal strength in these brain regions and these changes are reflected in the choice behavior exhibited by the subjects.

METHODS

Subjects

Thirteen healthy volunteers (eight females) with normal or corrected-to-normal vision participated in the experiments (mean age = 26.25 yr, SD = 5.77 yr). Subjects gave written informed consent in accordance with the protocols approved by the Ethical Committee of the University of Regensburg.

Stimuli

A high-contrast female face, female hand, and their Fourier phase randomized version served as adaptors (Kovács et al. 2008; mean luminance: 18 cd/m2, size: 4.3° radius; Kovács et al. 2006). As test stimuli we used female faces and hands other than the adaptors. First, we superimposed the images for spatial frequency, luminance, contrast, and average magnitude spectrum. We then manipulated their phase spectra using the weighted mean phase technique (Dakin et al. 2002). We created five images with phase-coherence levels ranging from 41 to 55% for the face images and from 53 to 90% for the hand stimuli. Finally, we superimposed the phase-coherence manipulated face and hand images, using Adobe Photoshop. In prior experiments we calibrated these face/hand composite images in a way that one was perceived predominantly as a face (on average 55% face phase...
coherence and 53% hand phase coherence), one predominantly as a hand (41% face/90% hand), and three images were ambiguous with respect to the assigned categorization (AMB; 53%/60%, 47%/70%, and 43%/80% face and hand, respectively).

To minimize local feature adaptation and apparent motion cues the size of the test stimuli was 25% smaller (3.5° radius) than that of the adapter images. Stimuli were back-projected via a liquid crystal display video projector (DLA-G20, 72 Hz, 800 × 600 resolution; JVC, Yokohama, Japan) onto a translucent circular screen (weighted echoplanar imaging sequence, repetition time [TR] 30 ms; flip angle 90°; 64 × 64 matrices; in-plane resolution: 3 × 3 mm; slice thickness: 3 mm). High-resolution sagittal T1-weighted images were acquired using a magnetization-prepared rapid gradient echo sequence (TR = 2,250 ms; TE = 2.6 ms; 1-mm isotropic voxel size) to obtain a three-dimensional structural scan.

Regions of interests (ROIs) were defined by block-design functional localizer runs (488 s long; 17-s epochs of faces, hands, and their Fourier randomized versions interleaved with 17 s of blank periods; 2 Hz; 300-ms exposition time; 200 ms blank).

Each subject underwent two scanning sessions (scanning time was ~45 min each). During one of the sessions the structural run and two event-related experimental runs, whereas during the other session the functional localizer run and two experimental runs were administered. One experimental run was a Control in each session, whereas the other experimental run was either the FaceA or the HandA adaptation run to minimize carryover effects (Aguirre 2007; Grill-Spector and Malach 2001). The order of the Control, FaceA, and HandA runs was randomized across subjects. To test whether adaptation to faces or to hands resulted in differential effects on subsequent AMB stimulus categorization, a one-way ANOVA was performed on the subjects’ category decisions with the adaptation condition as factor (three levels: Control, FaceA, and HandA).

Details of preprocessing and statistical analysis are given elsewhere (Kovács et al. 2008). Briefly, the functional images were corrected for acquisition delay, realigned, normalized to the Montreal Neurological Institute (MNI)-152 space, resampled to 2 × 2 × 2-mm resolution, and spatially smoothed with a Gaussian kernel of 8-mm full width at half-maximum (SPM5, Welcome Department of Imaging Neuroscience, London, UK).

Face-responsive areas were determined individually as areas responding more strongly to faces than to hands in the functional localizer scans (Puncorrected < 0.0001; T = 3.8). We could define the occipital face area (OFA) in 9 subjects [average Talairach coordinates (±SE): 45(1), −72(1), −5(1) and −44(2), −76(1), 5(2) for left and right hemispheres] and FFA in 10 subjects [43(1), −59(3), −12(1) and −41(1), −52(2), −14(1)] bilaterally (Hemond et al. 2007). Areas selectively responding to hands were determined by comparing the activity for hands versus faces [11 subjects bilaterally; Puncorrected < 0.0001; T = 3.8; 48(2), −68(2), 5(1) and −48(2), −69(2), 7(1)]. Areas of these subjects, matching our anatomical criteria and lying closest to the corresponding reference cluster (resulting from the random-effects analysis on the group data for differential contrasts; Puncorrected < 0.0001; T = 6.4), were considered as their appropriate equivalents on the single-subject level. To prove that the independent localizer scans and the experimental scans lead to the activation of the same areas we also conducted a random-effects whole-brain analysis (with threshold Puncorrected < 0.005; T = 3.1) from our Cont experimental sessions by contrasting all unambiguous face and hand stimuli. The resulting coordinates for bilateral FFA, right OFA, and left EBA were virtually identical to those of the functional localizer scans, whereas the left OFA and right EBA could not be identified from these contrasts.

A time series of the mean voxel value within a 4-mm-radius sphere around the local peak of the areas of interest was calculated and extracted from our event-related sessions (MARSBAR 0.38; Brett 2002), using finite impulse response (FIR) models (Ollinger et al. 2001). For each of the experimental conditions we collapsed our data across the three AMB phase-coherence levels and modeled events at the onset of these stimuli. Variance that could be explained by the previous measurements was excluded using an autoregressive AR(1) model and movement-related variance was accounted for by the spatial parameters resulting from the realignment procedure. The resulting regressors were fitted to the observed functional time series.

For reporting, stereotaxic MNI coordinates were converted into Ta-

FIG. 1. A: procedures and example stimuli. Timeline depicts the adaptor stimuli (either face, hand, or Fourier-scrambled image) and examples of the test stimuli (composite hand-face stimuli; see METHODS). B: behavioral adaptation effects. Percentage of trials endorsed as faces for the unambiguous hand, ambiguous stimuli, and unambiguous face. Results are shown for the Control condition (i.e., following adaptation to Fourier stimulus), for the Face Adapt (after adaptation to a face [FaceA]), and for the Hand Adapt (after adaptation to a hand [HandA]) conditions. C: the average response latencies for the ambiguous stimuli (AMB) during trials judged as faces (gray) and for trials judged as hands (black).
lairach (TAL) space using Wake Forest University Pickatlas (WFU-Pickatlas, version 1.02; Maldjian et al. 2003).

The peak of the event-related averages in a window from 5.1 to 6.8 s was used as an estimate of the magnitude of the response and averaged across observers. First, we performed a three-way ANOVA for each area with hemisphere (2), adaptation condition (3 levels: Cont, FaceA, and HandA), and perceived category (2 levels: face and hand) for each area. Since this analysis led neither to a significant effect of hemisphere [FFA: \(F(1,62) = 0.3, P = 0.6;\) OFA: \(F(1,52) = 0.15, P = 0.7;\) and EBA: \(F(1,66) = 1.4, P = 0.24\)] nor to significant interaction of hemisphere with adaptation \([F(2,124) = 1.9, P = 0.15;\) OFA: \(F(2,104) = 0.55, P = 0.58;\) and EBA: \(F(2,132) = 0.01, P = 0.99\)] we averaged the data across the two hemispheres.

To determine whether fMRIs is present, the peak percentage signal change values were compared by two-way ANOVAs [adaptation condition (2 levels: Cont and FaceA or Cont and HandA), perceived category (2 levels: face and hand) separately for FaceA and HandA conditions.

To compare the activity of FFA and EBA we performed an additional analysis. First, we normalized the signal changes for the FaceA and HandA conditions by dividing the percentage signal changes of each condition by the average signal change observed for the preferred unambiguous stimulus of the area during the Control condition. Next, we divided the normalized AMB responses from the FFA with that of the EBA, creating an index that is greater in FFA than that in EBA and <1 if EBA > FFA.

To make the link between the behavioral aftereffect and fMRIs stronger we performed a correlation analysis between the response latencies and the BOLD signal, obtained for the AMB stimuli. For this we first extracted the BOLD signal for each subject, condition, and trial separately. Next, we calculated the appropriate response latencies on those trials. Third, for each adaptation condition we calculated the average reaction times across subjects and trials in eleven 100-ms-long time bins (100–200, 200–300, . . . , 1000–1100, and >1100 ms) and calculated the average BOLD signals of the corresponding bins for each condition. Finally, we correlated the average response latencies with the average BOLD signals for each condition separately.

**RESULTS**

**Behavioral findings**

Whereas subjects reported the composite images with dominant hand information mainly as hands and the images with dominant face information as faces (Fig. 1B), the AMB stimuli were judged on average 49% (±2%) as faces and the remaining time as hands. This suggests that these intermediate stimuli have equal sensory evidences for the two stimulus categories and are indeed ambiguous to category decisions.

Adaptation led to category-specific aftereffects for the AMB stimuli [main effect of adaptation: \(F(2,189) = 31, P = 0.00001;\)] with significantly more trials judged as hands after FaceA and more trials judged as faces after HandA (Fig. 1B). This shows that prolonged adaptation to a complex stimulus leads to category-specific aftereffects during the perception of ambiguous stimulus composites.

The average response latencies of subjects (Fig. 1C) were analyzed by a two-way ANOVA with adaptation condition (3) and response (2: face or hand) as within-subject factors for the AMB stimuli. The lack of main effect of adaptation condition \([F(2,39) = 0.31, P = 0.7]\) suggests that, on average, the subjects used similar response strategies during Cont, FaceA, and HandA. However, we observed a significant interaction between the behavioral response latencies and the adaptation condition \([F(2,39) = 13.4, P = 0.00004;\)] which was due to the fact that response latencies were shorter for trials when the face or hand adaptors biased categorization toward the opposite category than for trials when it was not strong enough to change the subject’s decision (Scheffé post hoc analysis: \(P = 0.002\) and \(P = 0.0006\) for FaceA and HandA, respectively). No such response-dependent latency differences were observed, however, during Cont (\(P = 0.89\)).

**fMRI findings**

Because the use of functional localizers is intensively debated in the literature (Friston et al. 1996), we determined the magnitude of the category-selective responses in FFA, OFA, and EBA in an unbiased way. For this we compared the signal obtained for the unambiguous face and hand images during the experimental event-related scans, which are independent of the functional localizer scans, used for defining the position of the areas (for a discussion of the question of independence see Poldrack and Mumford 2009; E. Vul et al. 2009). Supplemental Fig. S1 shows that the selected areas are indeed category selective: both FFA and OFA show larger responses for the unambiguous faces, whereas EBA shows larger responses for the unambiguous hands.\(^1\)

Our behavioral results suggest that the AMB stimuli contain the same amount of stimulus-specific information about faces and hands. Since we were interested in the neural correlates related to the adaptation-induced aftereffects of such stimuli here we just present fMRIs data regarding the AMB stimuli. Figure 2A shows the average time course of FFA activity plotted as a function of time in Cont, FaceA, and HandA, separately for trials categorized as faces and as hands. The averaged peak responses in the FFA are shown in Fig. 2B. Similar to previous studies (Furey et al. 2006; Hasson et al. 2001; O’Craven et al. 1999) we have found that during the Cont condition the BOLD signal was significantly larger for trials perceived as faces than as hands [one-way ANOVA with perceived category as within-subject factor: \(F(1,59) = 4.4, P = 0.04\)].

FaceA led to a significant decline in activity compared with the Cont condition [main effect of adaptation: \(F(1,59) = 46, P = 0.0001;\)] Surprisingly, however, the observed fMRIs was more pronounced for trials when subjects perceived the AMB stimuli as hands compared with when they perceived them as faces [interaction of adaptation condition and perceived category: \(F(1,59) = 11, P = 0.002\)]. This shows that the effects of fMRIs in FFA are larger for trials when FaceA biases categorization toward the opposite category than for trials when it was not strong enough to change the subject’s decision. Although HandA also led to a significant fMRI effect in FFA [main effect of adaptation: \(F(1,59) = 19, P = 0.0001\)], this reduction in activity was smaller when compared with FaceA [main effect of adaptation with FaceA and HandA and face/ hand responses as factors: \(F(1,59) = 6, P = 0.02\)] and it was independent of the perceived category [interaction of Cont and HandA conditions and perceived category: \(F(1,59) = 3, P = 0.1, n.s.\)].

Correlation analysis (see Methods) of the response latencies and BOLD signal of the FFA revealed that the smaller the

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\(^{1}\) The online version of this article contains supplemental data.
BOLD signal in the FFA (or in other words, the larger the fMRIa) during FaceA, the shorter the response latency of the subjects ($R = 0.5$, $P < 0.02$). No significant correlations were observed during Cont ($R = 0.3$, $P = 0.1$) and HandA ($R = 0.2$, $P = 0.4$).

We found similar results in the EBA (Fig. 2, C and D). Exposure to the optimal stimulus of the area (a human hand during HandA) led to a significant signal adaptation as well in EBA [main effect of adaptation condition: $F(1,59) = 16$, $P = 0.0002$]. Again, the reduction in activity depended on the perceived category of the test stimulus [interaction of the adapting and perceived category: $F(1,59) = 19$, $P = 0.00004$]; it was significantly larger for trials categorized as faces (or in other words when HandA led to a category-specific aftereffect) compared with trials categorized as hands, without observed aftereffect.

Correlation analysis of the response latencies and BOLD signal of the EBA revealed that the smaller the BOLD signal in the EBA during HandA, the shorter the response latency ($R = 0.46$, $P < 0.04$). No such correlations were observed during Cont ($R = 0.9$, $P = 0.09$) and FaceA ($R = 0.4$, $P = 0.1$), suggesting the strong connection of EBA activity and behavior during HandA.

We also found differences in the BOLD signal in EBA when compared with FFA. First, the BOLD signal was similar for trials perceived as faces or hands in the Cont condition [one-way ANOVA with perceived category as within-subject factor: $F(1,59) = 0.9$, $P = 0.8$]. This suggests that in EBA, unlike in FFA (Furey et al. 2006; Hasson et al. 2001; O’Craven et al. 1999), the BOLD signal is not larger when the perception of an ambiguous stimulus is shifted toward the preferred interpretation for that area.

Second, unlike in FFA, adaptation to the nonpreferred stimulus (FaceA) did not lead to any fMRIa in EBA; in fact we even observed a slight, nonsignificant increase of the signal [main effect of adaptation: $F(1,59) = 2$, $P = 0.1$]. This would suggest that the EBA is more category selective than the FFA.

Occipital face area (OFA) showed a significantly larger BOLD signal for trials in which subjects perceived the ambiguous stimuli as faces rather than as hands [one-way ANOVA with perceived category as within-subject factor: $F(1,53) = 4.1$, $P = 0.05$] in the Cont condition.

We also observed significant fMRIa in OFA after both types of adaptation but the signal decrease in OFA, unlike that in FFA and EBA, was independent of the perceived category of the stimulus (for details see Supplemental Fig. S2).

To analyze our results further we compared the relative activity ratio of FFA and EBA separately for the two adapted conditions and for the trials perceived as faces or hands. First, we normalized the responses of both areas and next we divided the normalized AMB responses from the FFA with that of the EBA (for details see METHODS). The created index is $>1$ if the relative activity is greater in FFA than that in EBA and $<1$ if EBA $> FFA$. The index is similar during FaceA and HandA if adaptation did not bias perception (trials perceived as faces during FaceA and trials perceived as hands during HandA). However, the index is significantly different for those trials when adaptation led to a shift in the response category (i.e., to the category opposite that of the adapting stimulus; Fig. 3). We hypothesized that if these two areas play a significant role in the biased decisions during adaptation aftereffects, then their relative activity should be significantly different for trials when FaceA and HandA biased decisions toward opposite categories, whereas it should be similar for trials when the aftereffects of adaptation were not observed. Indeed, this is what we have found: the FFA/EBA index was significantly larger for trials perceived as faces following HandA than that for trials perceived as hands after FaceA. On the other hand, no such difference was observed during trials without aftereffects (face trials during FaceA and hand trials during HandA).
suggests that adaptation aftereffects are the direct result of the altered activity of category-specific occipitotemporal areas.

Whole-brain analyses

To test whether other areas reflect the adaptation processes as well, we also performed a whole-brain random-effects analysis for the AMB stimuli during Cont > FaceA, FaceA > Cont, and during Cont > HandA and HandA > Cont. These contrasts led to no significant activations in additional brain regions even at the liberal threshold of $P_{uncorrected} < 0.001$.

Finally, to test whether there is any other area that reflects the perceptual judgments for the AMB stimuli we also compared the BOLD signal obtained during trials judged as faces versus hands for each adaptation condition separately.

In the Cont condition no areas showed a differential BOLD signal for face and hand judged trials. However, in the FaceA condition (Fig. 4, A and E, top) we observed higher activations during trials judged as faces when compared with trials judged as hands ($P_{corrected} < 0.001$) in an area at the anterior cingulate cortex (ACC; 4, 34, 46) and in the anterior part of right insula (42, 24, 0). Surprisingly, the same two areas were also activated ($P_{corrected} < 0.005$) in the HandA condition (Fig. 4, A and E, bottom), but only for the opposite contrast (hand responses > face responses; anterior cingulate: 6, 28, 38, anterior insula: 44, 20, −2).

These results were confirmed by the imaging data extracted from a spherical ROI ($r = 10 \text{ mm}$) centered on the peak voxel from these ROIs (Fig. 4, B and F): BOLD responses were modulated by the percept both in FaceA ($t$-test for the peak activations between face and hand responses for both ACC and right insula: $P < 0.005, t > 3.2$) and HandA ($P < 0.03, t < −2.4$) conditions, whereas no such differences were observed in Cont ($P > 0.3, t < 1.12$).

These results suggest that the percept reported by the subjects is associated with the response in these regions, which is similar to that found for the FFA during FaceA and to that found for the EBA during HandA. To test this relationship we performed a correlation analysis on the peak activations of these areas across subjects and adaptation conditions and responses. We found that the activity of both FFA and EBA correlated positively with both ACC and right insula and these correlations were significant (Fig. 4, C and D and G and H; $P < 0.001$ for each correlation). These positive correlations suggest that the ACC and the right insula are involved in the same aspect of the perceptual decision process.

Discussion

Adaptation to a face or hand stimulus biased the categorization of subsequent ambiguous face/hand composite stimuli toward the opposite category. Our results show, for the first time, that prolonged adaptation to a complex stimulus leads to category-specific aftereffects during the perception of ambiguous stimulus composites. Although such stimulus composites have been used to study mechanisms of selective object-based attention (Furey et al. 2006; O’Craven et al. 1999) and decision making (Philliastides and Sajda 2006; Philiastides et al. 2006), we are not aware of any study showing that adaptation to high-level stimuli leads to the bias in category discrimination of such stimuli. Previous studies of high-level adaptation using continuously varying parameters (point-by-point morphing: Leopold et al. 2001; Rhodes et al. 2003; Webster et al. 2004; changes of viewpoint; Fang et al. 2005; eye-gaze direction: Jenkins et al. 2006) could not test aftereffects for categories more distant in object space (Op de Beeck et al. 2008). Our method makes the study of such category-specific adaptation aftereffects possible. Furthermore, the fact that we observed high-level object category-specific aftereffects, using noisy, ambiguous overlapping face/hand composites as test images supports recent results regarding the effect of adaptation of neurons in higher levels of the visual system as well (Clifford et al. 2007; Watson and Clifford 2003).

The observed fMRI in the face-sensitive FFA (but not in OFA) and in the body-part–sensitive EBA was significantly different for trials when adaptation biased perception and when it was not strong enough to change our decisions. Adaptation to the preferred stimulus of the given area led to larger fMRI during trials when it biased category decisions behaviorally than during trials when it could not overtly affect perception.

These results support recent findings that suggest that the fMRI repetition suppression is modulated by top-down effects (Henson et al. 2000, 2002; Ishai et al. 2004; Yi and Chun 2005). To our knowledge, however, this is the first fMRI study that found evidence for the involvement of category-specific areas in high-level category-specific aftereffects. Recent fMRI studies, using prolonged adaptation similar to that of the present study, have implicated the FFA in face viewpoint adaptation (Fang et al. 2007) and in position-invariant face gender adaptation (Kovács et al. 2008). However, no previous study compared the reduction of BOLD signal during trials with and without measurable perceptual aftereffects. The only study that tested the interaction of adapted and perceived face expressions/identities, using ambiguous face morphs (Furl et al. 2007), failed to find any modulation of the fMRI by the behavioral aftereffects and concluded that adaptation-induced perception is mediated by activity in the medial temporal regions, downstream to the earlier occipitotemporal areas that show signal reductions due to stimulus repetition. This conclusion is not at odds with the results of the present study if one considers that even the adaptation-improved spatial resolution...
(Grill-Spector et al. 1999) of a group-based fMRI study might well exceed the size of cellular patches sensitive to different facial characteristics (Op de Beeck et al. 2008; Tsao et al. 2008). This makes it difficult to disentangle the different face coding neural populations during adaptation. In our study, however, we chose two stimulus categories with cortical loci, which are well separable by standard fMRI methods. This enabled us to detect the perceptual modulation of fMRI signal adaptation and to show that adaptation-induced face/hand category decision biases are mediated by the relative activity of FFA and EBA. On the other hand, the fact that fMRI in OFA was similar after face and hand adaptation and that it was independent of the perceived category suggests that category representation in FFA is downstream to OFA (Fairhall and Ishai 2007).

The whole-brain analysis revealed that the ACC and right insula show similar adaptation condition \times behavioral response interaction to that of the FFA and EBA (Fig. 4). Both ACC and insula have previously been implicated in repetition-related decision processes (Maccotta and Buckner 2004; Wig et al. 2005). In a recent study Xu et al. (2007) found that the activity of these two areas mirrored the behavioral response pattern of subjects in two repetition-related tasks: they showed larger responses for the less similar than the very similar images in a scene-matching task, whereas a lower response for the less similar than the very similar images in an image-discrimination task, suggesting the correlation of fMRI and perceptual decisions in the frontal cortex and insula. Our results support this conclusion but also suggest that, at least
during adaptation-induced aftereffects, the occipitotemporal category-specific areas show similar perceptual modulations.

The response-dependent differential adaptation effect was not present after adaptation to the nonpreferred stimulus: fMRIs after hand adaptation was similar when the stimulus was categorized as face or hand in FFA, whereas no signal reduction was observed in EBA as a result of face adaptation.

These results have implications regarding the current debate if neural response selectivity and the selectivity of neural adaptation are similar or different. Results of macaque inferior temporal cortex, for example, suggest that as long as a stimulus activates a neuron it also will lead to adaptation, but this neuronal adaptation has greater selectivity than the response of the corresponding neuron (Sawamura et al. 2006). Our results agree with these single-cell data, in the sense that both the preferred and nonpreferred stimuli of the area cause signal reduction in FFA, but this reduction in activity is smaller for the nonpreferred adaptor. Moreover, in EBA we have not observed any adaptation for the nonpreferred adaptor, a stimulus that clearly activates the area (for results from OFA, see Supplemental Fig. S2). This suggests that the FFA is less category selective than the EBA. Indeed, recent results suggest that there is a body-selective area in the human fusiform gyrus (fusiform body area [FBA]; Peelen and Downing 2005; Schwarzlose et al. 2005), overlapping with FFA (average Talairach coordinates: 38, −41, −17; Taylor et al. 2007).

Since in our study we made no attempt to separate FFA from EBA it is possible that the fMRIs affect for the nonpreferred (hand) adaptor is due to the existence of body-part–selective neurons in FFA, an explanation requiring further studies. An alternative hypothesis would be that FaceA and HandA cause BOLD signal saturation in EBA that is larger for the preferred adaptor stimulus of the area. However, the fact that there is a significant difference in BOLD signal during HandA between face- and hand-perceived trials argues against this explanation. Altogether, our results agree with the conclusion that the selectivity of fMRIs effects reflects the underlying neural selectivity more faithfully than the stimulus-specific variations of the BOLD signal.

Recent findings suggest that the spontaneous prestimulus variations in the activity of the FFA (Hesselmann et al. 2008a,b) have an impact on decisions. Such fluctuations of the ongoing activity, just like the stimulus-evoked activations of the present study, are correlated with the judgments of ambiguous stimuli. Thus one possible account of the present results would be that the observed perceptual modulations of the FFA and EBA responses are simply due to the decision-related prestimulus signal fluctuations.

However, recent results suggest that the spontaneous variations of the prestimulus signal and the perceptual modulation of the stimulus-evoked activations do not reflect a single decision-related effect, extending from prestimulus baseline activity until poststimulus responses. Rather, the existence of independent contributions of prestimulus and evoked response modulations to perceptual decisions has been suggested (Hesselmann et al. 2008a). This means that the current results cannot simply be assigned to prestimulus ongoing signal fluctuations. Nevertheless, our current design was aimed at studying the effects of the aftereffect of adaptation on the BOLD signal, manifest in the stimulus-evoked responses. Such experimental designs of adaptation aftereffects (Fang et al. 2007; Furl et al. 2007; Kovács et al. 2008), because of the frequent and long-term presentation of adaptor stimuli, are not ideal to study ongoing spontaneous activity fluctuations, which usually require prolonged periods of rest (Fox and Raichle 2007; Fox et al. 2007). Thus the exact relationship between adaptation aftereffects and the fluctuations of spontaneous activity will require further investigation.

Recently, Summerfield et al. (2008) showed that the repetition-related fMRIs of FAA depends on the expectation of the subjects: it was larger when subjects expected repeated stimuli than when they did not. Thus it would be possible that the fMRIs differences observed in FAA and EBA between FaceA and HandA are due to the different probability of the responses and to the different expectations of the subjects. Indeed, during FaceA and HandA subjects perceived the AMB stimuli predominantly either as hands or faces, respectively, in which cases fMRIs was smaller than that during the more frequently occurring responses. However, there is one major difference between the Summerfield et al. (2008) and our own study: whereas in their case the repetition of the stimuli was more or less frequent, in our case the probability of the actual physical stimulus presentation was identical and only the frequency of a given response varied as a consequence of adaptation. Nevertheless, the possible connection between adaptation aftereffects and expectation (and in general predictive coding) is an exciting issue that requires further studies.

Our results also provide direct evidences of the two-pool model of high-level adaptation (Robbins et al. 2007), originally described for low- and midlevel features (Regan and Hamstra 1992). According to this model, two broadly tuned, overlapping neuronal populations code in an opponent fashion the stimulus space and adaptation cause each pool to decrease its activity in proportion to the strength of the unadapted response to the adapting stimulus: FaceA would therefore decrease the activity more in FAA than in EBA, whereas HandA would decrease more in EBA than in FAA. Indeed, this finding has been demonstrated in Fig. 4 for trials when aftereffects are observed. The role of FAA and EBA in category-specific adaptation aftereffects is also emphasized by the fact that the response latencies correlated significantly with the BOLD signal in FAA and EBA when adapted with the preferred stimulus of the area.

In summary, our results show that the fMRI signal adaptation, caused by the prolonged exposure of the preferred stimulus of FAA and EBA, is larger for trials when behavioral aftereffects are observed compared with trials without the aftereffect. Our results suggest that high-level category-specific adaptation aftereffects are based on the activity of category-sensitive occipitotemporal areas.

GRANTS

This work was supported by European Union Information Systems Technology Cognitive Systems Project 027198 (“Decisions in Motion”), Deutsche Forschungsgemeinschaft Grant KO 3918/1–1, Deutscher Akademischer Aus- tauschdienst Grant DAAD-MöB/821, and Hungarian Scientific Research Fund Grant T049467 to G. Kovács.

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