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The Timing of Perceptual Decisions for Ambiguous Face Stimuli in the Human Ventral Visual Cortex

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When observers must discriminate a weak sensory signal in noise, early sensory areas seem to reflect the instantaneous strength of the sensory signal. In contrast, high-level parietal and prefrontal areas appear to integrate these signals over time with activity peaking at the time of the observer's decision. Here, we used functional magnetic resonance imaging to investigate how the brain forms perceptual decisions about complex visual forms in a challenging task, requiring the discrimination of ambiguous 2-tone Mooney faces and visually similar nonface images. Face-selective areas in the ventral visual cortex showed greater activity when subjects reported perceiving a face as compared with a nonface, even on error trials. More important, activity was closely related to the time of the subject's decision for face judgments, even on individual trials, and resembled the time course of activity in motor cortex corresponding to the subject's behavioral report. These results indicate that perceptual decisions about ambiguous face-like stimuli are reflected early in the sensorimotor pathway, in face-selective regions of the ventral visual cortex. Activity in these areas may represent a potential rate-limiting step in the pathway from sensation to action when subjects must reach a decision about ambiguous face-like stimuli.

Keywords: consciousness, face perception, fusiform face area, object recognition, occipital face area, visual awareness

Introduction

How does the brain determine what might be present in the physical world when incoming sensory signals are weak, variable, or ambiguous? Presumably, the brain must analyze, integrate, and interpret the relevant sensory signals to form a perceptual decision, which can then be used to guide the behavior. Examples of perceptual decisions include recognizing if a person is a teammate or opponent, determining if the opponent is dodging to the left or to the right, predicting how fast the opponent will move, and the ability to use this information to select an appropriate behavioral response, such as intercepting the opponent. Forming a perceptual decision is thought to involve the classification of sensory signals (e.g., opponent dodging leftward or rightward) and the conversion of this information into a representational format that can guide the action (e.g., intercept left or right). An important question concerns how perceptual decisions are represented in the brain. In particular, where along the pathway from sensation to action do the critical neural processes take place that determine the outcome and the timing of perceptual decisions?

Neurophysiological studies suggest that parietal and prefrontal areas, implicated in attentional selection and motor planning, have a critical role in the formation of perceptual decisions (Gold and Shadlen 2001; Romo and Salinas 2001; Schall 2001). In these experiments, monkeys must discriminate a sensory signal in the presence of noise. Weaker sensory signals lead to longer response times to reach a decision. In early sensory areas, activity reflects the instantaneous strength of the sensory signal and remains steady over time irrespective of the time required to reach a perceptual decision (Britten and others 1992, 1996; Bradley and others 1998; Dodd and others 2001; Cook and Maunsell 2002). In contrast, high-level parietal and prefrontal areas can integrate these weak sensory signals over time, with activity peaking at around the time that the animal is ready to report its decision (Shadlen and Newsome 1996; Kim and Shadlen 1999; Gold and Shadlen 2000; Cook and Maunsell 2002; Hernandez and others 2002; Roitman and Shadlen 2002). Recent human neuroimaging studies suggest a similar dissociation between early perceptual areas and prefrontal areas during perceptual decision making (Binder and others 2004; Heekeren and others 2004). For example, a recent study showed that the activity in face- and house-selective regions of the human ventral visual cortex closely reflects the strength of sensory signals for faces and houses presented in visual noise, whereas high-level prefrontal areas seem to integrate these sensory signals to reach a perceptual decision (Heekeren and others 2004). Taken together, the above studies demonstrate the importance of high-level areas in forming decisions when weak sensory signals must be integrated over time to minimize perceptual uncertainty.

However, not all perceptual decisions appear to involve the steady accrual of weak sensory signals over time. For example, deciding if a face might be present in an ambiguous 2-tone "Mooney" image involves pattern recognition of a salient but camouflaged visual form (Mooney 1957; Moore and Cavanagh 1998; Ramachandran and others 1998). Mooney stimuli such as those shown in Figure 1*A* may appear uninterpretable for several seconds until the observer suddenly perceives the emergence of a salient face. After a grayscale face image is thresholded and converted into a 2-tone Mooney image, the local features of the face often become too ambiguous to be recognized individually (Fig. 1*C*). As a consequence, local features must be disambiguated based on their context within a global facial configuration, a process that depends on top–down knowledge of facial structure (Moore and Cavanagh 1998). We hypothesized that the ability to disambiguate Mooney stimuli may depend on pattern recognition mechanisms in the human ventral visual cortex, especially face-selective regions such as the fusiform face area (FFA) (Kanwisher and others 1997; McCarthy and others 1997; Tong and others 1998, 2000).

This led us to predict that the time course of activity in face-selective visual areas, but not other visual areas, should be closely associated with the time required to reach a perceptual

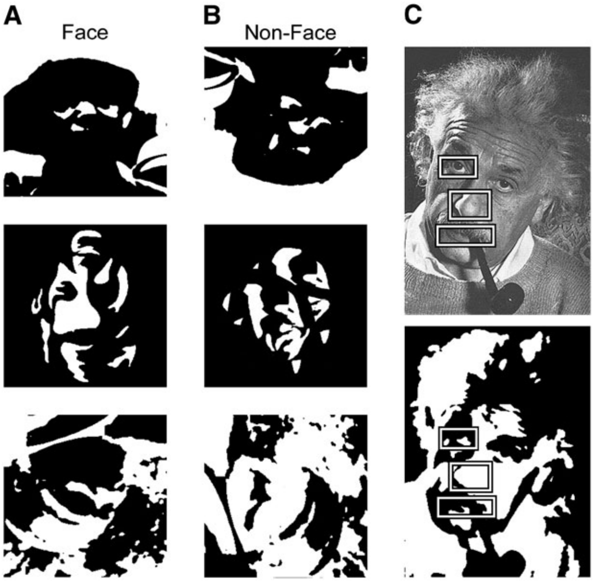

Figure 1. Examples of (*A*) Mooney face stimuli and (*B*) nonface stimuli. Nonface stimuli were generated by scrambling and altering intact Mooney faces. Note that most Mooney faces were not presented upright and could appear in any orientation, in order to increase the time required to perceive the face. (*C*) Comparison of local feature information in a grayscale and a thresholded Mooney face. Thresholding severely impairs recognition of individual features; however, the entire face can still be recognized based on the global configuration of these ambiguous local features.

decision about these ambiguous face-like stimuli. Previous neuroimaging studies have shown that the FFA responds with a stronger amplitude to perceived than unperceived faces (Dolan and others 1997; Kanwisher and others 1998; Tong and others 1998; Grill-Spector and others 2000, 2004; Bar and others 2001; Andrews and Schluppeck 2004; Summerfield and others 2006). Similar amplitude differences have been found in object-sensitive regions for perceived versus unperceived objects (Grill-Spector and others 2000, 2004; Bar and others 2001; Moore and Engel 2001). However, such amplitude effects fail to address whether cortical activity corresponds to the time of the subject's perceptual decision. Neurophysiological studies find that cortical visual activity fails to reflect the timing of perceptual decisions, even though the amplitude of activity does correspond to the final perceptual decision (Britten and others 1992, 1996; Bradley and others 1998; Dodd and others 2001; Cook and Maunsell 2002). Perhaps, due to the sluggish nature of the blood oxygen level–dependent (BOLD) response, only a few neuroimaging studies have reported evidence of a relationship between the time course of activity in ventral object areas and the time of object perception (Tong and others 1998; James and others 2000). A potential concern in these studies, however, is that either the visual stimulus itself physically varied over time (James and others 2000) or the perceptual visibility of the stimulus changed over time (Tong and others 1998) as a consequence of early sensory gating in V1 (Tong and Engel 2001). It remains an open question as to whether a temporal relationship between cortical activity and perceptual decisions would still be observed under stringent conditions in which the physical stimuli remain constant over time and are continuously visible. Such stringent conditions are necessary if one is to ensure that the dynamic changes in activity can only be attributed to changes in the perceptual interpretation of an object over time, independent of changes in the physical stimulus or its perceptual visibility.

To address this issue, we used event-related functional magnetic resonance imaging (fMRI) to measure the time course of cortical activity while subjects were required to make perceptual decisions about ambiguous Mooney stimuli over a prolonged time period. On each trial, a novel example of a Mooney face (Fig. 1*A*) or a scrambled nonface image (Fig. 1*B*) was steadily presented for a 12-s period. Subjects were instructed to press a button indicating whether they perceived a "face" or "nonface" as soon as they were confident of their decision and often required several seconds to form each new decision, indicating the challenging nature of the task. Event-related fMRI analyses were performed to investigate relationships between the time of the subject's decisional response and the timing of fMRI responses from multiple sites along the sensorimotor pathway. Primary regions of interest (ROIs) included early sensory areas (primary visual cortex), the FFA, object-selective visual areas, and motor cortex. We predicted that if the FFA is involved in the formation of perceptual decisions for ambiguous faces, then the time course of activity from this region should be correlated with the time of the subject's perceptual decision. Moreover, the time course of activity in the FFA should differ from that of other stimulus-driven visual areas and should instead resemble the activity in motor cortex corresponding to the behavioral report of the subject's decision for faces.

Methods

Subjects

Six healthy, right-handed university students (5 males and 1 female, ages 26–33 years, mean age 29.2 years) participated in the experiment after providing informed written consent. All subjects had normal or corrected-to-normal visual acuity and were naive to the purpose of the experiment.

Magnetic Resonance Imaging Acquisition

Subjects were scanned at the Princeton Center for the Study of Brain, Mind, and Behavior on a 3-T Siemens Magnetom Allegra head-dedicated scanner using a standard head coil. A high-resolution, 3-dimensional (3D), T_1-weighted anatomical magnetization prepared rapid gradient-echo scan was collected (time repetition [TR] = 11.08 ms, echo time [TE] = 4.3 ms, flip angle = 8°, 256 × 256 matrix, voxel resolution = 1 mm^3). Standard T_2^*-weighted gradient-echo echo planar imaging was used to measure BOLD contrast for whole-brain functional imaging (TR = 2000 ms, TE = 30 ms, flip angle = 90°, in-plane resolution 3 × 3 mm, 25 slices, slice thickness 4–5 mm, gap = 1 mm).

Stimuli

Stimuli consisted of 2-tone, thresholded images of faces and nonface stimuli that were created by scrambling the Mooney faces (see Fig. 1). To increase the difficulty of the face/nonface discrimination task, Mooney faces and their nonface counterparts could appear in any possible orientation in the picture plane and included front, three-quarter and profile view images of Mooney faces to maximize the heterogeneity of the stimulus set. Stimuli were presented on a black background, 10.6° × 10.6° in size, and spanned almost the entire area. The entire stimulus set consisted of 36 Mooney faces and 36 nonfaces.

Experimental Design

Each experimental fMRI run consisted of 12 stimulus trials interleaved between 12-s fixation baseline periods. On each stimulus trial, a novel example of a Mooney face image or nonface image was presented for a 12-s viewing period, and subjects were instructed to respond if the stimulus was a face or nonface by pressing the corresponding button on a response box. The instructions emphasized that subjects should respond as soon as they were confident of whether they were seeing

Table 1

Average Talairach positions and volumes of the ROIs across all subjects

	Right hemisphere		Left hemisphere	
	Talairach position	Volume (mm^3)	Talairach position	Volume (mm^3)
Primary ROIs				
FFA	37, −44, −12	353	−38, −52, −13	325
Motor cortex	n/a	n/a	−33, −22, 57	644
Striate cortex	10, −86, 2	1886	−7, −89, 1	1852
Parahippocampal gyrus	25, −51, −8	2459	−27, −53, −9	2779
Additional ROIs				
OFA	39, −68, −12	260	−42, −66, −12	394
LOC	42, −66, −4	2131	−30, −52, 1	2492
IPS	30, −38, 28	827	−34, −27, 27	691
DLPFC	38, 18, 24	2471	n/a	n/a

Note: Primary ROIs included the FFA, left motor cortex, striate cortex, and object-selective regions in the parahippocampal gyrus. Other ROIs included the OFA, the LOC, the IPS, and the right DLPFC. Lateralized regions that were not part of the analysis are listed as not applicable (n/a).

a face stimulus or nonface stimulus. To ensure that the perceptual discrimination task was feasible and as naturalistic as possible, subjects were allowed to make eye movements. Previous studies have shown that the FFA responds robustly to unambiguous faces under conditions of naturalistic free viewing (Hasson and others 2004). Moreover, we did not expect to find modulations in FFA activity as a function of shifts in eye position, given that the FFA responds robustly to faces across a wide range of eccentricities (Levy and others 2001), and our face stimuli were large, centrally presented, and spanned almost the entire image. Subjects completed 6 experimental fMRI runs involving the Mooney stimuli and received a total of 36 face trials and 36 nonface trials. The order of stimulus presentation was randomized, and each image was presented only once throughout the entire experiment.

fMRI Data Preprocessing

Functional data were motion corrected using automated image registration (Woods and others 1998). Subsequent preprocessing steps were performed using Brain Voyager (Brain Innovation, Maastricht, The Netherlands). Slice scan-time correction was applied to the fMRI time series, and linear trends were removed. No temporal or spatial smoothing was applied. fMRI data were aligned to the structural 3D image and transformed into Talairach coordinates.

Primary ROIs

Primary ROIs were identified in individual subjects based on independent a priori criteria. Time courses of activity were later extracted from these regions to test for effects of perceptual decision making. Face- and object-selective regions in the ventral visual cortex were identified based on fMRI activity from 2 separate runs, during which subjects alternately viewed stimulus blocks of faces and common objects (12 blocks/stimulus type), with fixation rest periods between stimulus blocks (Kanwisher and others 1997; Tong and others 1998).

Multiple regression analysis was performed using predicted hemodynamic time courses derived by convolving the time course of each stimulus type with a gamma function to account for hemodynamic lag. The FFA was identified in individual subjects as the region in the fusiform gyrus that responded significantly more to faces than objects using a minimum statistical threshold of $t > 5.2$, $P < 0.025$ corrected for multiple comparisons. Object-selective visual areas served as a control to assess whether any effects found in the FFA were specific to that cortical region. We identified object-selective regions in the parahippocampal gyrus by selecting voxels that responded significantly more to objects than faces using the same minimum threshold of $t > 5.2$. The final ROIs used for experimental analyses were additionally constrained by selecting activated voxels within the predefined FFA and object-selective parahippocampal region that revealed greater activity for all experimental trials than fixation baseline, using a minimum statistical threshold of $t > 4.0$, $P < 0.0001$ uncorrected.

All subjects showed reliable FFA activations according to these dual criteria (see Table 1 for average Talairach positions and volumes of all ROIs). Bilateral object-selective regions in the parahippocampal gyrus were reliably identified in 5 out of 6 subjects; the remaining subject who showed unreliable activation was excluded from further analyses of this region. The location of these parahippocampal activations corresponded well with previous reports of the locus of the parahippocampal place area (PPA) (Epstein and others 2003), as one might expect given that the PPA responds most strongly to scenes and houses, moderately to common objects, and weakly to faces (Epstein and Kanwisher 1998).

Primary visual cortex was identified in 4 subjects using standard retinotopic mapping techniques to delineate the boundaries between retinotopic visual areas (Sereno and others 1995; DeYoe and others 1996; Engel and others 1997). Details of our specific procedures for retinotopic mapping can be found in previous reports (Awater and others 2005). We identified activated voxels within V1 that showed greater activity across all experimental stimulus conditions compared with a fixation baseline, using a minimum statistical threshold of $t > 5.6$, $P < 0.0001$ corrected. In 2 other subjects, retinotopic maps were not available, and voxels corresponding to primary visual cortex were selected from the fundus of the calcarine sulcus, which invariably corresponds to V1 (Stensaas and others 1974; Tong and Engel 2001). All subjects showed similar time courses in fMRI activity, irrespective of the method of V1 localization. For each subject, we also localized the motor cortex region that corresponded to the finger representation. We selected the region within the primary motor cortex, as indicated by sulcal and gyral anatomy, that responded positively to all trials in which the subject made a finger response, using a minimum statistical threshold of $t > 5.6$. One subject, who failed to show reliable motor cortex activation, was excluded from the analyses involving motor cortex.

Additional ROIs

Although not a primary focus of the present study, we conducted analyses of several additional ROIs to assess whether the decision-related activity might also be evident in other relevant brain areas. These additional regions included the occipital face area (OFA), the lateral occipital complex (LOC), the intraparietal sulcus (IPS), and the right dorsolateral prefrontal cortex (DLPFC) (see Table 1). These regions were selected because of their possible involvement in face perception, object perception, or perceptual decision making. The OFA, which is positioned more posterior and lateral to the FFA, also responds more strongly to face stimuli than to other objects (Gauthier and others 2000; Yovel and Kanwisher 2005). Area LOC has been implicated in object perception and recognition (Malach and others 1995; Grill-Spector and others 2000). Both the IPS region and the DLPFC have recently been implicated in perceptual decision making, with a role in integrating information from earlier perceptual areas (Schall 2001; Shadlen and Newsome 2001; Heekeren and others 2004; Huk and Shadlen 2005). The OFA was functionally defined as a region within the inferior occipital gyrus that responded significantly more to faces than objects during the face–object localizer scans, using a minimum statistical threshold of $t > 5.2$, $P < 0.025$ corrected. All other ROIs were selected based on their established anatomical locations, by identifying the appropriate sulcus or gyrus in individual subjects and further selecting all voxels that showed positive activation during the Mooney experiment at a threshold of $t > 5.6$.

Time Course Analyses

The time courses of activity in the primary ROIs were analyzed by comparing event-related averages for the subset of trials that led to the fastest (0–25th percentile) and slowest (75–100th percentile) response times for perceptual decisions about faces (see Fig. 3 and Results for details). Event-related averages were computed across all relevant experimental trials and conditions for the fMRI activity found in each ROI. Activity levels for each trial were normalized by calculating the percent change in magnetic resonance intensity relative to the intensity observed at the start of each trial at the time of 0 s. To determine the time point at which activity first rose significantly above baseline (see Fig. 4), we first performed a 2-way analysis of variance with response category (face short and face long) and time (0–22 s) as separate factors. The resulting mean squared error and associated degrees of freedom were then used to perform planned pairwise comparisons between the activity level observed at time point 0 and each subsequent time point until a reliable difference was observed at the $P < 0.05$ level. This method of identifying the first fMRI time point that was significantly greater than baseline proved to be sensitive and reliable; in all cases, we observed that the subsequent time point was also significantly greater than baseline.

Individual Trial Analysis

Additional analyses were performed to investigate the relationship between the time of rising fMRI activity (fMRI rise time) and behavioral response times. fMRI rise times were calculated for each trial by fitting a sinusoid function to the fMRI time course and using the inflection point of the fitted function as an objective estimate of when fMRI activity rose above baseline. Previous studies have shown that the temporal onset of visual neuronal activity is better predicted by the inflection point in the rising portion of the BOLD response than by other measures such as the time of peak activity (Menon and others 1998). The frequency, phase, amplitude, and vertical displacement of the sinusoid function were adjusted using a standard algorithm in Matlab to minimize the mean squared error between actual and fitted data over time points –4 to +16 s relative to stimulus onset. Correlation and linear regression values were then calculated to assess the strength of the relationship between fMRI rise times and behavioral response times for each condition and ROI.

Results

The behavioral data revealed the challenging nature of the task; subjects often required several seconds to decide if a face was present in the stimulus or not (mean response time 5.8 s, range 0.7–11.7 s). Nonetheless, accuracy was quite high. On face stimulus trials, subjects correctly responded "face" on 75% of trials (hits) and failed to respond "face" on only 20% of trials (misses). Subjects failed to respond within the 12-s stimulus period on the remaining 5% of trials. When a nonface was presented, subjects correctly responded "nonface" on 76% of trials (correct rejections), erroneously classified the nonface stimulus as a face on 14% of trials (false alarms), and failed to respond in time on 10% of the trials. The distributions of all response times for correct face judgments were generally faster than those for correct nonface judgments (mean ± standard deviation [SD] for face and nonface responses, 3.90 ± 2.67 s and 7.31 ± 2.03 s, respectively), and a comparison of mean response times for individual subjects revealed a significant difference ($F_{1,5} = 68.41$, $P < 0.001$). These results are consistent with the possibility that subjects may have responded "nonface" if they had difficulty perceiving a face after inspecting the stimulus for an extended time period.

Figure 2 shows the time course of fMRI activity in the FFA for correct and incorrect behavioral responses to face and nonface stimuli. As predicted, FFA activity was significantly greater for correctly identified faces than for correctly identified nonfaces (red vs. blue solid curves, respectively, $F_{1,120} = 17.38$, $P < 0.0001$). More interestingly, activity in this region also corresponded to the subject's perceptual interpretation of the stimulus. FFA responses to face stimuli were significantly greater when subjects successfully perceived the face than when they failed to detect the face (red solid vs. red dashed curves, $F_{1,120} = 5.05$, $P < 0.05$), consistent with findings from previous studies (Dolan and others 1997; Kanwisher and others 1998; Andrews and Schluppeck 2004; Grill-Spector and others 2004; Wild and Busey 2004). Perhaps more surprisingly, FFA activity was also significantly greater when nonface stimuli were mistakenly perceived as faces than when they were correctly classified as nonfaces (blue dashed vs. blue solid curves, $F_{1,120} = 4.13$, $P < 0.05$). These findings concur with recent reports that face-related activity may be greater even when subjects mistakenly perceive a face when none is present (Wild and Busey 2004; Summerfield and others 2005). The present results indicate that the "amplitude" of the FFA response closely reflects the subject's perceptual decision about these ambiguous Mooney stimuli.

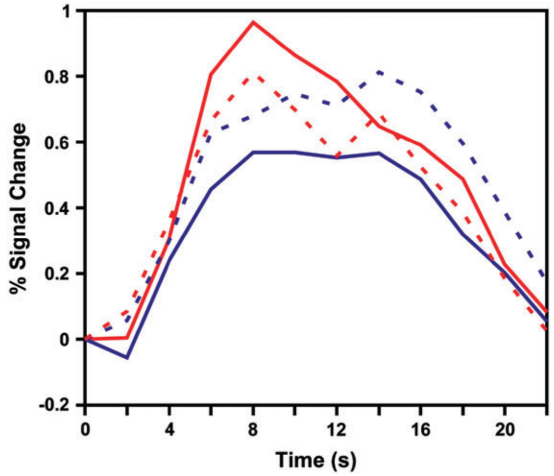

Figure 2. Time course of fMRI activity in the FFA for correctly and incorrectly classified faces and nonfaces. FFA activity was significantly greater when face stimuli were correctly identified as faces (red solid curve) than when they were incorrectly classified as nonfaces (red dashed curve). FFA activity was also greater when nonface stimuli were incorrectly classified as faces (blue dashed curve) than when they were correctly identified as nonfaces (blue solid curve). fMRI data were normalized by converting magnetic resonance signal intensities to percent signal change relative to time point 0 s for each trial. The stimulus was presented from time 0 to 2 s and replaced by a fixation point from time 12 to 24 s. Average fMRI time courses were calculated for each of the 5 subjects who made errors in this task and then analyzed using within-subjects analysis of variance (ANOVA) with response category and time (time points 2–22 s, TR 2 s) as separate factors. Planned contrasts were performed using the mean squared error and degrees of freedom from the 2-way ANOVA to test for differences in fMRI peak amplitudes (time points 6–12 s) across conditions.

Time Course of FFA Activity during Perceptual Decisions

To determine if activity in the FFA reflects the "timing" of perceptual decisions, we separately analyzed fMRI trials according to whether the subject required a short or long amount of time to reach a decision. Figure 3*A* shows a histogram of response times on correct face-response trials for a representative subject. The vertical dashed lines indicate the 25th and 75th percentiles of the distribution, which were used to separately bin the fMRI data according to the shortest quartile of response times (face-short trials) and the longest quartile of response times (face-long trials). Figure 3*B* shows these response times pooled across all subjects with vertical dashed lines, indicating the mean value of the 25th and 75th percentiles across subjects.

Figure 4*A* shows the time course of FFA activity on face-short and face-long trials; significant deviations above baseline (indicated by arrows) reflect the onset of face-specific activity (see Methods for analysis' details). In Figure 4*A*, the average time course for correct nonface trials was subtracted from the time course of each correct face-response trial to isolate the face-specific component of FFA activity. This subtraction was not applied to other ROIs that lacked face-selective activity. FFA activity for face-short responses (black solid curve) first rose significantly above baseline at 6-s poststimulus onset ($F_{1,55} = 6.74$, $P < 0.05$), consistent with the typical lag associated with

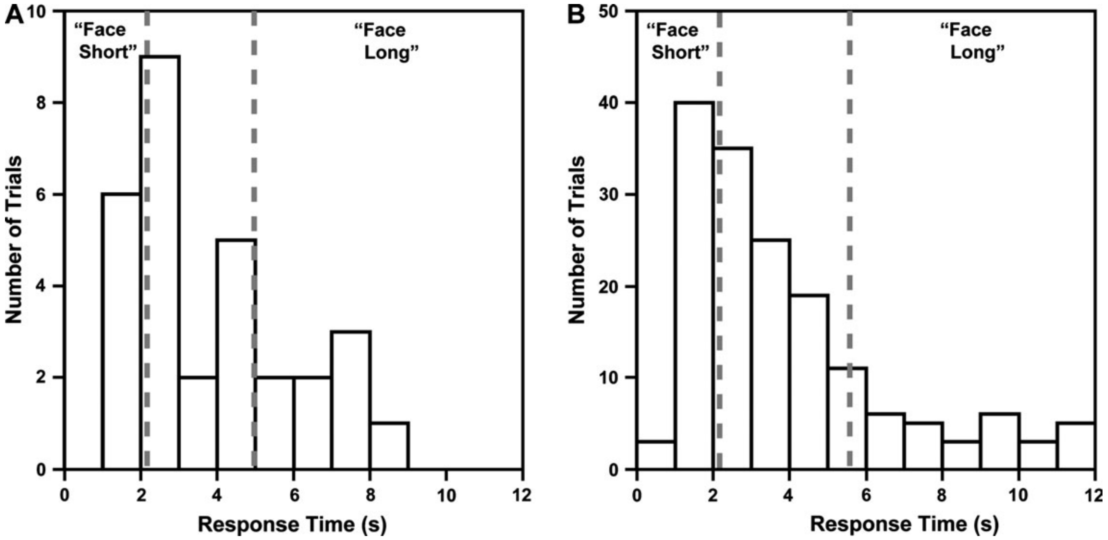

Figure 3. Histograms of behavioral response times for correct face responses. Response times are tallied in 1-s bins for 1 representative subject (*A*) and all subjects (*B*). Dashed lines indicate upper and lower quartile boundaries. The fastest 25% of response times for each subject were labeled as face-short responses (mean 1.66 s, SD across subjects 0.47 s); the slowest 25% of response times were labeled as face-long responses (mean 7.68 s, SD 2.14 s). Valid responses had to occur within the 12-s stimulus presentation period.

the hemodynamic BOLD response. In contrast, face-long activity (gray dashed curve) rose above baseline activity much later in time, at 10-s poststimulus onset ($F_{1,55} = 5.10$, $P < 0.05$). These results suggest a strong coupling between FFA activity and the time of the subject's perceptual decision. Even though the Mooney stimulus remained physically present on the screen for several seconds prior to the subject's decision, the onset of face-specific activity did not emerge until a much later point in time on face-long trials, reflecting the additional time required by the subject to form a perceptual decision.

Time Course of Activity in Motor Cortex

FFA activity was further compared with the time course of activity in motor cortex, which directly reflects the behavioral instantiation of the subject's decision. The motor ROI was successfully identified in 5 out of 6 subjects based on reliable activations found in the left precentral gyrus for all experimental trials when compared with fixation baseline. Figure 4*B* shows that the fMRI activity corresponding to the finger representation in motor cortex first rose significantly above baseline levels at 6-s poststimulus onset for face-short responses ($F_{1,44} = 14.69$, $P < 0.0005$) and at 10-s poststimulus onset for face-long responses ($F_{1,44} = 7.86$, $P < 0.01$). These fMRI rise times in motor cortex closely resemble those found in the FFA (Fig. 4*A*,*B*), indicating that activity in face-selective visual areas was time locked to the formation and behavioral instantiation of the perceptual decision.

Absence of Decision-Related Activity in Nonface-Selective Visual Areas

For comparison, we analyzed activity in nonface-selective visual areas to assess whether the decision-related activity found in the FFA might instead be attributable to nonspecific factors, such as a general increase in physiological arousal, visual attention, or the frequency of eye movements. If so, then other nonface-selective visual areas should also show evidence of decision-related activity. Instead, we predicted that visual areas that lack face selectivity should fail to show activity changes associated with the time of the perceptual decision.

Activity in the primary visual cortex (V1) was tightly coupled to the time of stimulus presentation and not to the perceptual decision (Fig. 4*C*). V1 activity rose significantly above baseline at 4 s after stimulus onset for both face-short and face-long trials ($F_{1,55} = 40.72$, $P < 0.0001$ and $F_{1,55} = 20.78$, $P < 0.0001$). The parahippocampal gyrus, which typically responds more strongly to nonface objects than to faces (Epstein and Kanwisher 1998), also showed similar fMRI rise times on face-short and face-long trials (Fig. 4*D*). Activity first rose above baseline at 4-s poststimulus onset ($F_{1,44} = 25.79$, $P < 0.0001$ and $F_{1,44} = 11.55$, $P < 0.001$) and showed no correspondence to the time of the subject's perceptual decision. Additional analyses of fMRI responses to nonface stimuli also revealed no consistent relationship between parahippocampal activity and the time of perceptual decisions (see below). Taken together, the above results indicate that the decision-related activity found in the FFA is not a general property of the visual system and cannot be explained in terms of global increases in arousal, visual attention, or eye movements. Instead, the FFA appears to convey specific information about the content and timing of perceptual decisions for ambiguous face stimuli.

Individual Trial Analysis: Correlations between the Timing of Perceptual Decisions and fMRI Activity

We further examined decision-related activity in the FFA by measuring the relationship between the rise time in fMRI activity and the time of subject's decision on individual trials, using a novel time-resolved analysis (see Methods). A sinusoid function was fitted to the fMRI time course of each trial, and the resulting inflection point served as an objective estimate of the rise time in fMRI activity (Fig. 5*A*). Next, we tested for significant correlations between the rise time in FFA activity and response time on correct face-response trials for each subject. Figure 5*B* shows the relationship between rise time in FFA activity and behavioral response time for a representative subject (S3). When subjects required a greater amount of time

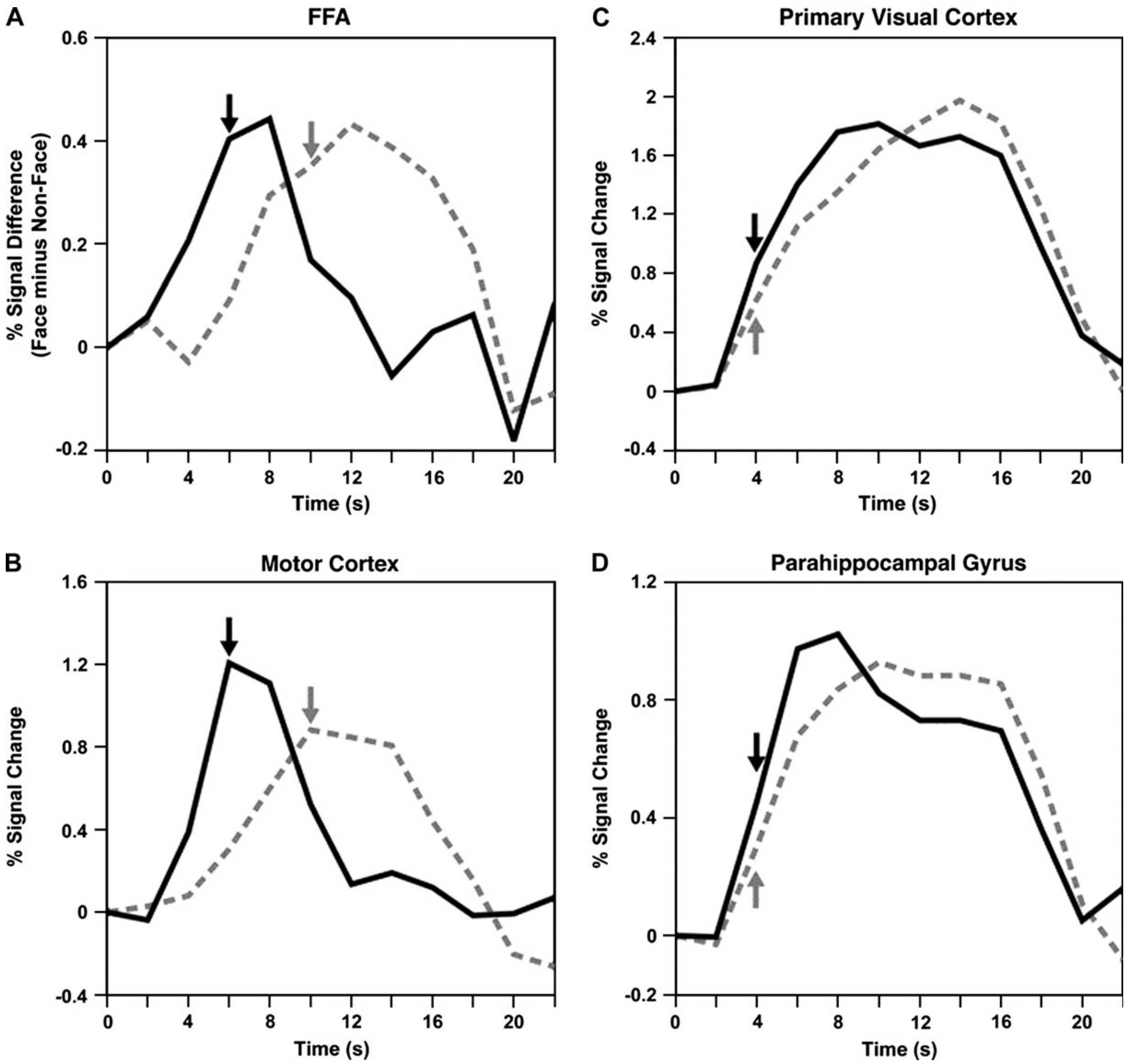

Figure 4. Time course of fMRI activity for face-short and face-long responses. Plots show fMRI time courses, averaged across subjects, for all correct face-short responses (black solid curves) and face-long responses (gray dashed curves) in 4 ROIs. Arrows indicate the time point at which activity first rose significantly above baseline levels. (*A*) Face-specific FFA activity rose significantly above baseline levels at 6 s after stimulus onset for face-short responses (black arrow) and at 10 s for face-long responses (gray arrow). (*B*) Effects of perceptual decision time in motor cortex are strikingly similar to those in the FFA, with activity increasing above baseline at 6 s for face-short responses and 10 s for face-long responses. (*C*) Primary visual cortex shows no effect of perceptual decision time; both face-short and face-long responses led to significant increases in activity at 4-s poststimulus onset, indicating the stimulus-driven nature of the fMRI response. (*D*) Object-selective regions of parahippocampal gyrus also show no effect of perceptual decision time.

to reach a decision about a face, there was a concomitant increase in the time required for FFA activity to rise.

For correct face-response trials, we observed a significant correlation between the time of rising activity in the FFA and behavioral response times in 5 out of 6 subjects (see Table 2). In contrast, there was no evidence of a relationship between FFA rise times and behavioral decision times when subjects responded correctly to nonface stimuli. The results indicate that activity in the FFA closely reflects the timing of perceptual decisions for face judgments but does not reflect the timing of nonface judgments.

In motor cortex, the time of rising activity was reliably correlated with behavioral response times for both correct face-response trials and correct nonface trials, in 5 out of 5 and 4 out of 5 subjects, respectively (Table 2). Unlike the FFA, motor cortex reflected the time of the subject's behavioral response, independent of the type of decision. Additional analyses revealed a significant correlation between rise times in the FFA and motor cortex on correct face-response trials in 4 out of 5 subjects, further suggesting a link between FFA activity and the motor instantiation of the perceptual decision for faces. As a general note, we found that correlation values provided a better indicator of the strength of the relationship between rising fMRI activity and behavioral response times than estimated slope values from the correlation–regression analysis. This is because any activity elicited by the onset of the stimulus or task, such as visually driven activity or motor preparation activity, would lead to slope values of less than 1. Average slope values for the FFA and motor cortex on correct face-response trials were 0.31 and 0.49, respectively, and did not reliably differ.

Unlike the robust decision-related activity found in the FFA, nonface-selective visual areas failed to show evidence of such effects. In primary visual cortex, none of our 6 subjects showed a significant relationship between fMRI rise times and

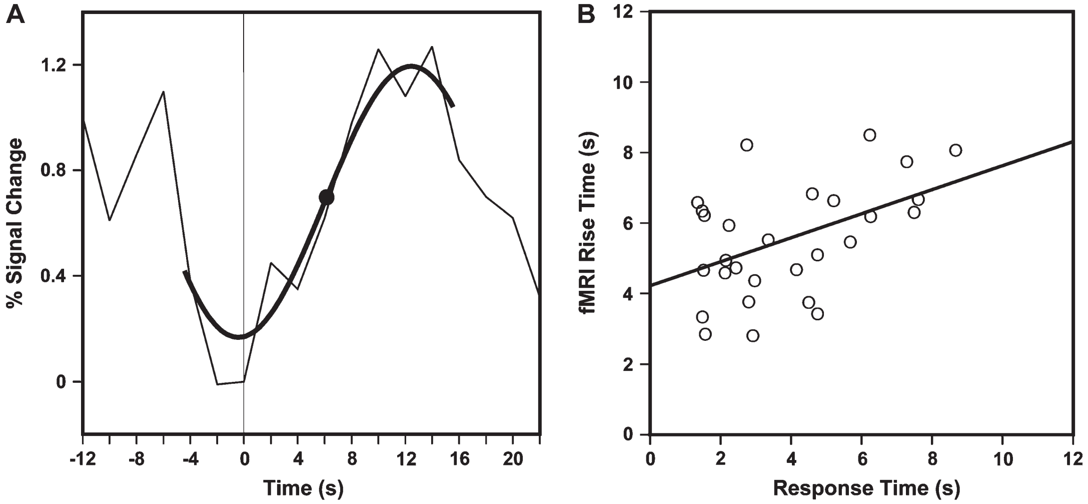

Figure 5. Relationship between behavioral response time and fMRI rise time across individual trials. (*A*) The time of rising fMRI activity was quantified on individual trials by calculating the best-fitting sine function and deriving the point of inflection as an objective estimate of when fMRI activity rose above baseline levels. (*B*) Correlation between fMRI rise times in the FFA and behavioral response times on correct face-response trials for a representative subject (S3).

Table 2

Correlation coefficients between the time of rising fMRI activity and behavioral response times for correct face responses (top) and correct nonface responses (bottom)

Subject	Primary ROIs				Other ROIs			
	FFA	MC	V1	PG	OFA	LOC	IPS	DLPFC
Correct face responses								
S1	**0.61**	**0.41**	0.15	**0.53**	**0.52**	**0.47**	**0.39**	0.02
S2	**0.52**	**0.61**	0.33	0.23	n/a	**0.39**	0.32	**0.47**
S3	**0.49**	**0.80**	0.31	0.13	**0.43**	0.35	**0.61**	0.34
S4	**0.46**	**0.59**	0.08	0.19	**0.40**	**0.43**	0.33	0.35
S5	0.14	**0.48**	0.01	−0.02	−0.25	−0.03	−0.08	−0.14
S6	**0.40**	n/a	0.37	n/a	n/a	−0.02	0.24	0.26
Correct nonface responses								
S1	0.03	**0.53**	0.27	0.26	0.05	0.20	**0.40**	0.30
S2	0.24	**0.40**	0.16	0.24	n/a	0.25	0.23	0.17
S3	0.16	**0.66**	0.37	0.24	0.14	0.06	0.22	0.13
S4	−0.01	0.25	−0.01	0.11	−0.03	−0.06	0.22	−0.29
S5	0.08	**0.67**	0.23	−0.04	0.06	0.04	0.14	0.03
S6	0.20	n/a	−0.37	n/a	n/a	−0.29	−0.28	−0.27

Note: Data are shown for primary regions (left) and additional ROIs (right). Significant correlations are indicated in bold ($P < 0.05$). If a given region was not reliably identified in a particular subject, the subject was excluded from the analysis (not applicable, n/a). For correct face responses (top), areas that showed reliable decision-related activity in the majority of subjects included the FFA, left motor cortex (MC), and OFA. In comparison, all other areas showed inconsistent or weak effects: primary visual cortex (V1), parahippocampal gyrus (PG), LOC, IPS, and DLPFC. Only the motor cortex showed reliable effects for nonface responses.

behavioral decision times for correct face responses. Similarly, only 1 out of 5 subjects showed significant effects in object-selective regions of the parahippocampal gyrus (one subject who lacked object-selective activity was excluded from this analysis). These results agree with our average time course analyses comparing short and long response times for face decisions in these regions and provide further evidence indicating that the decision-related activity found in the FFA cannot be explained in terms of global modulations throughout the visual pathway. Analyses of correct nonface responses also revealed no evidence of decision-related activity in these regions.

Individual Trial Analysis of Additional ROIs

Although not a primary focus of the present study, we performed the same individual trial analysis on several additional ROIs to assess whether decision-related activity might also be evident in other brain areas implicated in face perception, object perception, or perceptual decision making. These additional regions included the OFA, LOC, IPS, and DLPFC (Malach and others 1995; Gauthier and others 2000; Shadlen and Newsome 2001; Heekeren and others 2004; Huk and Shadlen 2005; Yovel and Kanwisher 2005). The OFA, which lies posterior and lateral to the FFA, was successfully localized in 4 out of 6 subjects by identifying voxels that responded more to faces than objects during the face–object localizer scans. All other ROIs were identified based on their anatomical location, and voxels that were reliably activated by the experimental task within these anatomical regions were selected for further analysis.

The right side of Table 2 shows the results of the individual trial analyses for these additional ROIs, with significant correlations indicated in bold text. In general, correlations between cortical activity and behavioral decision times were more prevalent in the FFA and motor cortex than in these other ROIs. Also, there was minimal evidence of decision-related activity in any of these regions during correct nonface responses.

Analyses of correct face trials revealed a reliable relationship between the time of rising fMRI activity and response times in the OFA in 3 out of 4 subjects, intermediate effects in area LOC (3 out of 6 subjects), and generally weaker effects in higher order areas of the IPS (2 out of 6 subjects) and DLPFC (1 out of 6 subjects). The more prevalent effects found in the OFA are consistent with the hypothesized role of this region in face perception and indicate that the activity in this region reflects not only a stimulus-driven preference for face stimuli (Gauthier and others 2000; Yovel and Kanwisher 2005) but also can reflect the perceptual interpretation of a face as it evolves over time. Area LOC has been strongly implicated in object perception and recognition and responds much more strongly to intact objects and faces than to scrambled stimuli (Malach and others 1995; Grill-Spector and others 2000). The response properties of LOC may explain why half of our subjects showed positive evidence of decision-related activity on correct face trials in this region. Greater activity may have reflected the perception of a coherent face rather than an uninterpretable set of fragmented shapes. In general, however, the effects found in area LOC were less consistent than those found in face-selective areas of ventral cortex.

Our analyses of higher order parietal–prefrontal areas, implicated in visual attention and perceptual decision-making studies, revealed surprisingly weak evidence of decision-related activity. Only 1–2 subjects showed evidence of decision-related activity on correct face-response trials in the IPS and DLPFC, and only 1 subject showed a reliable effect on correct nonface response trials in the IPS. These results greatly differ from the highly reliable effects found in the motor cortex of our subjects. What might account for the difference between our results and previous neurophysiological studies, which have found strong effects of perceptual decision making in the frontal eye fields and lateral IPS? In these previous studies, monkeys were required to maintain fixation until they were ready to report their decision by making an eye movement to 1 of 2 targets, and decision-related activity was usually measured in neurons that were involved in selecting the potential targets for eye movements. In contrast, our subjects were not constrained when viewing the stimulus and were allowed to shift their eyes and attention freely and could report their decision independently of the oculomotor system by making finger movements. Therefore, our study effectively decoupled shifts of visual attention and eye movements from the subject's behavioral report of the decision, which may account for the weak decision-related effects that we found in attention-related frontal–parietal areas.

Discussion

The present study revealed a close relationship between activity in the human ventral visual cortex and the time required to form perceptual decisions about face-like stimuli. Using fMRI, we were able to monitor activity from multiple sites along the sensorimotor pathway, while subjects had to distinguish ambiguous faces from visually similar nonfaces. Activity in face-selective visual areas, in particular the FFA, was tightly linked to the time of the subject's decision, even on a trial-by-trial basis. Activity in these face-selective areas reflected the timing of perceptual decisions specifically for faces, but not for nonface judgments, and closely resembled the timing of activity in motor cortex corresponding to the subject's behavioral response. Therefore, activity in the FFA (as well as the OFA of some subjects) corresponded to both the perceptual content and the timing of the subject's decision about faces. These results indicate that the timing of perceptual decisions can be reflected at an early stage of processing along the sensorimotor pathway.

Our results indicate that face-selective regions in the ventral visual cortex are closely associated with the timing of perceptual decisions for faces and may have an important role in forming decisions about ambiguous face stimuli. Intermediate effects were found in area LOC, suggesting that these perceptual decisions might be partially distributed across multiple visual areas. However, we found no evidence of decision-related activity in area V1 or object-selective regions of the parahippocampal gyrus, indicating that these effects are not evenly distributed throughout the visual cortex. Weak effects were also observed in attention-related regions of the parietal and prefrontal cortex, perhaps because our subjects were allowed to report their decision with a finger movement, unlike previous neurophysiological studies that required animals to make an eye movement to report their decision. Taken as a whole, the above results are consistent with the notion that face-selective areas of the human brain may be especially important for forming decisions about their preferred stimulus category.

One might ask does this decision-related activity arise in face-selective areas and whether this activity results from bottom–up processing and integrative activity within the ventral visual cortex proper or from top–down signals sent by higher order areas. We found that high-level frontal–parietal areas, previously implicated in visual attention and perceptual decision making, showed weak or negligible effects of decision-related activity, unlike the robust effects found in motor cortex. Therefore, these higher areas cannot readily account for the decision-related timing effects found in the FFA and OFA. Moreover, it is unclear how higher order areas might disambiguate Mooney images unless one assumes that these regions contain detailed visual representations of facial attributes, and evidence of finely tuned face representations has been primarily found in the ventral visual pathway (Gross 1994; Sugase and others 1999; Tsao and others 2006). For these reasons, the decision-related activity found in the FFA and OFA is difficult to explain in terms of top–down feedback from frontal–parietal areas and, instead, appears to reflect integrative processing within the ventral visual cortex.

More generally, our results suggest that ventral visual areas may be important for the formation of perceptual decisions about ambiguous visual forms. Previous neuroimaging studies of object perception have primarily focused on the amplitude of activity changes without regard to timing (Dolan and others 1997; Kanwisher and others 1998; Tong and others 1998; Grill-Spector and others 2000, 2004; Bar and others 2001; Andrews and Schluppeck 2004; Summerfield and others 2006). Only a few studies have shown that activity in ventral areas is associated with the time of object perception, such as during binocular rivalry (Tong and others 1998), when the visibility of a stimulus fluctuates over time due to early neural competition between conflicting monocular signals (Tong and Engel 2001), and also during object memory priming, when a previous encounter with an object can facilitate the visual threshold at which that item is later recognized during a staircase procedure in which the object is gradually uncovered over time (James and others 2000). Our results add to this previous body of work by establishing a clear link between cortical activity and the time required to reach a perceptual decision about novel stimuli, under conditions in which the visual stimuli remain constant and continuously visible over time. Therefore, the activity changes observed here cannot be attributed to changes in perceptual visibility, changes in physical visibility, or shifts in visual threshold resulting from previous experience with an object. Moreover, our results provide evidence of the specificity of this temporal relationship between neural activity and perceptual content (e.g., activity in the FFA was specific to face judgments). This was observed even at a fine-grained level of analysis of individual trials.

Our results indicate that activity in ventral visual areas can closely reflect the timing of perceptual decisions for ambiguous stimuli that remain constant over time. Unlike the robust decision-related effects found here in face-selective visual areas, previous neurophysiological and neuroimaging studies have reported that activity changes in early perceptual areas were independent of the time required to reach a decision. In these previous studies, subjects had to discriminate weak motion signals, face images, or complex objects in visual noise, and only parietal and prefrontal cortical areas proved capable of integrating these weak visual signals over time (Shadlen and Newsome 1996; Kim and Shadlen 1999; Heekeren and others 2004). Although there is some evidence that population activity in the middle temporal area (MT) can be pooled over time to predict the time of an animal's decision, neuronal response latencies in MT remain independent of decision times, whereas response latencies in parietal regions are strongly associated with decision times (Cook and Maunsell 2002). The pattern of FFA activity found here closely resembles the decision-related activity found previously in higher order areas, with activity rising above baseline at much later times for longer decisions. This temporal relationship was observed even though subjects displayed a wide range of decision times (1–12 s), much longer than those reported in previous studies. Our findings provide new evidence to suggest that activity in ventral visual areas may be closely linked to the time of perceptual decisions. Whereas most studies of perceptual decision making have relied on the presentation of weak sensory signals in noise, we used ambiguous Mooney images to delay the onset of perception. Mooney images can lead to many possible 2D and 3D perceptual interpretations, which lead to delays in converging on the final interpretation. Typically, when subjects first see a novel, ambiguous Mooney face, they initially perceive an unfamiliar 2D pattern of black and white fragments. Only by applying representational knowledge of facial structure is the subject eventually able to organize these jumbled 2D fragments into a coherent and salient 3D interpretation of a face (Moore and Cavanagh 1998; Ramachandran and others 1998). Our results suggest that the knowledge required for reorganizing and reinterpreting an ambiguous face stimulus may depend on the neural activation of appropriate face templates in the ventral visual cortex, which may be strongly represented in the FFA, OFA, and perhaps also area LOC (which also responds quite well to intact visual faces). As a consequence, these face representations in the ventral pathway may reflect an important processing stage necessary for transforming ambiguous sensory input into an appropriate response about face perception.

If this interpretation is correct, then our results suggest that the neural basis of perceptual decision making may be better understood by considering the many rate-limiting steps that might occur in the sequence of neural computations required to transform sensory input into visually guided action. Just as any series of chemical reactions may be gated by a single rate-limiting step, the time required to reach a perceptual decision could likewise result from a bottleneck in neural processing anywhere along the sensorimotor pathway (Sato and others 2001; Parker and Krug 2003). Previous studies have established the importance of parietal and prefrontal areas in integrating weak sensory signals over time to reach a decision. The present study further suggests that face-selective visual areas, and in particular the FFA, may be important for forming decisions about ambiguous face-like stimuli. These results shed light on the potential contributions of different brain regions along the sensorimotor pathway, when one must decide among competing alternatives under conditions of uncertainty.

Notes

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