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Brief article

The effect of face inversion on the human fusiform face area

Nancy Kanwisher^{a,b,*}, Frank Tong^c, Ken Nakayama^c

^a*Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology,
Cambridge, MA 02139, USA*

^b*Massachusetts General Hospital Nuclear Magnetic Resonance Center,
Charlestown, MA 02129, USA*

^c*Department of Psychology, Harvard University,
Cambridge, MA 02138, USA*

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Abstract

Inversion severely impairs the recognition of greyscale faces and the ability to see the stimulus as a face in two-tone Mooney images. We used functional magnetic resonance imaging to study the effect of face inversion on the human fusiform face area (FFA). MR signal intensity from the FFA was reduced when greyscale faces were presented upside-down, but this effect was small and inconsistent across subjects when subjects were required to attend to both upright and inverted faces. However when two-tone faces were inverted, the MR signal from the FFA was substantially reduced for all subjects. We conclude that (i) the FFA responds to faces *per se*, rather than to the low-level visual features present in faces, and (ii) inverted greyscale faces can strongly activate this face-specific mechanism. © 1998 Elsevier Science B.V. All rights reserved

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1. Introduction

Evidence from a wide variety of sources suggests that the perception of faces may be ‘special’ in two senses. First, the processes involved in face recognition may be qualitatively different from those involved in the recognition of other kinds of objects. This claim is supported by behavioural experiments showing that the disruption of recognition performance that results when a face is presented upside-

* Corresponding author. Fax: +1 617 2539767.

down is considerably greater than the analogous inversion cost for the recognition of objects (Yin, 1969; see Valentine, 1988 for a review; but also see Diamond and Carey, 1986). Second, neuropsychological double dissociations between face and object recognition suggest that these processes are subserved by different regions of the brain (e.g. Newcombe et al., 1994).

Perhaps the most striking evidence for the specialness of face processing comes from the recently reported neurological patient CK (Moscovitch et al., 1997). Although severely impaired at a wide range of visual tasks including the recognition of words and objects, CK is absolutely normal at recognising upright faces. Further, CK exhibits a face inversion cost that is six times greater than that observed in normal subjects. Moscovitch et al. explain this result by arguing that the face-specific mechanisms preserved in CK are unable to process inverted faces (see also Farah et al., 1995).

In another line of evidence for the specialness of faces, several imaging studies (Ishai et al., 1997; Kanwisher et al., 1997a; McCarthy et al., 1997) have demonstrated a focal region in the fusiform gyrus called the fusiform face area or FFA (see Fig. 1) that responds in a highly selective fashion to faces, compared to a wide variety of other stimulus types. However, the evidence for the selectivity of the FFA is based on comparisons of the response to different stimulus types, so it remains logically possible that this area responds not to faces per se, but to some confounding low-level visual feature which is present in face stimuli.

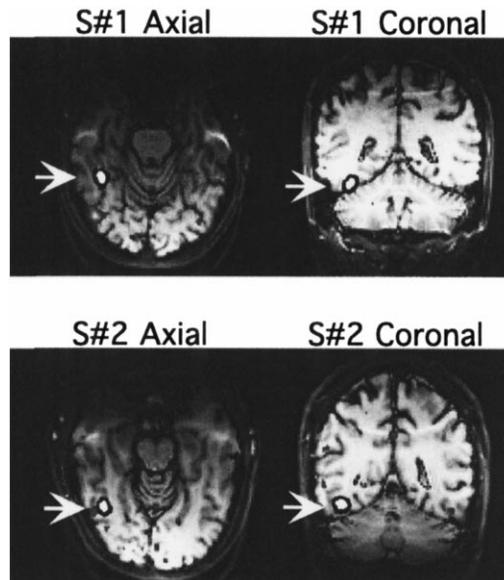


Fig. 1. An axial and coronal slice showing the fusiform face area (FFA) in two subjects. The arrow points to the FFA (the white spot outlined in black) in each image. This region responded significantly more during passive viewing of faces than passive viewing of objects in the functional localiser scan, $P < 0.0001$ (uncorrected). Right hemisphere is shown on the left in all images.

The present study measured fMRI responses in the FFA to upright and inverted faces in order to address two questions. First, does the FFA respond to faces per se, or to a confounding visual feature which tends to be present in faces? Second, is it true that inverted faces cannot engage face-specific mechanisms (Moscovitch et al., 1997)? If the FFA were found to respond only to upright faces (or to a much greater degree to upright than to inverted faces) then both questions could be answered affirmatively. This result would show that face-specific mechanisms are engaged only (or predominantly) by upright faces. And because the identical stimulus would be presented in upright and inverted conditions, any differential activation for the two cases would have to reflect face processing per se rather than differences in the low-level features present in the stimuli.

However, there were reasons to suspect that the FFA might not show a face-inversion effect. Both single-unit recordings from face-selective neurons in macaque temporal cortex (Perrett et al., 1988) and scalp recordings from humans (Jeffreys, 1989) have revealed comparable response amplitudes to upright and inverted faces, but greater response latencies to inverted faces. Such response latency effects would be extremely difficult to detect with fMRI.

The current study used both greyscale and two-tone Mooney (1957) faces to test two different kinds of face-inversion effect. Inversion of a greyscale face disrupts the ability to recognise the face, but not the ability to detect a face, that is, to see that a face is present. By contrast, inversion of a Mooney (1957) face disrupts face detection (George et al., 1997). Thus inversion effects for greyscale faces should reflect face recognition processes, whereas inversion effects for Mooney faces should reflect face detection processes.

2. Experiment 1: greyscale faces

Each subject's FFA was localised functionally by finding the region of his or her mid-fusiform gyrus that responded more strongly to faces than to either objects or houses in an independent localiser scan as described previously (Kanwisher et al., 1997a; Wojciulik et al., 1998). Fig. 1 shows examples of the localised FFA for two subjects taken from axial and coronal slices on independent sessions. After individually localising each subject's FFA, we then tested the hypothesis that the MR signal in this same region would be higher during presentation of upright than inverted greyscale faces in a separate set of functional scans run on the same subject in the same session. To control for attentional effects which are known to modulate the strength of the FFA response (Clark et al., 1996; Wojciulik et al., 1998), subjects performed passive viewing and 1-back matching tasks in separate scans. Because the 1-back task required if anything more attentional engagement on inverted than upright faces, whereas the opposite pattern of attentional engagement might be expected for the passive viewing task, our criterion for a genuine face-inversion effect was a consistent pattern of results across both tasks.

2.1. Method

2.1.1. Subjects

Ten healthy normal adults (six women), ages 21–38, with normal or corrected-to-normal vision, volunteered or participated for payment. All subjects gave informed written consent.

2.1.2. Stimuli

Greyscale face images consisted of 44 three-quarter view photographs taken at the Harvard Vision Sciences Laboratory (see Fig. 2a for examples).

2.1.3. Experimental procedures

Each subject was run on (i) two or more functional localiser scans containing

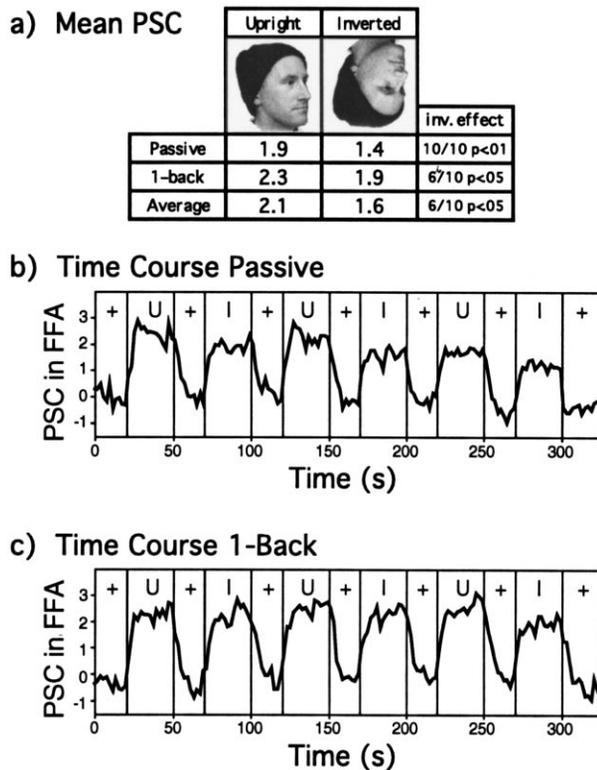


Fig. 2. (a) Example stimuli from Experiment 1 and the percent signal change (PSC) in the FFA (averaged over all voxels in each subjects predefined FFA, and then averaged over subjects) during viewing of upright and inverted greyscale faces in the passive viewing versus 1-back tasks. The number of subjects whose mean FFA PSC was higher for upright than inverted faces and the significance of the comparison is shown in the column at the right. At the bottom are shown the time courses of raw PSC (from the fixation baseline) averaged over all subjects' FFAs over the period of the scan, for (b) passive viewing and (c) 1-back tasks. +, fixation; U, upright greyscale faces; I, inverted greyscale faces.

epochs of faces and either objects or houses, and (ii) two or more scans each for the passive and 1-back tasks on upright versus inverted greyscale faces. Half of the subjects received passive viewing scans followed by the 1-back matching scans and other half received the reverse order. In the 1-back task, subjects were instructed to press a button whenever they saw two identical pictures in a row. Typically, one or two repetitions occurred in each epoch. Each scan lasted 5 min and 20 s and consisted of alternating 30-s epochs of upright and inverted faces (six epochs/scan) interleaved with 20-s fixation periods (see Fig. 2b,c). Faces were centrally presented in a random sequence at a rate of one every 667 ms (stimulus duration 450 ms, ISI 217 ms). The images subtended approximately $12^\circ \times 12^\circ$ and alternated between a top right or bottom left offset of 10% of the image width to discourage the use of low-level matching strategies.

2.1.4. MRI scanning procedures

Scanning was done on the 1.5 T scanner at the MGH-NMR Center in Charlestown, MA, using a bite-bar to minimise head motion and a bilateral surface coil which provided a high signal-to-noise ratio in posterior brain regions. Standard imaging procedures were used (TR, 2 s; TE, 70 ms; flip angle, 90° , 180° offset, 25 ms; 165 images/slice). Twelve 6- or 7-mm-thick coronal or axial slices covered the entire occipital lobe as well as the posterior portion of the temporal lobes, including the FFA. In all other respects, imaging procedures were identical to those reported by Kanwisher et al. (1997b).

2.1.5. Data analysis

Each subject's FFA was identified from the functional localiser scans as the set of all contiguous voxels in the fusiform gyrus that showed significantly greater activation to greyscale front view faces compared to houses or to common objects on a Kolmogorov–Smirnov test using a criterion of $P < 0.0001$ (uncorrected). For the analysis of the main experiment, image data for passive viewing and 1-back scans were separately averaged for each subject, and a time course of the magnetic resonance (MR) signal intensity was extracted from each subject's FFA (averaging over all voxels identified in the localiser scan for that subject). The average percent signal change in the FFA was calculated for each subject, stimulus condition, and task (incorporating an estimated 6-s haemodynamic lag), using the average signal intensity during fixation epochs for the same subject, experiment, and task as a baseline. An ANOVA across subjects was run on the average percent signal change in each of the conditions in each experiment. Because data were analysed within independently defined regions of interest, no correction for multiple voxel-wise comparisons was made.

2.2. Results and discussion

The FFA was localised in all ten subjects¹. The percent signal change (PSC) from

¹This high success rate reflects the fact that when possible we selected subjects who had revealed clear FFA activations in previous experiments in our lab. Typically, the FFA can be found in about 75% of subjects.

fixation for each condition in each subject's individually-localised FFA was calculated; the average PSC values across subjects are shown in Fig. 2a. An ANOVA across subjects on the PSC for each condition yielded a main effect of higher signal for upright than inverted faces ($F(1,9) = 10.6, P < 0.01$), and a main effect of higher signal in the 1-back than passive viewing task ($F(1,9) = 31.2, P < 0.0005$). The interaction of stimulus orientation by task did not reach significance ($F(1,9) = 2.95, P = 0.12$); however, a trend toward such an interaction was suggested in the data. In particular, the lower response for inverted compared to upright faces was seen in all ten subjects for the passive viewing condition ($t(9) = 3.8, P < 0.005$), but was seen in only six out of ten subjects for the 1-back task ($t(9) = 2.4, P < 0.05$)².

Although these data reveal a significant FFA inversion effect, it is small in magnitude and not found consistently across subjects in the critical 1-back condition. The response to inverted greyscale faces was much greater than the 0.5–1% signal changes typically observed in past studies for non-face control stimuli (Kanwisher et al., 1997b). Moreover, the FFA activity for inverted faces during 1-back matching was as strong as the activity for upright faces during passive viewing. Thus, inverted greyscale faces clearly can activate the FFA to a considerable extent. These results argue against the strong claim that inverted faces cannot activate face-specific mechanisms such as the FFA, and instead suggest a more subtle quantitative distinction between upright and inverted faces.

The behavioural data from the 1-back task replicated the well-known behavioural inversion effect: all of our subjects were more successful at detecting consecutive repetitions when faces were upright (91% hits minus false alarms) than inverted (57% hits minus false alarms), $t(9) = 6.08, P < 0.001$. Thus subjects were evidently processing the inverted faces much less effectively than the upright faces during the 1-back scans. Yet the FFA response was only about 15% lower for inverted compared to upright faces while subjects carried out this task.

When greyscale faces are inverted, recognition performance deteriorates but face detection is preserved. The next experiment tested whether face inversion might produce a stronger effect for Mooney faces, which are hard to perceive as faces at all when inverted.

3. Experiment 2: Mooney faces

In this experiment we presented upright and inverted two-tone Mooney faces³. Greyscale photos of faces and objects were also presented in the same scans to provide comparison values of maximal and minimal FFA responses, respectively. Methods were identical to those of Experiment 1 except as follows.

²The familiarity of the faces did not appear to interact with face-inversion effects: for subjects who were familiar with many of the stimulus faces ($n = 7$), the mean PSC was 2.05 for upright and 1.60 for inverted faces, and for subjects unfamiliar with the stimulus faces ($n = 3$), mean PSC was 2.10 for upright and 1.74 for inverted faces.

³The two-tone Mooney faces used in this study differed from the two-tone faces used by Kanwisher et al. (1997a) which were not Mooney-type faces and provided many more visual cues for face recognition.

3.1. Methods

3.1.1. Subjects

Eleven subjects were run. Data sets from three subjects were not included because two showed no FFA activation on the independent localiser scans and there were technical problems with the scans from the third. Of the eight remaining subjects, two subjects had participated in Experiment 1 in a previous session, and two subjects participated in Experiments 1 and 2 in the same session.

3.1.2. Stimuli

A set of 25 pictures was used for each of the four stimulus conditions: greyscale objects, inverted Mooney faces, upright Mooney faces and upright greyscale faces (see Fig. 3a for examples). To minimise potential transfer of learning effects between upright and inverted Mooney faces, half of the subjects viewed one set of 25 Mooney faces upright and the other set of 25 faces inverted. The remaining subjects viewed the reverse configuration. To accentuate the difficulty in perceiving the Mooney faces, a more rapid presentation rate of one image every 333 ms (stimulus duration 200 ms, ISI 133 ms) was used.

3.1.3. Experimental design

Each scan consisted of four blocks of four consecutive 16-s stimulus epochs (one epoch for each stimulus condition) with a 16-s fixation epoch between each block. Across the four blocks, each condition appeared once in each serial position within a block. Each subject performed two test scans. Half of the subjects performed the passive task and the remaining half performed 1-back matching.

3.2. Results and discussion

Subjects reported seeing the stimulus as a face more often in the upright than inverted Mooney images, replicating the results of George et al. (1997).

All eight subjects showed greater FFA activity to upright than inverted two-tone faces and this effect was highly consistent across passive and 1-back viewing conditions (see Fig. 3). An ANOVA revealed a highly-significant overall effect of stimulus condition, $F(3,18) = 66.6$, $P < 0.00001$, but no significant effect of task type ($F(1,6) < 1$)⁴ or interaction with task type ($F(3,18) = 1.6$, $P = 0.22$). Planned contrasts revealed a significantly greater FFA response to upright than inverted two-tone faces ($t(7) = 9.5$, $P < 0.00005$). Significantly greater FFA activity was also found for upright greyscale versus upright Mooney faces ($t(7) = 3.2$, $P < 0.05$), and for inverted Mooney faces versus common objects ($t(7) = 2.4$, $P < 0.05$).

In sum, the FFA response was much lower for inverted than upright Mooney faces, and this effect was found consistently across subjects and tasks. Although the

⁴The apparently larger activation during passive viewing than 1-back was unreliable and was largely due to data from one subject in the passive group who had particularly strong FFA activations.

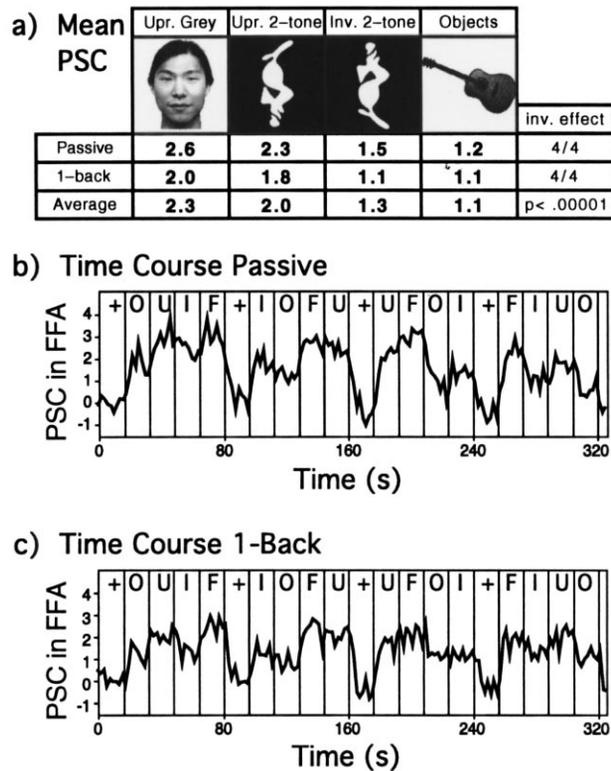


Fig. 3. (a) Example stimuli from Experiment 2 and the percent signal change (PSC) in the FFA during viewing all four stimulus conditions in the passive viewing versus 1-back tasks. The number of subjects whose FFA PSC was higher for upright than inverted two-tone faces is shown in the column at the right. At the bottom are the time-courses of raw PSC (from the fixation baseline) averaged over all subjects' FFAs over the period of the scan, for (b) passive viewing and (c) 1-back tasks. +, fixation; U, upright two-tone faces; I, inverted two-tone faces; F, upright greyscale faces; O, objects.

response was slightly higher to inverted Mooney faces than to objects, this may reflect the fact that all subjects reported seeing a face in some of the inverted Mooney images.

4. General discussion

These experiments demonstrate that inverted greyscale faces produce a strong FFA response, albeit somewhat weaker than the response to upright greyscale faces. However, inverted Mooney faces produce a considerably lower FFA response than upright Mooney faces. These results provide clear answers to the two questions posed above. First, the consistently lower response to inverted Mooney faces than to the identical images presented upright demonstrates that the FFA response cannot

be explained in terms of the presence of any specific low-level visual features⁵. Instead, the FFA response is correlated with the perception of a face. Second, the large response to inverted greyscale faces allows us to reject the strong version of the hypothesis (Moscovitch et al., 1997) that inverted faces cannot engage face-specific mechanisms. However, even though the FFA is apparently one face-specific mechanism that is engaged by inverted greyscale faces, it remains possible that there are other face-specific mechanisms which cannot be engaged by inverted faces⁶, and if so it could be those mechanisms that are preserved in patient CK.

Several further questions remain to be answered. First, would the inversion effect be significantly stronger for two-tone than greyscale faces when all the conditions are run within subjects and when other factors (like stimulus presentation rate) are equated across stimulus types? Second, does the FFA respond more strongly to an inverted face that had previously been viewed upright (which was usually the case in Experiment 1) than one that had not (as in Experiment 2)? While the answers to these questions are of some interest, they are not critical to the main issues addressed in this paper.

What clues do the present data provide about the exact operations that are carried out in the FFA? Recall that subjects performed much better at discriminating between upright than inverted greyscale faces. Yet during performance of this same task their FFA response was only slightly lower for inverted than upright faces (and only six out of ten subjects showed the effect in this direction). One interpretation of this finding is that the FFA may be involved in face *detection* but not face *recognition*. That is, the FFA may simply be triggered by the presence of a face (perhaps in order to alert and engage other systems), but may not itself carry out the processes involved in discriminating between faces. Consistent with this hypothesis, the FFA response was drastically reduced when face detection was impaired by the inversion of Mooney faces. Also supporting this view, in other studies we have found that cat and cartoon faces activate the FFA as strongly as human faces (Kanwisher et al., 1997b). Therefore, the FFA may not be dedicated to the sole task of discriminating or recognising human faces. However, the present data cannot rule out the possibility that the FFA is involved in face recognition, either in terms of structural encoding, memory storage or retrieval. It is entirely possible that strong inversion effects are not observed for greyscale faces because neural activity in the FFA can reflect computational effort at face recognition as well as computational success.

The present data dovetail with previous findings of face-specific responses recorded from human ERPs (Jeffreys, 1989) and from single neurons in the superior temporal sulcus of monkeys (Perrett et al., 1988). No reduction in amplitude is found

⁵It should be noted that face inversion does reverse the relative position of low-level features on the retina which could lead to differences in retinotopic stimulation. However, it is unlikely that retinotopic differences can account for our data because the FFA lies anterior to retinotopic cortex (Halgren et al., 1997).

⁶Our data provide no evidence for such additional face-specific mechanisms, but they could nonetheless exist (e.g. beyond our spatial resolution or statistical power to detect them or beyond the brain regions scanned in our study).

for either of these physiological responses when greyscale faces are inverted, although in both cases the response to inverted faces is delayed. On the other hand, the magnitude of the ERP response to Mooney faces is drastically reduced when these stimuli are presented upside-down (Jeffreys, 1989). Given that the fMRI response would be expected to reveal differences in magnitude but not latency, there is a striking consistency in the face-inversion effects observed with fMRI of the FFA, responses of face-specific neurons, and face-specific ERPs, suggesting that all of these physiological markers may reflect the same underlying process. It remains for future work to determine whether that process is face detection, face discrimination, or some other face-related process.

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