Spatiotemporal characteristics of form analysis in the human visual cortex revealed by rapid event-related fMRI adaptation

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The integration of local elements to coherent forms is at the core of understanding visual perception. Accumulating evidence suggests that both early retinotopic and higher occipitotemporal areas contribute to the integration of local elements to global forms. However, the spatiotemporal characteristics of form analysis in the human visual cortex remain largely unknown. The aim of this study was to investigate form analysis at different spatial (global vs. local structure) and temporal (different stimulus presentation rates) scales across stages of visual analysis (from V1 to the lateral occipital complex—LOC) in the human brain. We used closed contours rendered by Gabor elements and manipulated either the global contour structure or the orientation of the local Gabor elements. Our rapid event-related fMRI adaptation studies suggest that contour integration and form processing in early visual areas is transient and limited within the local neighborhood of their cells' receptive field. In contrast, higher visual areas appear to process the perceived global form in a more sustained manner. Finally, we demonstrate that these spatiotemporal properties of form processing in the visual cortex are modulated by attention. Attention to the global form maintains sustained processing in occipitotemporal areas, whereas attention to local elements enhances their integration in early visual areas. These findings provide novel neuroimaging evidence for form analysis at different spatiotemporal scales across human visual areas and validate the use of rapid event-related fMRI adaptation for investigating processing across stages of visual analysis in the human brain.
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Prompt and successful recognition of objects in our complex environments entails that we extract information about their properties and interpret their shape structure. Understanding the analysis of shape properties by the visual system and characterizing their representations have been the central goal for theoretical

(Riesenhuber and Poggio, 2000), neurophysiological (Logothetis and Sheinberg, 1996) and imaging (Grill-Spector, 2003) approaches to visual recognition. Traditional approaches of visual processing (Maunsell and Newsome, 1987; Felleman and Van Essen, 1991; Van Essen et al., 1992) suggest that the analysis of local image features involves early visual areas (i.e. striate and extrastriate retinotopic regions), while higher visual areas (i.e. regions in the inferotemporal cortex) mediate the perception and recognition of global shapes. Recently, there is accumulating evidence that early visual areas may also respond to global rather than simple local features (Allman et al., 1985; Gilbert, 1992, 1998; Lamme et al., 1998; Fitzpatrick, 2000). Our recent fMRI studies (Altmann et al., 2003; Kourtzi et al., 2003b) provide evidence that both early and higher occipitotemporal visual areas are involved in the integration of local elements to global forms. However, the spatiotemporal characteristics of form analysis in early and higher visual areas in the human brain remain largely unknown. The aim of this study was to investigate the contribution of early and higher visual areas to form analysis at different spatial (global vs. local structure) and temporal (different stimulus presentation rates) scales.

To address these questions, we used human fMRI. We employed a rapid event-related adaptation paradigm in which decreased responses are observed in trials where the same stimulus is presented repeatedly compared with trials in which two different stimuli are presented sequentially (Kourtzi and Kanwisher, 2000, 2001). This technique (Schacter and Buckner, 1998; Wiggs and Martin, 1998; Grill-Spector and Malach, 2001; Henson, 2003; Henson and Rugg, 2003) capitalizes on neural adaptation (Carandini et al., 1997; Lisberger and Movshon, 1999; Mueller et al., 1999) or repetition suppression (Miller et al., 1991; Li et al., 1993; Desimone, 1996) effects whereby neural activity is lower for stimuli that have been viewed recently than for stimuli that have not. By comparing the adapted response evoked by the same stimulus shown twice with increased responses (rebound effect) evoked by two different stimuli in a trial, we can deduce sensitivity in the neural populations to changes between stimuli. fMRI adaptation paradigms have been used extensively (Tootell et al., 1995, 1998; Buckner et al., 1998; Grill-Spector et al., 1999; Engel

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and Furmanski, 2001; Huk et al., 2001; Naccache and Dehaene, 2001; Avidan et al., 2002; Vuilleumier et al., 2002; Rotshtein et al., 2005) as a powerful tool for studying neuronal populations beyond the limited spatial resolution of the conventional fMRI paradigms that average across populations which may respond differentially to different stimulus attributes.

Our stimuli consisted of global closed contours that were rendered by Gabor elements. Such displays yield the perception of global figures (Fig. 1) and are thought to emerge from the integration of oriented local elements into global configurations (Field et al., 1993; Kovacs and Julesz, 1993, 1994; Hess et al., 2003). Our previous studies have shown that analysis of this type of stimuli involves both early retinotopic areas (V1, V2, Vp, V4) and the lateral occipital complex (LOC), a region in the lateral occipital cortex extending anterior in the temporal cortex (Fig. 2) that is thought to be involved in the analysis of object shape (Malach et al., 1995; Kanwisher et al., 1996) and processes of object recognition (Grill-Spector et al., 2000; Bar et al., 2001). In this study, we tested form processing at different spatiotemporal scales in these early and higher visual areas. In particular, in Experiment 1, we tested sensitivity to form changes in both early and higher visual areas by presenting stimuli with the same or different global contours in a trial. We examined the temporal characteristics of form processing in these areas by manipulating the temporal interval between the two stimuli presented in a trial. In Experiment 2, we investigated form processing at different spatial scales by testing sensitivity to local orientation changes compared to global contour changes. Our findings showed sensitivity for changes in form contours in both early and higher visual areas, suggesting that these areas are involved in the processing of shape features. However, differences in the spatiotemporal properties of processing in early and higher visual areas suggest a differential contribution of these regions in form analysis. That is, early visual areas encode local form information in a transient manner, whereas higher visual areas are involved in sustained processing of the perceived global shape. Finally, our findings suggest that attention modulates these spatiotemporal properties of perceptual integration in the visual cortex. That is, attention to the global form maintains sustained processing in occipitotemporal areas, whereas attention to local elements enhances their integration in early visual areas.

Materials and methods

Observers

Twelve observers participated in Experiment 1 and fifteen in Experiment 2. Four observers were excluded from the analysis in Experiment 2 due to excessive head movement. All observers had normal or corrected to normal vision, were paid for participation and gave their informed consent.

Stimuli

In Experiment 1, observers were presented with closed contours rendered with Gabor elements; that is, oriented sinusoidal luminance features with Gaussian envelopes that model roughly the RF structure of V1 simple cells. The elements were aligned along the contours (co-aligned), as described in previous studies (Kovacs, 1996; Braun, 1999; Altmann et al., 2003; Kourtzi et al., 2003b) (Fig. 1a). The contours covered an average area of $6° \times 6°$ and were presented on a mean luminance gray background. We used seventy-eight different contours with Gabor size of 0.25° and 0.30° distance between neighboring Gabor elements.

In Experiment 2, observers were presented with symmetrical contours that were rendered with Gabor elements of the same orientation and parallel to each other (co-oriented) but that were not aligned along the contour (Fig. 1b). These stimuli allowed us to independently manipulate the form structure at the local (orientation of Gabor elements) and global (global contour) level. In particular, in Experiment 1, changes in the global contour resulted in small changes in the local orientation of the local elements. However, in Experiment 2, different global contours were rendered with Gabor elements of the same orientation. For each presentation of a shape, the Gabor elements were presented at the same position in one of twelve possible orientations (0°, 15°, 30°, 45°, 60°, 75°, 90°, 105°, 120°, 135°, 150°, 165°). Furthermore, each contour was rotated at six different orientations along its axis of symmetry (15°, 45°, 75°, 105°, 135°, 165°). We used twenty-four different shapes (each presented at six orientations and rendered at twelve Gabor orientations) with 0.5° Gabor size and 0.5° distance between two neighboring Gabor elements, as in previous studies (Kourtzi et al., 2003b). The shapes covered an average area of $8.9° \times 8.9°$ and were presented on a mean luminance gray background.
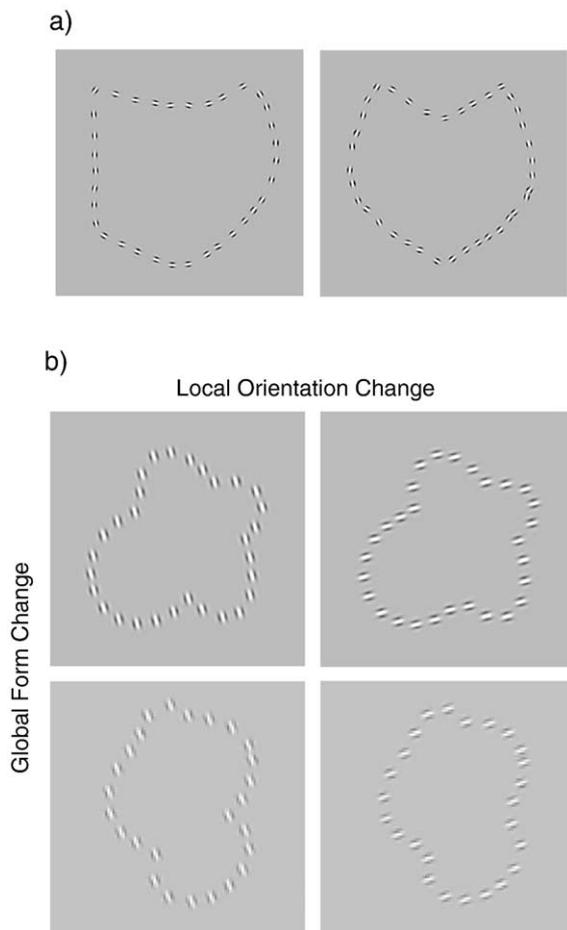

Fig. 1. Stimuli. Examples of stimuli used in (a) Experiment 1: two sample stimuli, and (b) Experiment 2: examples of local orientation change and global form change. Seventy-eight stimuli were used in Experiment 1 and twenty-four in Experiment 2. All stimuli were matched for the covered area.
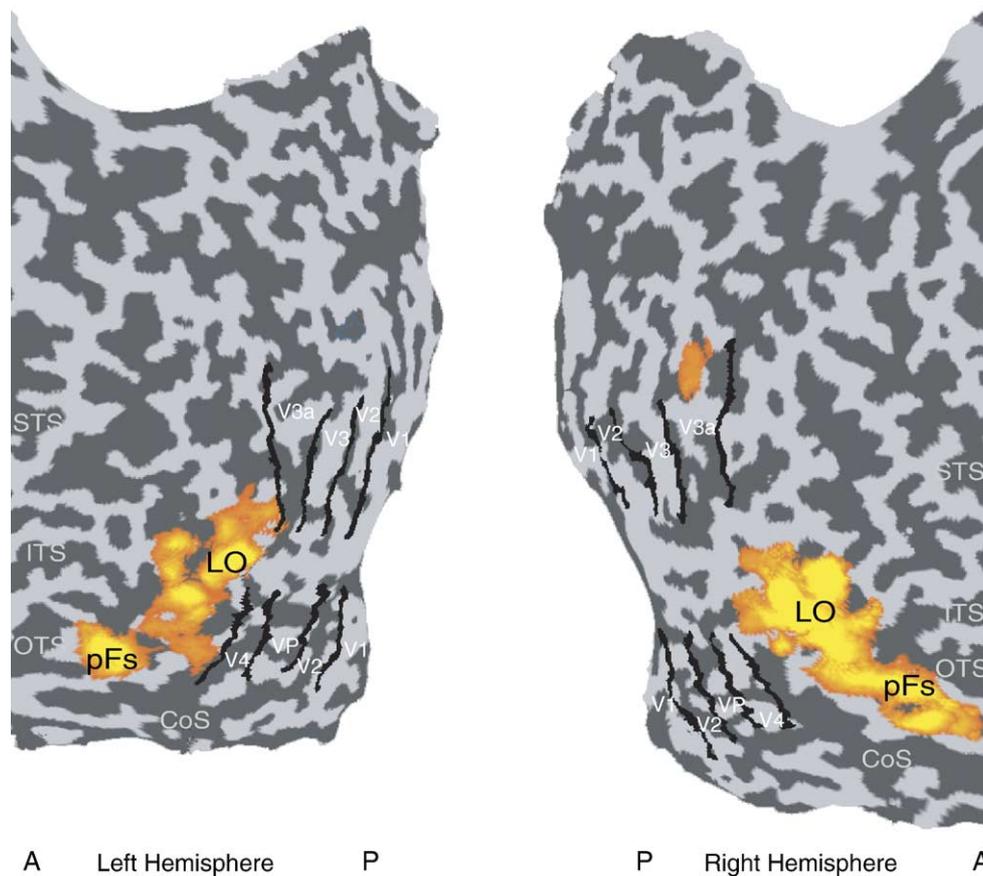
Fig. 2. Regions of interest. Functional activation maps for one subject showing the early retinotopic ventral (V1, V2, VP, V4) and dorsal (V1, V2, V3, V3a) areas and the LOC. The LOC was defined as the set of all voxels in the ventral occipitotemporal cortex that were activated more strongly ($P < 10^{-4}$) by intact than scrambled images of objects. Two subregions of the LOC were identified: the LO (lateral occipital) at the posterior part of the inferior–temporal sulcus and the pFs (posterior fusiform) in the posterior fusiform gyrus. Functional activations are superimposed on flattened cortical surfaces of the right and left hemispheres. A: anterior, P: posterior, STS: superior temporal sulcus, ITS: inferior temporal sulcus, OTS: occipitotemporal sulcus, CoS: collateral sulcus.

For the LOC localizer scans, we used grayscale images of novel and familiar objects as well as scrambled versions of each set, as described previously (Kourtzi and Kanwisher, 2001). For mapping the borders and the eccentricity of the retinotopic visual areas, we used rotating triangular wedge stimuli and concentric rings, respectively. These stimuli consisted of either gray-level natural images or black and white objects-from-texture images that were presented at temporal frequency of 2 Hz as described in previous studies (Grill-Spector et al., 1998).

Design and procedure

For each experiment, observers participated in four event-related scans for the experiment, two LOC localizer scans and two retinotopic mapping scans. The order of the scans was counterbalanced across observers. Before the scanning session, the observers participated in a practice session during which they were familiarized with the types of stimuli used in the experiment.

The event-related scans consisted of 25 trials per experimental condition and 25 fixation trials that were interleaved with the experimental trials. Each scan started with a 16-s fixation epoch and ended with an 8-s fixation epoch. As in previous studies (Kourtzi and Kanwisher, 2000, 2001), the order of trials was counterbalanced so that trials from each condition, including the

fixation condition, were preceded (2 trials back) equally often by trials from each of the other conditions. Each trial lasted 3 s and consisted of two sequentially presented stimuli.

In Experiment 1, we tested trials in which the two consecutively presented stimuli had the same (Identical Stimulus) or different shape (Different Stimulus) and manipulated the temporal interval between the stimuli (ISI: inter-stimulus interval). Each trial consisted of the first stimulus presented for 300 ms followed by a blank screen (ISI) for 100 or 400 ms and then a second stimulus that was presented for 300 ms. A blank screen (inter-trial interval) was then presented for 2300 ms or 2000 ms, depending on the duration of the ISI. Thus, the observers were tested in four conditions: (a) Identical Stimulus-Short ISI, (b) Different Stimulus-Short ISI, (c) Identical Stimulus-Long ISI and (d) Different Stimulus-Long ISI. Observers were instructed to report via button presses whether the two shapes presented in a trial were the same or different.

In Experiment 2, each stimulus was presented for 300 ms with a 65 ms inter-stimulus interval (ISI) followed by a blank interval of 2335. This brief ISI was chosen based on the results of Experiment 1 that showed stronger adaptation effects for an ISI of 100 than 400 ms. Observers were tested in four conditions in which the two stimuli in a trial had: (a) the same global shape and were rendered with Gabors at the same orientation (Identical), (b) the same global shape but differed at the orientation (90°) of their Gabor elements (Different Local Orientation), (c) a different global shape but were

rendered with Gabor elements at the same orientation (Different Global Form) and (d) a different global shape and were rendered with Gabors at a different orientation (90°) (Different Local Orientation and Global Form). The different contours presented in the Different Global Form and the Different Local Orientation and Global Form conditions differed also in the orientation (90°) of their symmetry axis. Observers performed a matching task on the symmetry axis of the contours (same or different orientation) or on the orientation of the local Gabor elements. Analysis of the behavioral data suggests that both global form and local orientation changes were visible and observers attended and performed both tasks successfully across all conditions. Accuracy performance in the global form matching task across conditions was: Identical: 97.3%, Different Local Orientation: 98.8%, Different Global Form: 98.3%, Different Local Orientation and Global Form: 92.6%. Accuracy performance in the local orientation matching task across conditions was: Identical: 86.7%, Different Local Orientation: 87.3%, Different Global Form: 85.6%, Different Local Orientation and Global Form: 86.2%.

For the LOC localizer scans, each stimulus condition (grayscale images of novel and familiar objects as well as scrambled versions of each set) was presented in a 16-s stimulus epoch (blocked design), as previously described (Kourtzi and Kanwisher, 2000). Observers performed a 1-back matching task that engaged their attention on all the stimulus types, i.e. both the intact and the scrambled images of objects. For the retinotopic mapping scans, eight wedge positions and eight eccentricity rings were presented each for 8 s and repeated eight times. Observers performed a dimming task (detection of luminance changes) on the fixation presented at the center of the display.

Imaging

The experiments were conducted in a 3T Siemens scanner at the University Clinics, Tübingen. Data were collected with a head coil from 11 axial ($3 \times 3 \times 5$ mm^3) slices that covered occipitotemporal regions using Gradient Echo pulse sequences (TR = 1 s, TE = 40 ms for the event-related scans; TR = 2 s, TE = 90 ms for the localizer scans).

Data analysis

fMRI data were processed using the Brain Voyager software package. Preprocessing of all the functional data included head movement correction, temporal filtering of high frequencies and removal of linear trends. The 2D functional images were aligned to 3D anatomical data, and the complete data set was transformed to Tailarach coordinates. Anatomical data were additionally inflated and unfolded.

For each individual observer, we identified the LOC and the early retinotopic areas along the ventral pathway (V1, V2, Vp, V4) as regions of interest (ROI) (Fig. 2). 3D statistical maps were calculated for each of these ROIs by correlating the signal time course with a reference function for each voxel based on the hemodynamic response properties (Boynton et al., 1996; Cohen, 1997). The LOC was defined as the set of voxels in the ventral occipitotemporal cortex that showed significantly stronger activation ($P < 10^{-4}$, corrected) to intact than scrambled images based on the averaged data of the two localizer scans. Two separate LOC subdivisions were identified as described in previous studies (Grill-Spector et al., 1999): a posterior lateral occipital region (LO) and

an anterior region in the posterior fusiform gyrus (pFs) (Fig. 2). Early visual areas (V1, V2, Vp, V4) were identified based on standard retinotopic mapping procedures (Sereno et al., 1995; DeYoe et al., 1996; Engel et al., 1997). Additionally, a subregion that matched the area covered by the experimental stimuli was localized within the retinotopic areas.

For each observer, we extracted fMRI responses by averaging the data from all the voxels within each of the independently defined ROIs in the event-related scans. In each scan, we averaged the signal intensity across all the trials in each condition at each of 10 corresponding time points (seconds). We then calculated the fMRI response in each condition as the percent signal change from the fixation baseline, as described previously (Kourtzi and Kanwisher, 2000, 2001). Finally, we averaged these time courses across scans and observers. As the hemodynamic response function peaks several seconds after the onset of the stimulus, we expected the largest differences across conditions at the peak of this function (Boynton et al., 1996; Cohen, 1997; Dale and Buckner, 1997). We identified the peak of the fMRI responses in each experiment by fitting a Gaussian model (Kruggel and von Cramon, 1999) to the average fMRI responses across observers. This analysis showed similar values for the average peak responses across conditions (Figs. S1, S2). Based on these analyses, we selected time points 3–5 s after the trial onset as the peak points of the hemodynamic response function across ROIs. The data analysis (ANOVAs and contrast analyses, Greenhouse–Geisser corrected) and figures report effects on the average of these fMRI peak responses across subjects for each condition.

Eye movements

To control for differences across conditions in eye movements, we recorded eye movements (from three subjects in Experiment 1 and four in Experiment 2) using an infrared camera system (Eyelink 2.02) while the subjects performed the experiment. These recordings showed no differences across conditions in the mean eye position (Experiment 1: x position: $F(2,6) = 1.22$; $P = 0.37$; y position: $F(2,6) = 2.18$; $P = 0.16$; Experiment 2: x position: $F(3,9) < 1$; $P = 0.93$; y position: $F(3,9) < 1$; $P = 0.65$), the number of saccades (Experiment 1: $F(2,6) < 1$; $P = 0.66$; Experiment 2: $F(3,9) = 1.99$; $P = 0.22$) and the mean saccade amplitude (Experiment 1: x amplitude: $F(2,6) = 1.42$; $P = 0.31$; y amplitude $F(2,6) = 2.08$; $P = 0.1$; Experiment 2: x amplitude: $F(3,9) = 1.49$; $P = 0.28$; y amplitude $F(3,9) < 1$; $P = 0.53$). These controls suggest that it is not likely that our results could be significantly confounded by eye movements.

Results

Experiment 1: fMRI adaptation at different temporal scales

In Experiment 1, we tested the temporal characteristics of fMRI adaptation across visual areas by manipulating the temporal interval between the two stimuli presented in a trial. We observed fMRI adaptation, that is, lower responses for identical than different forms in both early (V1, V2, Vp, V4) and higher (LO, pFs) visual areas as reported previously (Kourtzi et al., 2003a,b). Interestingly, these adaptation effects were observed only for brief temporal delays (100 ms) between stimuli in early visual areas. In contrast, these form adaptation effects were observed for both brief
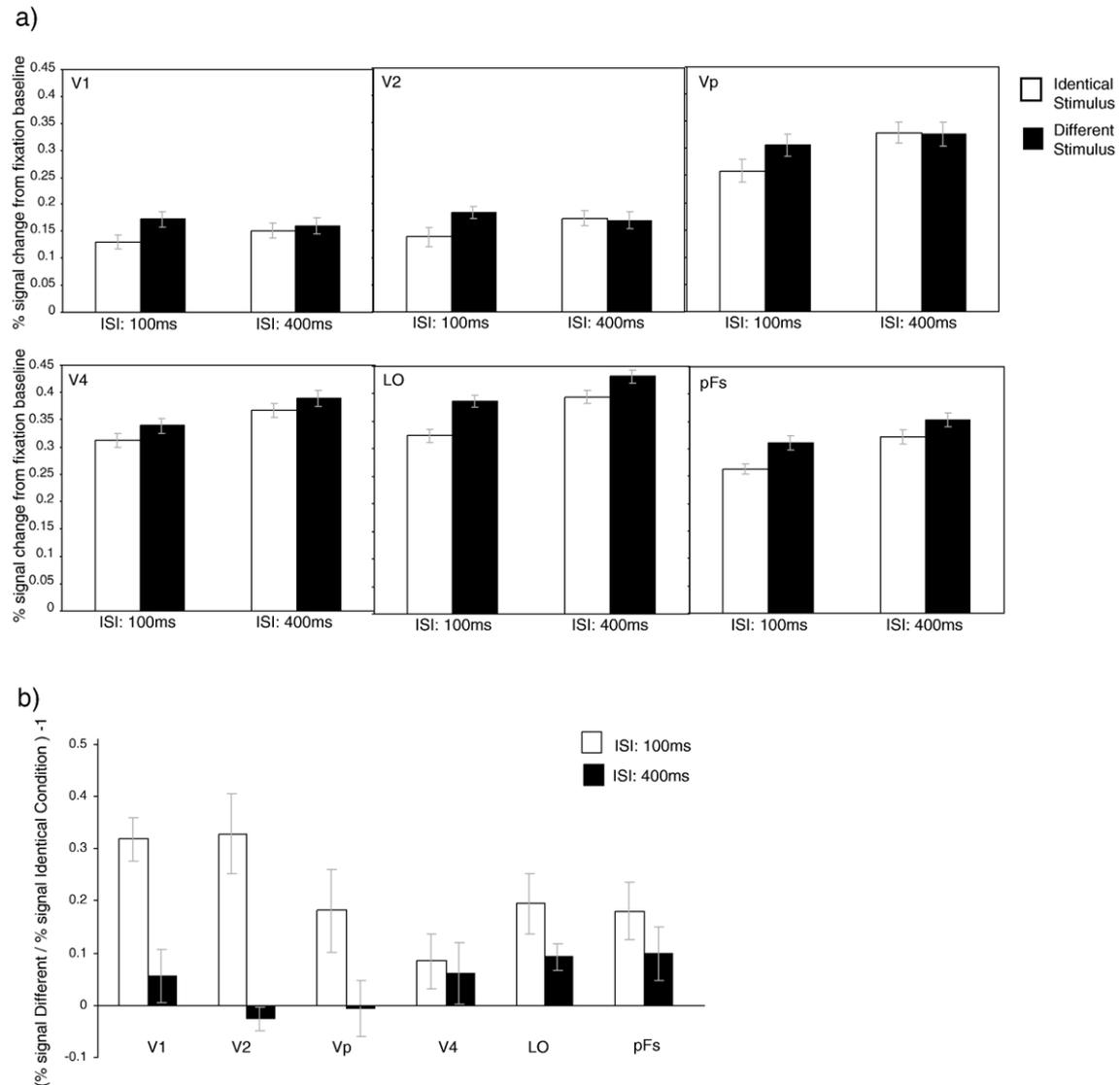
Fig. 3. Results for Experiment 1. (a) fMRI responses (% signal change from fixation baseline) across visual areas for the Identical and Different Stimulus conditions at ISI of 100 and 400 ms. Error bars indicate the standard error of the mean (SEM) across subjects. (b) Rebound effects (% signal change for Different Stimulus condition divided by the Identical Stimulus condition minus 1) across visual areas for ISI of 100 and 400 ms. Zero indicates adaptation, whereas higher responses than zero indicate release from adaptation (rebound). Error bars: SEM across subjects.

(100 ms) and longer (400 ms) temporal delays between stimuli in the LOC subregions (Fig. 3).

Specifically, lower fMRI responses were observed for identical than different forms in a trial, consistent with previous findings (Kourtzi and Kanwisher, 2000, 2001). Additionally, we observed stronger responses for the longer than the brief temporal delays between stimuli. That is, a repeated measures ANOVA for Stimulus (Identical, Different), ISI (100 ms, 400 ms) and ROI (V1, V2, Vp, V4, LO and pFs) showed significant effects of Stimulus ($F(1,50) = 8.774$, $P = 0.01$), ISI ($F(1,50) = 12.465$, $P < 0.01$) and ROI ($F(2,23) = 8.275$, $P < 0.01$). More importantly, we observed significant interactions of ROI and Stimulus ($F(2,28) = 3.34$, $P < 0.05$) and ROI and ISI ($F(2,33) = 8.82$, $P < 0.001$). Contrast analysis showed significantly stronger responses for different than identical forms across all ROIs when the stimuli in a trial were separated by a brief temporal interval: V1 ($F(1,21) = 9.32$, $P < 0.05$), V2 ($F(1,21) = 11.09$, $P = 0.01$), Vp ($F(1,21) = 11.95$, $P = 0.01$), V4 ($F(1,21) = 3.74$, $P < 0.05$), LO ($F(1,21) =$

21.51, $P = 0.01$) and pFs ($F(1,21) = 12.09$, $P < 0.01$). However, significantly stronger responses for different than identical forms for a longer temporal delay between stimuli in a trial were observed only in LO ($F(1,21) = 7.33$; $P < 0.05$) and pFs ($F(1,21) = 5.40$, $P < 0.05$), but not in V1 ($F(1,21) < 1$, $P = 0.36$), V2 ($F(1,21) < 1$, $P = 0.51$), Vp ($F(1,21) < 1$, $P = 0.63$) or V4 ($F(1,21) = 2.71$, $P = 0.12$).

In summary, we observed form adaptation in both early and higher visual areas when the temporal interval between the two stimuli in a trial was brief, whereas adaptation effects for longer temporal separations were observed only in the LOC. Fig. 3b provides a summary of these fMRI adaptation effects at different temporal scales across visual areas. The presented graph depicts release from adaptation as indicated by a rebound index. To obtain this index, we divided the fMRI responses for the Different Stimulus condition by the fMRI responses for the Identical Stimulus condition and subtracted one. Zero indicates adaptation, whereas an index higher than zero indicates neural

sensitivity to changes between the presented form stimuli in the measured visual areas. From the graphs, it is apparent that sensitivity to form changes was more transient in early than higher visual areas; that is, form adaptation for extended temporal delays was observed in the higher but not early visual areas. These findings are consistent with previous imaging studies showing that BOLD decreases for repeated stimulus presentation (Dale and Buckner, 1997; Friston et al., 1998; Huettel and McCarthy, 2000) are stronger for shorter than longer temporal separations between stimuli and differ across areas (Huettel and McCarthy, 2001; Huettel et al., 2004). Furthermore, our findings are consistent with previous neurophysiological studies showing that neural adaptation in V1 cells for rapidly presented and repeated stimuli decreases for delays longer than 100–200 ms (Mueller et al., 1999). Thus, our findings suggest a transient analysis of form features in early visual areas compared to more sustained processing in higher visual areas.

Might the form adaptation effects observed in the early visual areas be due to changes in the local position and orientation of the Gabor elements rather than their global contour? All the seventy-eight stimuli used in the experiment covered the same area and had an average overlap of 92.20% within an area of 1.0° (approximate size of receptive fields in V1 at an eccentricity of 6°), suggesting only very small position differences between shapes. Experiment 2 investigated further the effect of local orientation changes without position changes in the processing of contours in early visual areas.

Attentional control

It could be argued that the decreased fMRI responses observed in the Identical condition were due to the fact that the observers paid less attention when there was no change in the stimulus than in conditions where a stimulus change was present in a trial. Analysis of the behavioral responses of the observers showed that they performed the matching task successfully (Identical Stimulus-Short ISI: 97.7%, Different Stimulus-Short ISI: 98.5%, Identical Stimulus-Long ISI: 95.9%, Different Stimulus-Long ISI: 98.3%) and without any significant differences across conditions ($F(3,30) = 1.73$, $P = 0.21$). To further control for this possible attentional confound, we conducted Experiment 1 with nine additional subjects while they performed a dimming task (detection of luminance changes) on the fixation point. This task was also of similar difficulty across conditions (Identical Stimulus-Short ISI: 95.5%, Different Stimulus-Short ISI: 93.8%, Identical Stimulus-Long ISI: 96.7%, Different Stimulus-Long ISI: 94.2%) and thus entailed similar attentional load across conditions. This experiment replicated the results observed in Experiment 1 (Fig. 4). That is, we observed significantly stronger fMRI responses for different than same forms across early (V1: $F(1,23) = 4.14$, $P = 0.05$, V2: $F(1,23) = 8.61$, $P < 0.01$, VP: $F(1,23) = 31.88$, $P < 0.001$, V4: $F(1,23) = 10.42$; $P < 0.01$) and higher (LO: $F(1,23) = 47.58$; $P < 0.001$ and pFs: $F(1,23) = 13.54$; $P < 0.001$) visual areas. These findings suggest that it is unlikely that the adaptation effects observed in Experiment 1 were confounded by differential attention across conditions. Interestingly, when attention was driven away from the stimulus to a fixation task, adaptation effects were limited to the brief temporal intervals. In particular, a significant interaction ($F(1,45) = 5.60$, $P < 0.05$) between Stimulus (Identical, Different) and ISI (100 ms, 400 ms) indicated adaptation effects for brief ($F(1,45) = 7.42$, $P < 0.05$) but not

longer ($F(1,45) < 1$, $P = 0.56$) temporal intervals between stimuli in a trial across all areas. These findings suggest that sensitivity of neural populations in the visual cortex to global form changes is more transient when attention is focused away from the stimulus; that is, form processing is less sustained under divided attention. These results are supported by a significant interaction between Experiment 1 and this attentional control experiment in the fMRI responses observed across conditions and areas $F(2,16) = 2.32$, $P < 0.05$). These findings are consistent with previous studies (Eger et al., 2004; Murray and Wojciulik, 2004; Rezec et al., 2004) reporting that attention modulates behavioral and fMRI adaptation effects.

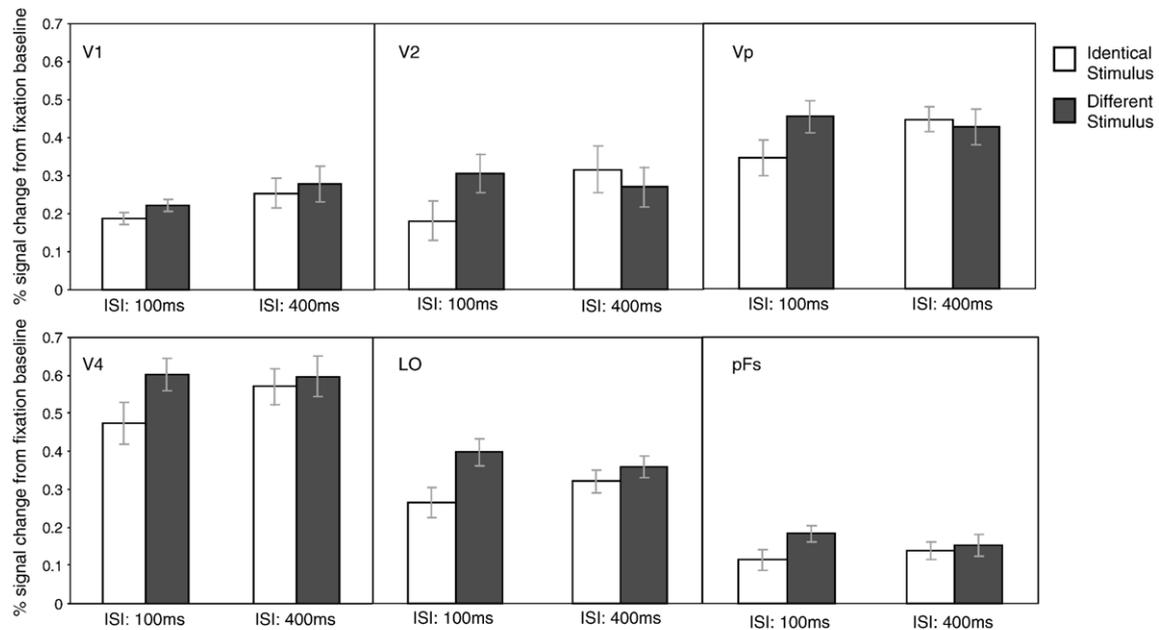### Experiment 2: fMRI adaptation at different spatial scales

In Experiment 2, we investigated fMRI adaptation at different spatial scales by changing either the global form of the stimulus or the orientation of the local Gabor elements or both the global form and the orientation of the local elements without changing their position. As shown in Fig. 5a, we observed release from adaptation (rebound effects) for global form changes in the LOC but not in the early visual areas. In contrast, for local orientation changes, we observed release from adaptation primarily in the early visual areas.

Specifically, a repeated measures ANOVA for Global Form Change (Identical, Different Local Orientation vs. Different Global Form, Different Local Orientation and Global Form), Local Orientation Change (Identical, Different Global Form vs. Different Local Orientation, Different Local Orientation and Global Form) and ROI (V1, V2, VP, V4, LO and pFs) showed a significant main effect of Local Orientation Change ($F(1,11) = 5.42$, $P < 0.05$) and an interaction of ROI and Global Form Change ($F(4,34) = 12.61$, $P < 0.001$). Furthermore, contrast analyses showed significantly stronger responses for stimuli with different than the same local orientation (Local Orientation Change) in V1 ($F(1,21) = 4.36$, $P < 0.05$), V2 ($F(1,21) = 19.14$, $P < 0.01$), Vp ($F(1,21) = 7.26$, $P < 0.05$) and V4 ($F(1,21) = 6.31$, $P < 0.05$), but no significant differences in LO ($F(1,21) = 2.12$, $P = 0.14$) or pFs ($F(1,21) = 1.16$, $P = 0.19$).

Similar analysis showed significantly stronger responses for stimuli with different than the same global forms (Global Form Change) in LO ($F(1,21) = 20.76$, $P < 0.001$) and pFs ($F(1,21) = 10.76$, $P < 0.01$), but no significant differences for global form changes in Vp ($F(1,21) < 1$, $P = 0.385$) or V4 ($F(1,21) < 1$, $P = 0.625$). Interestingly, the opposite pattern of results was observed in areas V1 and V2. That is, we observed significantly stronger responses for stimuli with the same than different global forms (V1: $F(1,21) = 5.55$, $P < 0.05$; V2: $F(1,21) = 25.32$, $P < 0.001$). As shown in Fig. 5a, this effect was due to the stronger fMRI responses observed in these areas for local orientation changes in stimuli with the same than different global form.

In summary, these results suggest sensitivity to local orientation changes across early visual areas, whereas sensitivity to global form changes primarily in the LOC. These findings suggest that early visual areas integrate contour information within local neighborhoods whereas higher occipitotemporal areas (LOC) at global scales, consistent with previous studies (Smith et al., 2002; Kourtzi et al., 2003b). Finally, our results suggest that global form analyses in higher visual areas may influence processing of local features in early stages of visual analyses. These results are consistent with recent theories on predictive coding (Rao and
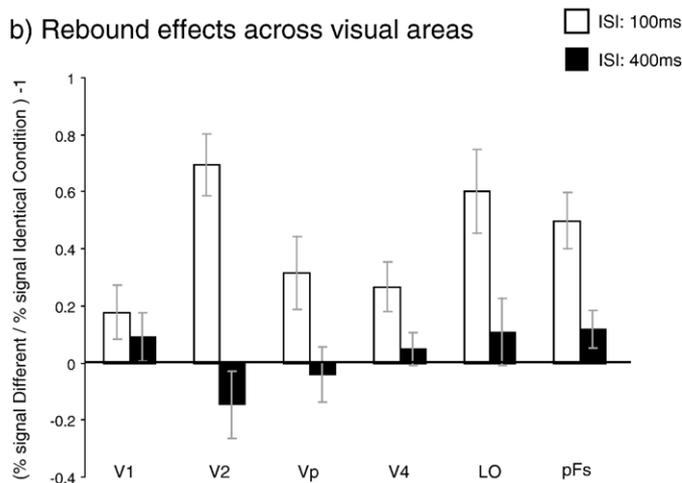
a) fMRI responses across visual areas

Fig. 4. Results for the attentional control experiment. (a) fMRI responses (% signal change from fixation baseline) across visual areas for the Identical and Different Stimulus conditions at ISI of 100 and 400 ms. Error bars: SEM across subjects. (b) Rebound effects (% signal change for Different Stimulus condition divided by the Identical Stimulus condition minus 1) across visual areas for ISI of 100 and 400 ms. Zero indicates adaptation, whereas higher responses than zero indicate release from adaptation (rebound). Error bars: SEM across subjects.

Ballard, 1999; Murray et al., 2002, 2004) suggesting that processing in early stages of visual analysis reflects the residual error after comparison of the physical input to the perceptual interpretation computed in higher areas. This error would be larger when local orientations changes occur in stimuli that have the same than different global form as indicated by the increased fMRI responses in early visual areas observed for the Different Global Form condition.

Attentional control

One possible limitation of this experiment is that the matching task on the orientation of the shape axis of symmetry required that

the observers attended more to the global form than the local elements. It is possible that attention to global forms enhances their representation in the LOC, whereas attention to the local elements could facilitate their integration in the early visual areas. We tested this hypothesis by presenting the observers with the same stimuli as in Experiment 1 but while performing a matching task on the orientation of the local elements.

The results of this experiment showed similar effects for local orientation changes as before. As shown in Fig. 5b, we observed release from adaptation for local orientation changes, primarily in the early visual areas rather than the LOC. In particular, we observed significantly stronger responses for stimuli with different than the same local orientation (Local Orientation Change) in V1
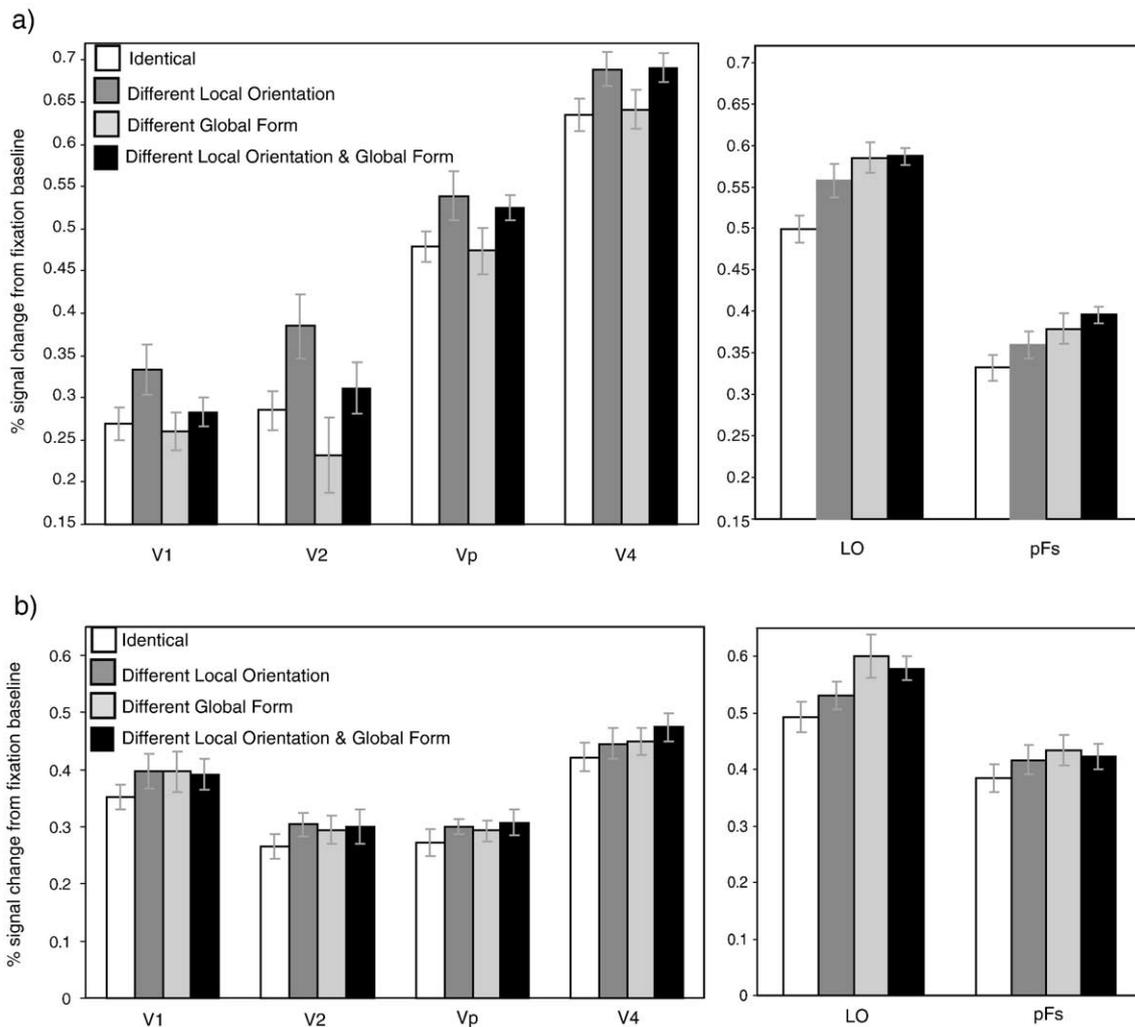
Fig. 5. Results for Experiment 2. (a) Global Form matching task, (b) Local Orientation matching task. fMRI responses (% signal change from fixation baseline) across visual areas and conditions. Error bars: SEM across subjects.

($F(1,25)$ = 5.94, $P < 0.05$), V2 ($F(1,25)$ = 6.56, $P < 0.05$), Vp ($F(1,25)$ = 5.79, $P < 0.05$) and V4 ($F(1,25)$ = 8.31, $P = 0.01$), but no significant differences in LO ($F(1,25) < 1$, $P = 0.29$) or pFs ($F(1,25)$ = 1.32, $P = 0.24$).

Interestingly, we observed release from adaptation for stimuli with different global forms when the local element orientation remained the same (Different Global Form) across all visual areas (V1: $F(1,25)$ = 11.00, $P < 0.01$, V2: $F(1,25)$ = 4.62, $P < 0.05$, Vp: $F(1,25)$ = 2.31, $P < 0.05$, V4: $F(1,25)$ = 3.89, $P < 0.05$, LO: $F(1,25)$ = 62.90, $P < 0.001$, pFs: $F(1,25)$ = 13.04, $P < 0.01$). As shown in Fig. 5b, these rebound effects were similar in magnitude to those observed for local orientation changes (Different Local Orientation, Different Local Orientation and Global Form). These findings suggest that attention to local elements may facilitate their integration to global forms and thus result in enhanced sensitivity to global form changes in early visual areas. This attentional effect was supported by a significant interaction ($F(3,24)$ = 3.05, $P < 0.05$) between tasks (matching of global shapes vs. matching of local orientations) across conditions and ROIs. Taken together, these findings propose that the integration of global forms is enhanced in early visual areas by attention to the local elements,

while global forms are represented independent of the spatial scale of attention in higher visual areas.

Orientation-specific fMRI adaptation

Were the local fMRI adaptation effects observed across visual areas orientation-specific? Orientation-specific fMRI adaptation appears to be a controversial issue as long adaptation studies have shown orientation adaptation in V1 (Tootell et al., 1998), whereas some rapid event-related fMRI adaptation studies have reported lack of orientation adaptation effects in V1 and V2 and increasing effects along the hierarchy of the ventral visual areas (Boynton and Finney, 2003).

To address this question, we conducted a control experiment in which we compared fMRI responses to a single stimulus (Single Presentation: field of randomly oriented and positioned Gabor elements) with fMRI responses to two sequentially presented stimuli (Repeated Presentation conditions). Two Repeated Presentation conditions were tested: (a) Identical Orientation, in which the same Gabor field was presented twice, and (b) Different Orientation, in which two stimuli that differed in their local orientation were

presented (90° rotation of each Gabor element with no position change). In all conditions, each stimulus was presented for 300 ms, and in the repeated presentations, the two stimuli in a trial were separated by a blank interval of 100 ms. Observers were engaged in a dimming task at fixation that was of similar difficulty across all conditions (Single Presentation: 95.8%, Identical Orientation: 96%, Different Orientation: 96.9%). Previous studies have shown that when two stimuli are presented in a pair, the fMRI responses for the second stimulus are decreased compared to responses to a single stimulus (Dale and Buckner, 1997; Friston et al., 1998; Huettel and McCarthy, 2000). Based on these studies, we predict that responses to the second stimulus in the repeated presentation conditions would be lower than responses to a single stimulus. Importantly, if this nonlinearity in the fMRI signal is related to neuronal adaptation (Huettel and McCarthy, 2001), then we would predict that responses to the second stimulus for the Identical Orientation condition would be lower than for the Different Orientation condition.

Fig. 6 shows the average peak fMRI response for single and repeated stimulus presentations. For repeated stimulus presentations, we plot responses to the second stimulus after subtracting the response to the single stimulus and shifting the difference in the fMRI responses back in time by 400 ms (Stimulus presentation time: 300 ms, plus ISI: 100 ms). The figure shows lower fMRI responses for repeated than single presentations in all areas (V1: $F(1,22) = 92.62$, $P < 0.001$, V2: $F(1,22) = 73.05$, $P < 0.001$, VP: $F(1,22) = 63.78$, $P < 0.001$, V4: $F(1,22) = 105.10$, $P < 0.001$), LO: $F(1,22) = 10.91$, $P < 0.05$ and pFs: $F(1,22) = 20.48$, $P < 0.01$). More importantly, this decrease in the fMRI responses for the repeated stimulus presentations was orientation-specific in the early retinotopic areas (V1, V2, VP and V4), the posterior (LO) but not the anterior (pFs) subregions of the LOC. In particular, we observed a significant ($F(2,22) = 7.207$; $P < 0.01$) interaction for Condition (Single Presentation, Identical Orientation, Different Orientation) and ROI (V1, V2, VP, V4, LO and pFs). Furthermore, contrast analysis showed significant stronger responses for different than identical orientations of Gabor elements in V1 ($F(1,22) = 10.11$, $P < 0.05$), V2 ($F(1,22) = 5.30$, $P < 0.05$), VP ($F(1,22) = 12.02$, $P < 0.05$), V4 ($F(1,22) = 5.29$, $P < 0.05$) and LO ($F(1,22) = 3.70$, $P = 0.05$), but no significant differences in pFs ($F(1,22) < 1$, $P = 0.28$). Interestingly, analysis of the time to peak from trial onset revealed delayed peak responses for repeated than single presentations ($F(2,10) = 13.80$, $P = 0.01$), consistent with previous studies (Huettel and McCarthy, 2000; Boynton and Finney, 2003), but no significant ($F(2,10) = 1.50$, $P = 0.23$)
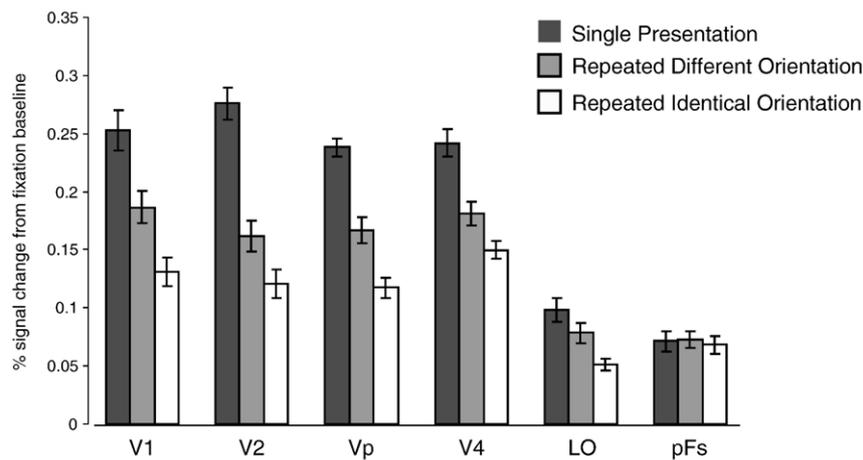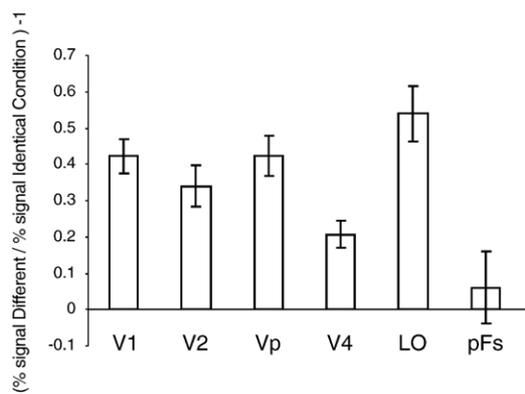

Fig. 6. Results for orientation-specific adaptation control. (a) Average peak fMRI responses for the second stimulus after subtracting the fMRI responses to the single stimulus from those of the repeated presentation conditions and shifting the difference in the fMRI responses back in time by 400 ms (Stimulus presentation time: 300 ms, plus ISI: 100 ms). Error bars: SEM across subjects. (b) Rebound effects for the average peak fMRI responses (Fig. S4b) across areas. Error bars: SEM across subjects.

differences between identical and different orientation conditions (Fig. S3). These orientation adaptation effects in early visual areas and LO but not in pFs are consistent with previous studies suggesting that posterior LOC subregions encode information about object parts, while anterior subregions show stronger invariance to image changes (Grill-Spector et al., 1999). These findings suggest that the fMRI adaptation effects observed in our experiments are orientation-specific and in accordance with higher fMRI sensitivity to orientation changes in occipital rather than anterior temporal regions. Although this experiment cannot rule out a possible contribution of vascular nonlinearities to the decreased BOLD responses observed after stimulus repetition (Huettel and McCarthy, 2000; Boynton and Finney, 2003; Huettel et al., 2004), our findings are consistent with previous physiological studies showing rapid orientation adaptation in primary visual cortex (Mueller et al., 1999) and suggesting a role for neuronal adaptation in orientation processing in early visual areas. Differences in the stimulus properties (e.g. spatial frequency) and the stimulus duration used in different fMRI studies could account for the different orientation adaptation effects reported and would be of interest for further investigation.

Discussion

Our findings advance our understanding of the characteristics of form integration in the human visual cortex and validate the use of rapid event-related fMRI adaptation for investigating processing across stages of visual analysis (early and higher visual areas) in the human brain. Our studies have focused in the perceptual integration of local elements to global form contours that is thought to engage early retinotopic and higher occipitotemporal areas (Smith et al., 2002; Kourtzi et al., 2003b). Future studies are necessary to investigate more complex integration processes (i.e. local contours to objects and multiple objects to scenes) that are shown to implicate higher temporal and parietal cortical areas (Fink et al., 1996).

In particular, our results showed transient processing of form contours in early visual areas while a more sustained analysis in the LOC (Experiment 1). These effects are consistent with recent human fMRI and EEG studies that show persistent activations after the presentation of objects in occipitotemporal (van Turennout et al., 2000, 2003; Ferber et al., 2003; Henson et al., 2004; Mukamel et al., 2004) rather than early visual areas or the human motion complex (hMT+/V5) (Ferber et al., 2003; Mukamel et al., 2004). Similarly, previous neurophysiological studies (Miyashita and Chang, 1988; Rolls and Tovee, 1994; Desimone, 1996; Brown and Xiang, 1998; Yakovlev et al., 1998; Keysers et al., 2001; Tamura and Tanaka, 2001) have shown sustained neural responses in the inferotemporal cortex after stimulus presentation. Taken together, these studies suggest neural processing of visual stimuli beyond the duration that they are present on the retina. This sustained processing may mediate visual short-term memory for objects as proposed by several behavioral studies (Potter, 1976; Intraub, 1980). Such a mechanism in higher visual areas could facilitate temporal associations and sequence learning (Yakovlev et al., 1998) that is useful for invariant object representations (Riesenhuber and Poggio, 2000).

Furthermore, Experiment 2 showed sensitivity to local orientation changes in primary visual cortex that decreased along the hierarchy of visual areas, whereas sensitivity to global contour changes in the LOC but not in early visual areas. This sensitivity to orientation changes in early visual areas was orientation-specific and is consistent with previous evidence for orientation adaptation effects and orientation selectivity in early visual areas (Carandini et al., 1997; Mueller et al., 1999).

At first glance, this sensitivity to local orientation but not global form changes observed in early visual areas for Experiment 2 appears to contradict the adaptation effects observed for global contours in Experiment 1. However, it is possible that the sensitivity to global form changes observed in Experiment 1 was due to small local orientation changes. In particular, global shape changes in the co-aligned stimuli used in Experiment 1 resulted in small local orientation changes. In contrast, when using co-oriented stimuli with different global contours but with local elements of the same orientation (Experiment 2), we did not observe any sensitivity to global form changes in early visual areas. Thus, taken together, the findings of Experiments 1 and 2 are consistent with previous studies suggesting that early visual areas contribute to global shape analysis by processing the local contour orientations and integrating elements within the local neighborhood of their receptive field (Sceniak et al., 1999; Rossi et al., 2001; Smith et al., 2002; Kourtzi et al., 2003a), while higher visual areas appear to represent salient shape regions (Stanley and Rubin, 2003) and the perceived global shape (Kourtzi and Kanwisher, 2001).

Interestingly, an alternative interpretation proposes that the different effects across experiments could be due to the nature of the stimuli. The stimuli in Experiment 1 were closed contours rendered by Gabor elements aligned along the contour (co-aligned), whereas the contour stimuli in Experiment 2 were rendered by Gabor elements of the same orientation that were parallel to each other (co-oriented) but were not aligned along the contour. Co-alignment of similarly oriented elements along shape contours is thought to be a highly consistent regularity observed in natural images, whereas parallel elements are usually encountered in textured surfaces (Geisler et al., 2001; Hess et al., 2003). Recent studies suggest that visual processing as early as in the primary visual cortex takes into account natural image regularities (Lee et al., 1998; Sigman et al., 2001). Sensitivity to 'good continuation' has been acknowledged as an important aspect of shape processing very early on (Koffka, 1935). In accordance, recent studies have shown that co-aligned contours are more easily detectable in cluttered scenes than contours rendered by elements orthogonal to the contour orientation (Field et al., 1993; Hess et al., 2003). Furthermore, responses of neurons in the primary visual cortex have been shown to be enhanced (Kapadia et al., 1995) by co-aligned elements and inhibited (Born and Tootell, 1991) by co-oriented elements. Thus, it is possible that early visual areas process information about naturally occurring global contours when rendered by co-aligned elements (Experiment 1) rather than co-oriented parallel elements (Experiment 2) that do not usually occur in natural shape contours. However, higher visual areas that are known to represent global shape representations invariant to local image changes may encode information about shape contours independent of the arrangement of their local elements.

This sensitivity to global contour changes in naturally occurring co-aligned contours observed in early visual areas could be accounted for by recurrent processing of visual information via local connections and feedback interactions. In particular, recent studies suggest that the primate brain has developed a network of recurrent connections that mediate integration of features based on regularities characteristic of natural scenes (e.g. collinearity).

Horizontal connections in macaque V1 have been proposed to link neurons of similar orientation tuning and mediate contour integration (Gilbert, 1992, 1998). Alternatively, feedback connections (Lamme et al., 1998; Lamme and Roelfsema, 2000; Bullier, 2001) from extrastriate visual areas may modulate processing in early visual areas. These feedback connections mediate the segmentation of target elements from their background and facilitate perceptual integration of global forms.

Finally, our findings suggest that attention modulates these spatiotemporal properties of perceptual integration in the visual cortex, consistent with previous studies showing a role of attention in form analysis and learning (Gilbert et al., 2000). Our results provide novel evidence that attention to global forms may facilitate their sustained visual processing, while attention to local elements may enhance global form processing in early visual areas possibly by facilitating their perceptual integration. Previous studies have suggested that integration of collinear contours is prominent under conditions of divided rather than focal attention (Ito et al., 1998; Ito and Gilbert, 1999; Roberts et al., 2005). These findings are consistent with the idea that the neural mechanisms underlying feature integration based on natural scene regularities have developed to mediate coherent visual perception when attentional resources are divided to different targets in complex environments. Interestingly, our results suggest that focal attention is necessary for the perceptual integration of co-oriented parallel elements that do not usually occur in natural shape contours and enhances sustained processing of global forms defined by co-aligned natural contours.

Conclusions

In summary, our studies demonstrate that rapid event-related fMRI adaptation paradigm can be used to study form analysis at different spatiotemporal scales across visual areas in the human brain. In particular, our results suggest that form integration and processing in early visual areas is transient and limited within the local neighborhood of their cells' receptive field. Thus, processing in early visual areas appears to be implemented at high spatiotemporal resolution that allows continuous sampling of the visual scenes at fine spatial scales. In contrast, higher visual areas appear to support encoding at a lower spatiotemporal resolution; that is, they encode the perceived global form in a more sustained manner. This type of processing may facilitate the representation of distinctive shape features and temporal associations (Miyashita and Chang, 1988; Miller et al., 1993; Yakovlev et al., 1998) that are critical for learning categories of objects and discriminating between their members. Recurrent processing between early and higher visual areas is implemented via feedforward and feedback projections that allow both fine-to-coarse and coarse-to-fine analysis of visual images. These intra-areal interactions shape the visual analysis of forms based on prior knowledge about regularities in natural scenes, attention and task context and demands (Gilbert et al., 2000).

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2005.06.017.

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