

Binocular Rivalry and Visual Awareness in Human Extrastriate Cortex

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Summary

We used functional magnetic resonance imaging (fMRI) to monitor stimulus-selective responses of the human fusiform face area (FFA) and parahippocampal place area (PPA) during binocular rivalry in which a face and a house stimulus were presented to different eyes. Though retinal stimulation remained constant, subjects perceived changes from house to face that were accompanied by increasing FFA and decreasing PPA activity; perceived changes from face to house led to the opposite pattern of responses. These responses during rivalry were equal in magnitude to those evoked by nonrivalrous stimulus alternation, suggesting that activity in the FFA and PPA reflects the perceived rather than the retinal stimulus, and that neural competition during binocular rivalry has been resolved by these stages of visual processing.

Introduction

Binocular vision normally leads to a single stable interpretation of the visual world. But when discrepant monocular images are presented to the two eyes, they rival for perceptual dominance such that only one monocular image is perceived at a time while the other is suppressed from awareness (e.g., Levelt, 1965). This phenomenon of binocular rivalry was originally thought to reflect competition between the inputs from each eye, either in the lateral geniculate nucleus or primary visual cortex (V1) (e.g., Blake, 1989). However, single unit recordings in alert monkeys have revealed that only a small percentage of neurons in V1/V2 (9%), V4 (18%), and MT (12%) show increased activity when their preferred stimulus is perceived during rivalry, and that some neurons in V4 (9%) and MT (11%) actually fire more when their preferred stimulus is phenomenally suppressed (Logothetis and Schall, 1989; Leopold and Logothetis, 1996).

These single unit studies suggest that competitive interactions in binocular rivalry are not restricted to mono-

cular neurons in V1 (see also Sengpiel and Blakemore, 1994) but continue to occur at much higher levels of the visual pathway, such as V4 and MT, well after inputs from the two eyes have converged in V1. However, these studies do not reveal if or when this competition is resolved, such that neural activity no longer reflects the presence of the suppressed stimulus and solely reflects the perceived stimulus. Although most neurons (84%) in the inferotemporal cortex of monkeys show significant changes in neural activity corresponding to perceived changes in a rivalrous stimulus, these neural changes are only about half the magnitude of those evoked by nonrivalrous stimulus changes (Sheinberg and Logothetis, 1997). If binocular rivalry were fully resolved, one would expect to find equivalent neural modulations for perceived changes during rivalry and actual stimulus changes.

The present study used functional magnetic resonance imaging (fMRI) to investigate whether activity in human extrastriate cortex is correlated to visual awareness during binocular rivalry, and, more specifically, whether activity changes during rivalry might be comparable to those found during nonrivalrous stimulus alternation. If equivalent responses were found in a specific neural region, this would indicate that binocular rivalry is resolved by this stage of the visual pathway. Such brain regions would not only provide a neural basis for phenomenal dominance and suppression during rivalry, but might also provide insights regarding visual awareness under general conditions of perceptual ambiguity (Crick, 1996; Leopold and Logothetis, 1996).

We capitalized on the stimulus-selective response properties of two high-level visual areas: the human fusiform face area (FFA), which responds selectively to faces as compared to a variety of nonface stimuli (Kanwisher et al., 1997; McCarthy et al., 1997; Tong et al., submitted), and the parahippocampal place area (PPA), which responds strongly to houses and places but not to faces (Epstein and Kanwisher, 1998). The differential response properties of these two regions allowed us to measure changes in fMRI signals during rivalry and nonrivalry alternations.

Three types of fMRI scans were performed: localizer, rivalry, and nonrivalry scans. On localizer scans, alternating sequences of nonrivalrous faces and houses were binocularly presented in order to functionally localize each subject's FFA and PPA. The FFA was defined as the region in the mid-fusiform gyrus that responded significantly more to faces than houses, and the PPA was defined as the region in the parahippocampal gyrus that responded significantly more to houses than faces. These two areas served as the regions of interest for subsequent rivalry and nonrivalry scans.

On rivalry scans, a face image was presented to one eye and a house image was presented to the other eye while subjects maintained fixation (see Figure 1a). Subjects used a button box to report when their dominant percept switched to that of a face or house. On subsequent nonrivalry scans, the stimulus alternated between nonrivalrous monocular presentations of either

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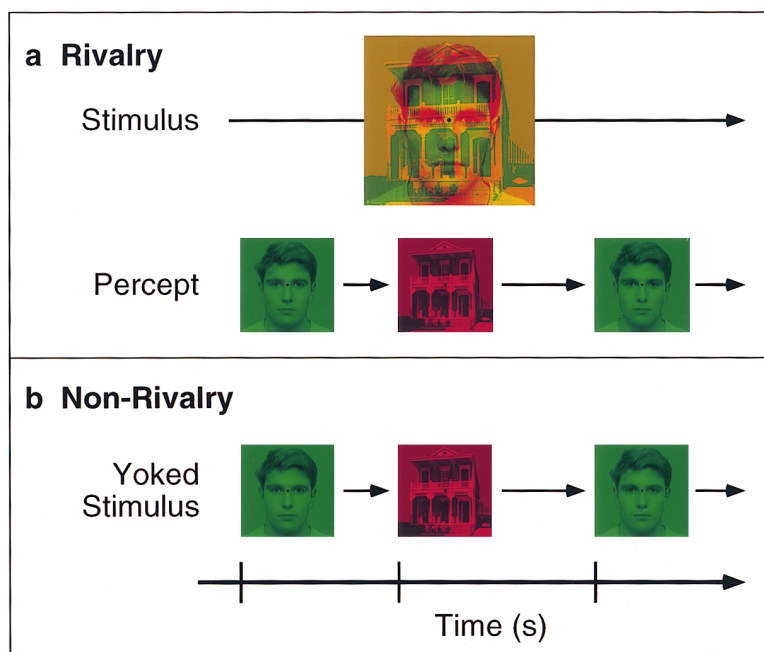


Figure 1. Experimental Design and Stimuli

(a) Ambiguous face/house stimulus used in rivalry scans. When viewed through red and green filter glasses, only the face could be seen through one eye and only the house through the other eye. This led to vigorous binocular rivalry as indicated by reported alternations between a face percept and house percept (typically every few seconds). (b) A timeline illustrating how nonrivalry scans presented nonrivalrous monocular images of either face or house alone using the same temporal sequence derived from the perceptual report of a previous rivalry scan.

face or house alone using the identical temporal sequences reported during previous rivalry scans in the same subject (see Figure 1b). Subjects maintained fixation and reported when the stimulus switched to a face or house. For rivalry and nonrivalry scans, fMRI activity in the predefined FFA and PPA was monitored every second and later analyzed in an event-related fashion time-locked to the subject's report of a change in percept.

Results

Localizer Scans

The FFA and PPA regions of interest were successfully localized in all subjects. The anatomical locus and extent of these regions were highly consistent with those described in previous studies (Kanwisher et al., 1997; McCarthy et al., 1997; Epstein and Kanwisher, 1998). The size of the FFA ranged from 4 to 8 voxels across the three subjects with unilateral FFA regions and comprised a total of 22 voxels in a subject with a bilateral FFA (median FFA size across subjects = 6.5 voxels; voxel size = $3.25 \times 3.25 \times 7$ mm). The PPA appeared bilaterally in all subjects and ranged in size from 25 to 49 voxels (median size = 36.5 voxels).

Figure 2a shows the localized FFA and PPA of one subject in two adjacent near-axial slices. Whereas the FFA is lateralized to the right fusiform gyrus in this subject, the PPA occurs bilaterally in parahippocampal cortex. Figure 2b shows the time course of MR signal for the FFA and PPA during localizer scans, averaged across all four subjects. During each of the 16 s stimulus periods, the FFA responded vigorously to sequentially presented faces but only weakly to houses, whereas the PPA responded strongly to houses and weakly to faces.

Rivalry Scans

All subjects reported strong perceptual alternations between a face-dominant and house-dominant percept

while they maintained fixation on the rivalrous face/house stimulus. The mean duration of these face percepts and house percepts were of comparable length for each subject but varied in length between subjects (ranging from 2.5 to 5.5 s). The perceptual durations of each subject were distributed according to a gamma-shaped function, as typically found in binocular rivalry studies (e.g., Levelt, 1965).

Figure 3 shows the raw fMRI activity and reported perceptual switches of one subject during a portion of a rivalry scan. (Note that for this figure alone, perceptual responses have been shifted forward by 4 s to compensate for the lag in the hemodynamic fMRI response). Even in the raw MR time course, a correspondence between FFA activity, PPA activity, and perceptual awareness could be seen (cf. Brown and Norcia, 1997). FFA activity was generally greater during face than house percepts, whereas PPA activity was greater during house than face percepts.

Average fMRI time course functions for each subject were constructed by separately averaging FFA and PPA signal intensities over all occurrences of a perceptual switch in a given direction (i.e., house to face versus face to house) time-locked to each reported switch. Figure 4a shows the average time course of subject S1. Changes from a house percept to a face percept were accompanied by a sharp rise in FFA activity and a sharp fall in PPA activity (left panel), whereas changes from face to house led to the opposite pattern of activity (right panel). These fMRI responses corresponded to the direction of the perceptual switch and thus the content of visual awareness.

Figure 5 reveals that all four subjects showed the same qualitative pattern of fMRI responses during rivalry. Switches to the preferred percept of a given region (e.g., house to face switches for the FFA) always led to significant increases in fMRI activity within the specified time window of -2 to $+4$ s (Figure 5a; 8/8 cases),

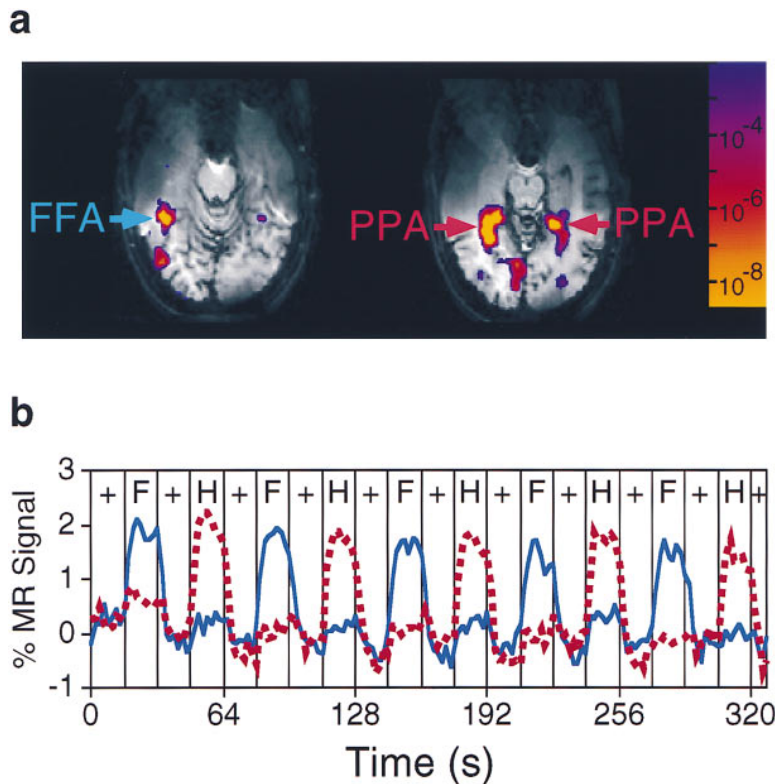


Figure 2. Localizer Data: FFA and PPA

(a) Two adjacent near-axial slices showing the localized FFA and PPA of one subject (S1). The FFA was localized as the region in the fusiform gyrus that responded more to faces than houses. The PPA was localized as the region in the parahippocampal gyrus that responded more to houses than faces. (These images follow radiological convention with the left hemisphere shown on the right and vice versa.)

(b) MR time course on localizer scans showing FFA (blue solid line) and PPA (red dotted line) activity (expressed in percent signal change relative to fixation baseline) averaged across all four subjects. Subjects viewed sequentially presented faces (F), houses (H), or a static fixation point (+).

whereas switches to a *nonpreferred* percept led to significant decreases in activity (Figure 5c; 7/8 cases). These fMRI responses were closely linked to the time of the reported perceptual switch in all subjects. For all reliable fMRI changes during rivalry, the initial peak or trough always occurred within a narrow time window of -2 to 0 s. These initial extrema significantly preceded the subject's own behavioral response (mean = -0.9 s; $t[14] = 4.5$; $p < 0.001$) and appeared to reflect the time of the perceptual switch itself. Final extrema in fMRI activity occurred 1 to 4 s after the subject's response, with durations ranging from 2 to 6 s from the initial to the final peak or trough.

The duration and magnitude of fMRI responses corresponded to the duration of the subject's reported percept. This is illustrated in Figure 6, which shows that for subject S2 during switches from face to house, increases in the perceived duration of house led to larger and longer responses from the PPA (rising activity, left

panel) and FFA (falling activity, right panel). Enough observations of varying percept durations were collected to reveal this increase in fMRI response magnitude and duration as a function of percept duration in three out of four subjects.

The above results indicate that FFA and PPA activity is tightly linked to visual awareness during rivalry, reflecting both the content and duration of each percept. The observed changes in fMRI activity as a function of percept duration further indicate that our measure of fMRI signals is sufficiently sensitive to detect rather small differences in fMRI responses and unlikely to be limited by response saturation. These points will be relevant when we next compare the magnitude of fMRI responses found during rivalry versus nonrivalry.

Rivalry versus Nonrivalry Scans

In order to determine the extent to which FFA and PPA activity reflected the perceived as opposed to the retinal

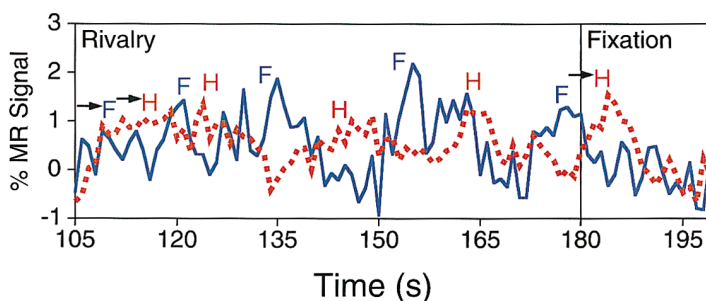


Figure 3. Example of Raw Data from Rivalry Scan

Raw MR time course (expressed in percent signal change relative to fixation baseline) showing FFA (blue solid line) and PPA (red dotted line) activity from part of a rivalry scan while the subject (S1) viewed a rivalrous face/house stimulus or static fixation point. All reported switches to a face percept (F) or house percept (H) have been shifted forward by 4 s (as illustrated by arrows) to compensate for the lag in the hemodynamic fMRI response. (This time shift was not applied to any other analysis or figure).

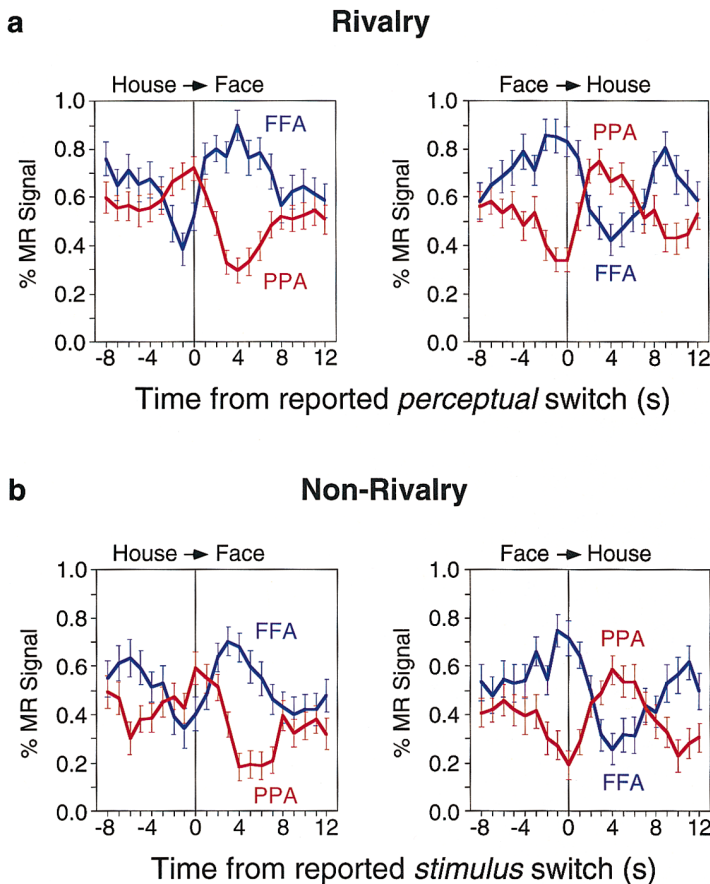


Figure 4. Rivalry versus Nonrivalry Data for Subject S1

Average FFA (blue) and PPA (red) activity during reported house-to-face switches (left) or face-to-house switches (right) for rivalry (a) and nonrivalry (b) scans for one subject (S1). Vertical line indicates the time of the subject's response (averaged to the nearest second). Vertical bars represent ± 1 SEM.

stimulus, fMRI signal changes during rivalry were compared with nonrivalrous changes in the retinal stimulus itself. Figure 4b shows the average fMRI time course during reported nonrivalrous stimulus switches for subject S1. Inspection of the rivalry and nonrivalry figures (Figures 4a and 4b) reveals a striking resemblance, not only in the qualitative pattern of FFA and PPA responses but also in the amplitude of these activity changes. This similarity can be seen for all subjects in Figure 5 by comparing individual fMRI responses for rivalry (columns a and c) and nonrivalry (columns b and d).

In order to quantify the effects of rivalry versus nonrivalry across subjects, the sign-preserving amplitude of each fMRI response (i.e., final minus initial peak or trough value) was measured for each condition, subject, switch type, and region of interest, as shown in Figure 5. The resulting scatterplot in Figure 7 reveals a remarkable correspondence in the fMRI responses found across subjects during rivalry (ordinate) versus nonrivalry (abscissa). All points cluster tightly around the line of identical amplitudes of MR responses for rivalry and nonrivalry. A line of best fit accounted for 94% of the variance (R^2), and yielded a slope of 0.91 and an intercept of 0.05, which did not significantly differ from a theoretical slope of 1 or intercept of 0. These results indicate that FFA and PPA responses during perceived changes in an ambiguous rivalrous stimulus are of equal magnitude to those evoked by unambiguous changes in the stimulus itself. This strongly suggests that competitive neural

interactions underlying binocular rivalry have been resolved by the time visual information reaches the FFA or PPA.

Overall, the timing of fMRI responses for rivalry and nonrivalry were quite similar (see Figure 5). The initial extrema for all reliable fMRI responses during nonrivalry always occurred within a narrow window of -1 to $+1$ s (relative to the reported switch) as compared to -2 to 0 s for rivalry. The somewhat earlier fMRI response for rivalry than nonrivalry (-0.9 s versus -0.1 s, respectively; $t[14] = 4.6$; $p < 0.001$) likely reflects the fact that subjects required more time to determine when a perceptual switch during rivalry had occurred, as well as the fact that a brief face/house blend was sometimes perceived during these switches. Final extrema for fMRI responses were generally comparable for rivalry and nonrivalry (mean = 2.9 s, range = $+1$ to $+4$ s for rivalry; mean = 3.3 s, range = $+2$ to $+4$ s for nonrivalry; $t[14] = 1.58$; ns), whereas the duration of fMRI responses, estimated by the time difference between the final and initial extrema, were somewhat longer for rivalry than nonrivalry (3.9 s versus 3.4 s, respectively; $t(14) = 2.17$; $p < 0.05$).

Discussion

The present study demonstrates a tight coupling between human visual awareness and neural activity in two extrastriate areas. When subjects viewed a rivalrous

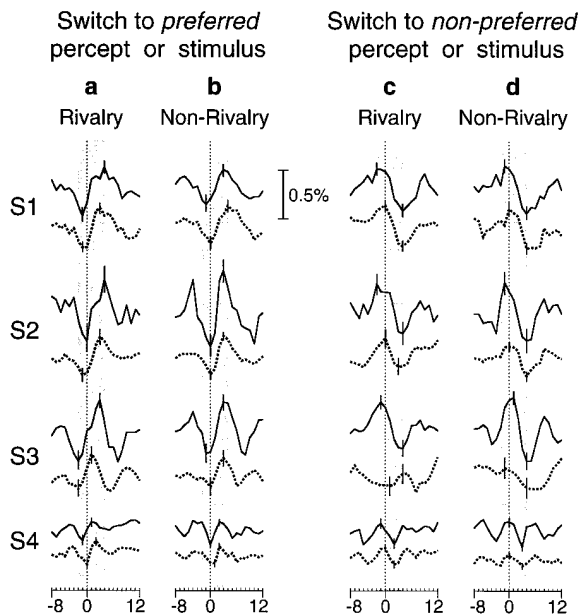


Figure 5. Rivalry versus Nonrivalry Data for All Subjects
FFA (solid) and PPA (dotted) time courses for switches to a preferred or nonpreferred percept (rivalry) or stimulus (nonrivalry) for all four subjects. Error bars representing ± 1 SEM indicate when activity reached a maximum or minimum within the specified time window of -2 to $+4$ s (gray region). Scale depicts 0.5% MR signal change. Switches to a preferred percept (a) or stimulus (b) led to significant increases in activity in 16 of 16 cases ($t > 3.3$; $p < 0.05$ Bonferroni corrected). Nonpreferred switches (c and d) led to significant decreases in activity in 14 of 16 cases (S3 showed nonsignificant PPA changes for both rivalry and nonrivalry).

face/house stimulus, they reported spontaneous alternations every few seconds between a face percept and a house percept, consistent with previous binocular rivalry studies (e.g., Levelt, 1965; Blake, 1989). Even though the retinal stimulation remained constant, perceptual alternations during rivalry were accompanied by time-locked fMRI responses in the FFA and PPA that were correlated with the content of visual awareness. Perceived switches from house to face led to sharp increases in FFA activity and decreases in PPA activity; perceived switches from face to house led to the opposite pattern of fMRI responses. Similar fMRI responses occurred when subjects viewed actual alternations between a nonrivalrous face stimulus and house stimulus

using the same temporal sequence reported by the subject on previous rivalry scans. Indeed, fMRI responses accompanying phenomenal changes during rivalry were identical in magnitude to those evoked by changes in the stimulus itself.

Our results provide an upper bound for the stage of processing at which binocular rivalry is resolved. Single unit studies of alert monkeys have revealed that only a small percentage of neurons in V1/V2, V4, and MT show increased activity when their preferred stimulus is perceived during rivalry and that some neurons in V4 and MT actually show activity changes corresponding to the suppressed stimulus (Logothetis and Schall, 1989; Leopold and Logothetis, 1996). This suggests that rivalrous information from the two eyes may not be resolved into a single dominant percept by these stages of the visual pathway. Although most neurons in inferotemporal cortex follow the perceived stimulus during rivalry, these neural changes are only about half the magnitude of those observed during nonrivalrous stimulus alternation (Sheinberg and Logothetis, 1997). In contrast, our results demonstrate that in the FFA and PPA, neural responses to a change in perceptual awareness with the stimulus held constant are as large as responses to a change in the stimulus itself. This suggests that competitive neural interactions underlying binocular rivalry are resolved by the time visual information reaches the FFA and PPA.

These findings provide an important contribution to our understanding of the neural basis of binocular rivalry. A number of previous studies have used EEG (e.g., Lansing, 1964; Cobb et al., 1967; Brown and Norcia, 1997) or MEG (Tononi et al., 1998) to demonstrate correlations between neural activity and human visual awareness during rivalry. However, these techniques provide rather coarse information about the cortical locus of awareness-related responses. A recent fMRI study of binocular rivalry used a design similar to ours to ask the orthogonal question of which brain regions are active during reported perceptual alternations (independent of the direction of the switch) compared to intervals in which no alternation occurred (Lumer et al., 1998). They found that parietal and frontal regions were more strongly activated by reported perceptual switches during rivalry than by reported stimulus switches during nonrivalry. They also briefly mention some evidence of fusiform activity correlated with the content of perception. Our study goes beyond these earlier reports to provide specific data regarding the cortical locus of

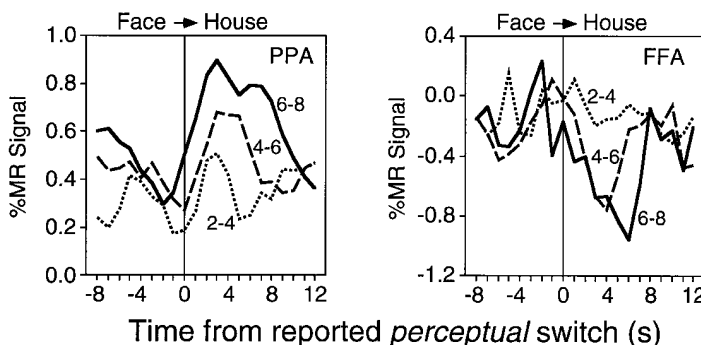


Figure 6. Effect of Percept Duration
Average PPA (right) and FFA (left) activity for perceived face-to-house switches during rivalry for one subject (S2). Data are plotted as a function of the duration of the house percept: dotted lines, 2-4 s; dashed lines, 4-6 s; solid lines, 6-8 s.

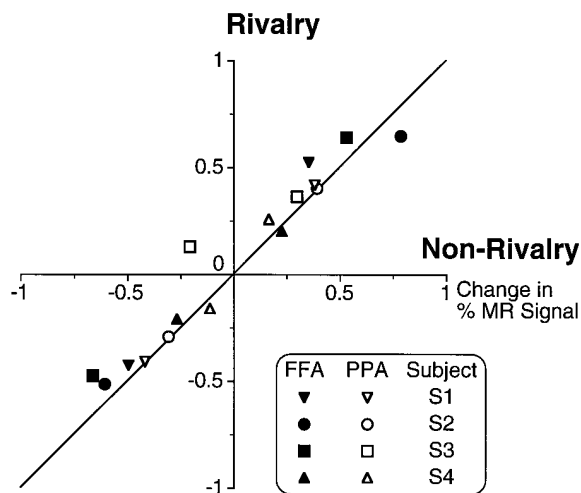


Figure 7. fMRI Response Amplitudes for Rivalry versus Nonrivalry Scatterplot comparing the amplitude of fMRI responses during rivalry (ordinate) and nonrivalry (abscissa) for each region, switch type, and subject (obtained from data shown in Figure 5). Positive points in the top right quadrant reflect increases in fMRI activity during switches to a preferred percept or stimulus; negative points in the bottom left quadrant reflect decreases in activity during non-preferred switches. Note that all points cluster tightly around the line of identical amplitudes of fMRI responses for rivalry and nonrivalry.

competitive interactions in binocular rivalry and the role of the FFA and PPA in visual awareness.

The identity in neural response for perceived changes during rivalry and actual stimulus changes during nonrivalry suggests that activity in the FFA and PPA reflects the perceived rather than the retinal stimulus. Consistent with this conclusion, recent studies have shown that FFA responses are strongly modulated by voluntary selective attention when the stimulus is held constant (Wojciulik et al., 1998) and that the FFA and PPA are respectively activated during mental imagery of faces or places, even when no visual stimulus is present at all (O'Craven and Kanwisher, submitted). In the present study, we found that these areas also respond during spontaneous reversals of perception during rivalry, demonstrating that awareness-related changes in these regions can occur without effortful voluntary acts of selective attention or mental imagery. These findings support the notion that multiple extrastriate regions such as the FFA and PPA participate in our awareness of specific attributes of the visual world.

Experimental Procedures

Subjects

Four experienced observers, ages 20–39, served as subjects. Subjects were right-handed healthy adults with normal or corrected-to-normal visual acuity and normal stereo-depth perception. All subjects reported vigorous binocular rivalry (i.e., frequent periods of exclusive phenomenal dominance) in a prior psychophysical testing session.

MRI Acquisition

Scanning was done on a 3T GE scanner at the MGH-NMR Center (Charlestown, MA), using a quadrature bilateral surface coil which provided a high signal-to-noise ratio in posterior brain regions. High

resolution anatomical and functional images were collected using six or seven slices, oriented either parallel or perpendicular to the subject's brain stem and centered over the occipitotemporal junction to encompass the FFA and PPA. Standard fMRI procedures were used (gradient echo, EPI acquisition, TE = 30 ms, flip angle = 90°, TR = 2 s for localizer scans; faster TR of 1 s for better temporal resolution on rivalry and nonrivalry scans). A bite bar minimized head motion.

Localizer Scans

Each subject's FFA and PPA were functionally localized based on two or three localizer scans (Figure 1), using previously described methods (Kanwisher et al., 1997). The FFA included all contiguous voxels in the mid-fusiform gyrus, which responded significantly more to faces than houses, whereas the PPA included all voxels in parahippocampal gyrus, which responded significantly more to houses than faces, using a minimum significance threshold of $p < 10^{-6}$ for each. Only after the precise regions of interest were established based on the independent localizer data did we proceed with subsequent rivalry and nonrivalry analyses.

Rivalry and Nonrivalry Scans

The rivalrous stimulus consisted of a superimposed face and house separately defined by red and green luminance variations (Figure 1a). When seen through a red filter over one eye and a green filter over the other, only the face was visible through one eye and only the house through the other eye (filters transmitted <4% of the unmatched versus matched luminance color). The nonrivalrous face and nonrivalrous house was defined by either red or green luminance variations alone (Figure 1b), which led to alternating monocular presentation through the filters. Both the color assignment (green face and red house or vice versa) and the placement of the filters (green left and red right or vice versa) were counterbalanced across the four subjects. The face/house stimulus subtended 5°–8° of visual angle. Centered within the stimulus was a dark circular fixation point which could be seen through both eyes.

Each subject received five or six rivalry scans and an equal number of nonrivalry scans. For rivalry scans, the rivalrous face/house stimulus was continuously presented for two 75 s periods interleaved within three 15 s fixation periods during which a central fixation point was presented on a yellow square (5°–8° in width). Subjects maintained fixation and reported when their dominant percept changed to that of a "face," "house," or "blend" by pressing one of three keys on a button box. Subjects were instructed to report face/house blends if they persisted over time and not to report blends that were briefly perceived during switches. Nonrivalry scans were identical to rivalry scans with the exception that the stimulus alternated between monocular presentations of either face or house alone using the identical temporal sequence reported on a previous rivalry scan in the same subject. When a blend was reported during rivalry (which happened infrequently), a face/house blend was presented for the corresponding nonrivalry stimulus period.

Activity in the FFA and PPA was analyzed relative to the time of each reported switch. A "face" response was coded as a valid house-to-face switch if it was immediately preceded by "house" or if an intervening "blend" response occurred <2 s prior to the "face" response. A house-to-face switch further required that the report of "face" last a minimum of 2 s before the next response. This was done because a brief face percept or face stimulus followed by "house" typically yielded a small and unreliable MR signal change that was soon followed by the opposite fMRI response (corresponding to house). By contrast, longer durations led to longer, larger, and more reliable responses (see Figure 6). The same method was used to code whether a "house" response was a valid face-to-house switch.

Percent MR signal change was calculated using each subject's average signal intensity during fixation epochs (shifted by 5 s to approximate the expected hemodynamic lag) as a baseline. This time shift was only used to calculate baseline fMRI activity and was not applied to any other analysis.

FFA and PPA activity data were sorted (to the nearest second) relative to the time of each reported switch to generate an average time course plot (see Figure 4). The average time course plot of

each subject comprised an average of 40–121 observations. The amplitude of fMRI change during reported switches for each subject, viewing condition, switch type, and region of interest was measured within the restricted time window of -2 to $+4$ s as shown in Figure 5. This method provided the simplest and most direct measure of fMRI response magnitudes, requiring minimal a priori assumptions regarding the precise shape or temporal lag of the hemodynamic response. To test the statistical significance of these fMRI activity changes, peak and trough fMRI values were compared using a conservative Bonferroni corrected t test ($t > 3.3$; $p < 0.05$) to account for the number of implicit comparisons within the restricted time window of -2 to $+4$ s.

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