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Location of Human Face-Selective Cortex With Respect to Retinotopic Areas

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Abstract: Functional Magnetic Resonance Imaging (fMRI) was used to identify a small area in the human posterior fusiform gyrus that responds selectively to faces (PF). In the same subjects, phase-encoded rotating and expanding checkerboards were used with fMRI to identify the retinotopic visual areas V1, V2, V3, V3A, VP and V4v. PF was found to lie anterior to area V4v, with a small gap present between them. Further recordings in some of the same subjects used moving low-contrast rings to identify the visual motion area MT. PF was found to lie ventral to MT. In addition, preliminary evidence was found using fMRI for a small area that responded to inanimate objects but not to faces in the collateral sulcus medial to PF. The retinotopic visual areas and MT responded equally to faces, control randomized stimuli, and objects. Weakly face-selective responses were also found in ventrolateral occipitotemporal cortex anterior to V4v, as well as in the middle temporal gyrus anterior to MT. We conclude that the fusiform face area in humans lies in non-retinotopic visual association cortex of the ventral form-processing stream, in an area that may be roughly homologous in location to area TF or CITv in monkeys. *Hum. Brain Mapping 7:29–37, 1999.* © 1999 Wiley-Liss, Inc.

Key words: fMRI; V4; inferotemporal cortex; objects

INTRODUCTION

The first indication that cortical face-processing may be localized was the description of discrete lesions that selectively impair the recognition of familiar faces (prosopagnosia) [Meadows, 1974]. These lesions usually include the posterior fusiform gyrus (PF), which lies at the base of the brain at the junction between the occipital and temporal lobes [Damasio et al., 1990]. Recently, changes in blood perfusion and/or oxygenation during face-processing in normal subjects have been localized to the same area using positron emission tomography (PET) [Sergent, 1993; Haxby et al., 1994] and fMRI [Puce et al., 1995; Clark et al., 1996; Kanwisher et al., 1996]. Magnetic fields highly selective for faces and peaking about 165 ms after stimulus onset have been estimated to arise from the same area [Sams et al., 1997; Halgren et al., submitted]. This inference has been confirmed by direct recordings of

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neuronal field potentials from the same area using intracranial electrodes [Allison et al., 1994; Halgren et al., 1991, 1994].

Functional interpretation of these findings, and in particular the construction of a neural model of face-processing, requires that PF be located relative to other areas in the visual processing stream. The visual processing stream has been extensively studied in macaque monkeys, where about 30 visual association areas have been distinguished on the basis of their cellular architecture, connectivity, retinotopy and response-properties [Felleman and VanEssen, 1991; Sereno and Allman, 1991; Sereno et al., 1994]. In general, the visual processing areas may be divided into early areas which contain point-to-point mappings of the visual field (''retinotopic areas'') and later areas lacking such mapping. The visual areas can also been divided into a ''dorsal stream'' concerned with location and motion, and a ''ventral stream'' more concerned with form [Ungerleider and Mishkin, 1982]. Although the two streams are not completely segregated, areas within each stream interact more closely with each other than with areas within the other stream [Felleman and VanEssen, 1991].

In macaques, the highest concentrations of face-selective neurons have so far been found in the anterior superior temporal polysensory (STPa) and dorsal anterior infero-temporal (AITd) areas [Perrett et al., 1992]. Anatomically, macaque STPa and AITd lie in the anterior part of the superior temporal sulcus (STS), dorsal and anterior in the temporal lobe, adjacent to auditory association cortex. In contrast, human PF lies ventral and posterior in the temporal lobe, adjacent to limbic cortex of the parahippocampal gyrus. Thus, homology between primate STS and human PF would require a phylogenetic stretching and rotation of the cortex that seems unlikely [Gross, 1992; VanEssen and Drury, 1997]. Furthermore, lesions of the primate STS do not produce specific deficits in face discrimination [Heywood and Cowey, 1993]. Consequently, other authors have proposed that PF may be homologous to macaque area V4v [Schneider et al., 1993; Haxby et al., 1994; Halgren et al., 1994], an area that receives input from early visual areas V1 and V2, and projects very widely to the ventral visual stream [Felleman and VanEssen, 1991]. However, no direct evidence for this hypothesis has been advanced.

Given that about 40 million years have passed since the evolutionary divergence of macaques and humans [Northcutt and Kaas, 1995], it is likely that the homologies between cortical processing areas would be inexact, especially at the higher levels of visual association cortex. For example, the motion sensitivity appears to be much greater in V3A, and less in V3, in humans compared to macaques [Tootell et al., 1997].

However, even if the homologies between the visual cortices of humans and macaques are only approximate, the general location of PF relative to retinotopic areas, and relative to the dorsal vs. ventral streams, would still have important implications. Specifically, if the human PF is homologous to the macaque STS, then it should lie in a nonretinotopic area more associated with the dorsal stream. Conversely, if PF is homologous to the macaque V4v, then it should lie in retinotopic cortex of the ventral stream.

Locating PF in a retinotopic area (e.g., human V4v) would imply that the calculations that it performs to detect faces are relatively low-level, i.e., specific for the location of the face in the visual field. In particular, the identity of faces presented in different visual field locations would depend on integration at higher levels. Similarly, if PF were in non-retinotopic regions farther in the ventral stream, then its input would include color and form information, and it would project to anteromedial temporal areas where memories and emotions associated with the face may be elaborated. Conversely, if PF is in the dorsal stream, then it would be expected to have less sensitivity to the fine structure of the face and more to its location and movement, or the location and movement of its parts. Thus, these alternatives would seem to have strongly divergent implications for the kinds of processing performed within PF, for the nature of input that it receives, and for the types of areas where the results of its processing are projected.

Recently, methods have been developed that allow the retinotopic and motion-sensitive areas in the human brain to be mapped with high accuracy using fMRI [Sereno et al., 1995; Tootell et al., 1996, 1997]. The goal of the current study is to map these (previously described) areas together with the face-selective areas in the same subjects.

MATERIALS AND METHODS

Grayscale full-face photographs of previously unfamiliar young caucasian adults, without facial hair, glasses, or other verbalizeable distinguishing features, were digitized and then processed so as to have the same luminance and size. The stimuli were edited to remove the photographed neck, clothing and background, and were placed uniformly within the frame so that the fixation point fell on the bridge of the nose. Control stimuli were the same faces which had been distorted by repeatedly moving randomly shaped

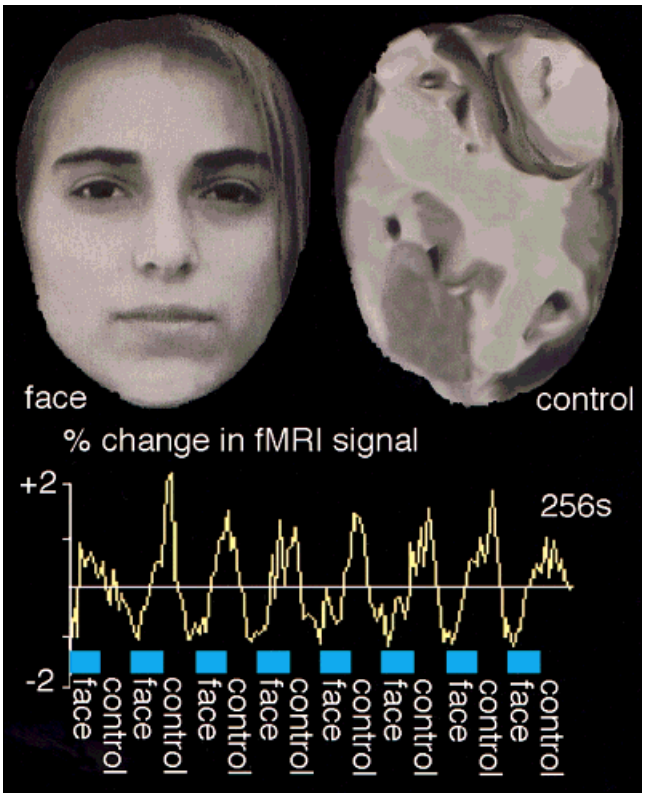

Figure 1.
Unfamiliar grayscale faces and control stimuli (above) were presented in eight cycles of 16 s blocks (24 different stimuli per block). A typical sequence of hemodynamic activation over one run in PF is shown below.

segments of the faces to new locations, while maintaining the face outline constant. The boundaries between the segments were then "smeared" to remove the edges which had been introduced, and would have made the control images systematically different from the controls. The resulting images were not recognizeable as faces, or even as containing parts of faces (see Fig. 1). The control stimuli closely matched the faces in shape, retinal location, mean luminance, and contrast. The same face stimuli had previously been used for MEG [Halgren et al., submitted] and intracranial EEG recordings [Halgren et al., 1994].

The stimuli, subtending a visual angle of 10 degree vertical × 8 degree horizontal, were presented at 640 × 480 resolution with an LCD projector onto a translucent rear-projection screen and adjustable 45 degree mirror [see Tootell et al., 1997, for details]. Stimuli were presented against a uniform gray background for 240 ms each, with an interstimulus interval (from stimulus onset to onset) of 667 ms. Each cycle consisted of 24 different faces in 16 s, followed by 24 different controls in 16 s. Each run consisted of eight cycles.

Subjects (n = 7) were scanned in a 1.5T GE MR scanner using echo-planar imaging (Advanced NMR) and a custom coil. The coil was a bilateral, receive-only quadrature surface coil, molded for relatively uniform sensitivity throughout the occipital cortex including posterior temporal and occipital cortices. Sixteen slices (4 mm thick) were oriented perpendicular to the calcarine fissure. In-plane resolution was 3.1 × 3.1 mm. Head motion was greatly minimized by the use of an individually molded bite bar. Any scans in which head motion exceeded 2 mm were discarded. An asymmetric spin-echo sequence (TR = 2000ms; TE = 70ms; offset = −25ms) was used to measure 'activation' (local increases in blood flow and oxygenation).

Fourier analysis was used to detect voxels whose dominant fMRI activation had the same frequency as the stimulus blocks [as described in Tootell et al., 1997]. Statistical significance was computed from the ratio of the power at the frequency of the stimulus blocks to that at other frequencies (except harmonics and very low frequencies). The cortical surface was reconstructed from the subject's structural MRI, as described elsewhere [Dale and Sereno, 1993; Sereno et al., 1995; Tootell et al., 1995]. Following surface reconstruction, the brain was "inflated" so as to allow sulcal as well as gyral cortex to be viewed. A flattened view of the entire hemisphere was also made by cutting around the corpus callosum and thalamus. The fMRI activations were visualized on the subjects' unfolded cortical surfaces. Visual area terminology follows that of Felleman and VanEssen [1991]; see, e.g., Zilles [1990] for alternative terminologies.

Retinotopic visual areas were mapped in the same subjects using fMRI to measure the polar angle and eccentricity of each location in the visually responsive areas [Sereno et al., 1995]. Polar angle was measured using a rotating wedge of flickering black-and-white checks; eccentricity was measured using an expanding ring of flickering checks. Since adjacent visual areas tend to map the retina in either a direct or a mirror image, boundaries between areas are clearly delineated by reversals of the visual field sign [Sereno et al., 1994]. For example, when viewed from above the cortical surface, the visual field is mapped in V1 as a mirror image, whereas the visual field is mapped in V2 as a non-mirror image (mirror image retinotopic areas are colored yellow in Figures 2 and 3, whereas non-mirror image retinotopic areas are colored blue). The visual motion area MT was identified in all subjects with fMRI using 16 s blocks of moving vs. stationary low contrast rings [Tootell et al., 1995]. The moving

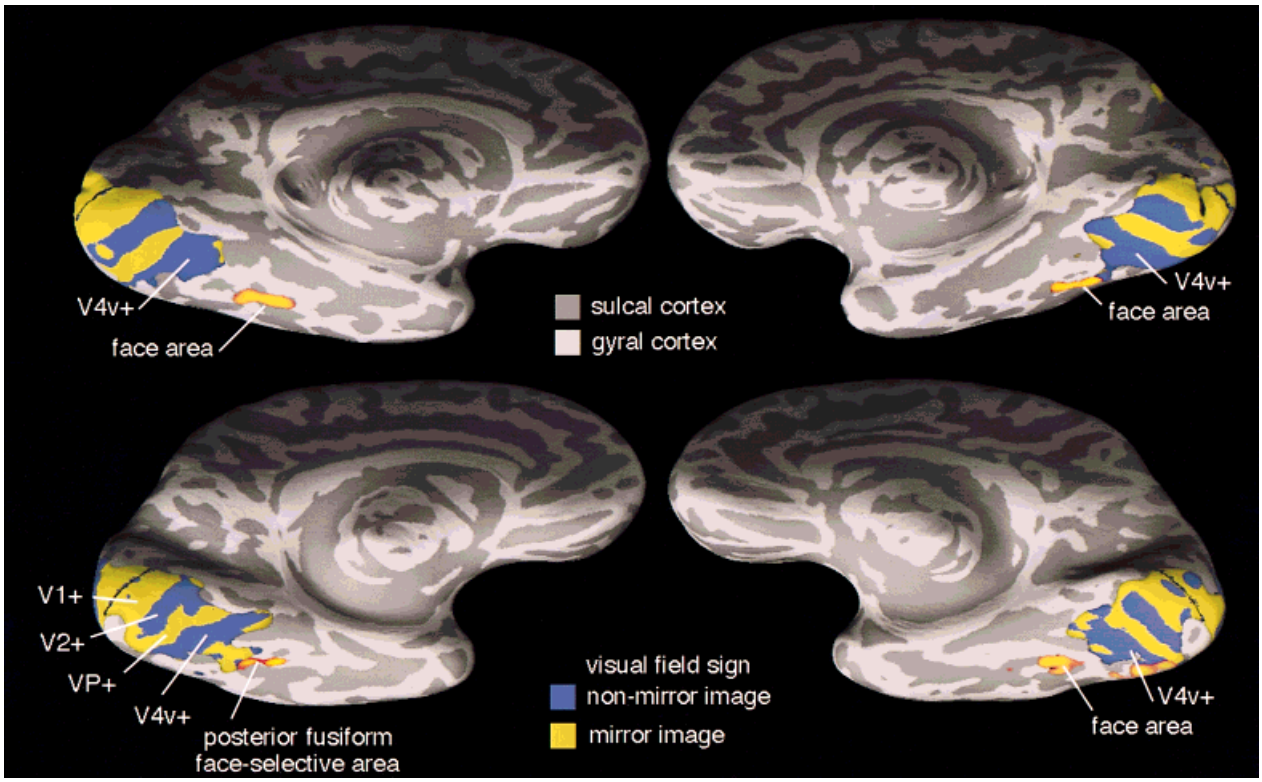

Figure 2.

Within-subject co-localization of the fusiform face area (PF) vs. retinotopic visual areas. Hemodynamic activations (voxels at $P < 0.00005$ for faces) are painted onto a ventromedial view of the subjects' inflated cortical surfaces. Sulcal cortex is coded as a darker gray than gyral cortex. The right and left hemispheres of two typical subjects are shown. In all subjects, the highest level of face-selective activation was in the base of the posterior fusiform g. or in the occipitotemporal sulcus separating it from the inferior temporal gyrus. This activation was bilateral in all except one subject. PF was always clearly anterior to V4v, and a small gap was typically present between the anterior boundary of V4v and PF.

rings alternated every second between expansion and contraction.

Some of the same subjects were examined with a further set of stimuli, consisting of blocks of grayscale face photographs, black-and-white face sketches, grayscale drawings of a variety of inanimate objects, or grayscale photographs of the fronts of cars (Fig. 3). The entire 256 s run consisted of 16 periods alternating between visual stimuli and resting fixation. Twenty-four different stimuli of a given category were shown in each active block.

RESULTS AND DISCUSSION

Figure 1A shows a typical sequence of activation in PF. This activation was bilateral in all except one subject, i.e., it was observed in 13 of the 14 hemispheres examined. The right and left hemispheres of two typical subjects are shown in Figure 2. In all subjects, the highest level of face-selective activation was in the base of the posterior fusiform gyrus or in the occipitotemporal sulcus separating it from the inferior temporal gyrus. The area of the region of the face response (significantly different from the controls at an uncorrected $P < 0.00005$) was 185 ± 109 mm in the right hemisphere and 173 ± 111 mm in the left. The Talairach [Talairach and Tournoux, 1988] coordinates of the centers of these areas were: 37, −52, −17 in the right hemisphere; and −42, −58, −18 in the left. These coordinates are similar to those that have been reported for face-selective responses in PF by other studies using PET [Sergent, 1993; Haxby et al., 1994], fMRI [Puce et al., 1995; Clark et al., 1996; Kanwisher et al., 1996], MEG [Halgren et al., submitted], and intracranial EEG [Halgren et al., 1994]. Thus, the location of this area relative to other visual areas should have a general validity for PF as identified in these other studies.

After identification of PF, phase encoding in the same normal subjects was used to identify the retinotopic visual areas areas V1, V2, V3, V3A, VP, and V4v (Figs. 2, 3). In all 13 hemispheres, PF was located *anterior* to the ventral part of visual area V4v. It is possible that PF may have shown retinotopy if we had used faces in different parts of the visual field as the test stimuli, rather than flickering checkerboards. However, the current data clearly indicate that PF is not in retinotopic cortex, as typically defined.

Moving low-contrast concentric rings were used in the same subjects to activate the visual motion area MT and the adjacent area MSTd ("MT+": Tootell et al. [1996]). PF was found to lie substantially more ventral than these areas (Fig. 3). Since MT+ is the most ventral outpost in the dorsal stream, this supports the idea that PF is in the ventral visual stream.

A 1–2 cm gap was typically present between the anterior limit of V4v and PF. Weak retinotopy opposite in visual field sign to V4v was often observed in these gaps, suggesting at least one interposed visual area. McKeefry and Zeki [1997] have reported a weakly retinotopic color-sensitive area in the same general region. The color area has been found with PET/fMRI [for review see VanEssen and Drury, 1997], and with intracranial recordings [Allison et al., 1994], to be adjacent to but posterior to the face area. The location of this interposed area anterior to V4v and its weak retinotopy suggests that it may be homologous to PITv, which lies just anterior to V4v in macaques [Boussaoud et al., 1991; Felleman and VanEssen, 1991]. If this is true, then PF would be homologous to the area just anterior to PITv. Two candidate areas satisfy this constraint: CITv ventrolaterally and TF ventromedially [Felleman and VanEssen, 1991]. Of these areas, TF seems the more likely candidate given the location of PF with respect to MT: whereas in macaques the dorsal boundary of area CIT lies close to MT/MSTd, PF was found to lie substantially more ventrally (Fig. 3). That is, in macaques, TF lies substantially ventral to MT, as does PF in humans according to our data.

Additional support for a possible homology between PF in humans and TF in macaques is found in their gross anatomical location and cytoarchitectonics. The fusiform g. in humans and area TF in macaques both lie immediately lateral to the collateral sulcus, and the face-selective part of the fusiform g. in humans and area TF in macaques both lie at about the level of the posterior limit of the corpus callosum. Furthermore, the cellular architecture of the fusiform gyrus at this level in humans is distinctive, and is similar to that of TF in macaques [von Economo and Koskinas, 1925; Braak, 1978; von Bonin and Bailey, 1947; Eslinger et al., 1996]. Thus, the location of PF relative to the retinotopic and motion-sensitive visual areas, its gross anatomical location, and its cellular architecture all suggest that it lies in an area corresponding to the macaque area TF.

The fMRI response to grayscale face photographs was also compared in four subjects to that evoked by grayscale images of objects and of cars, and black-on-white sketches of faces (Fig. 3). The time-courses of fMRI activation were calculated for the various functional regions described above. All of the retinotopic visual areas were strongly activated by all four stimulus categories, to an approximately equal extent. In particular, no difference was found in the response of V4v to the faces as compared to objects, providing further evidence that the face-selective area does not correspond to V4v. Conversely, the equivalent responses of the retinotopic cortices to all categories suggest that they were roughly equivalent on sensory grounds. MT appeared to respond weakly to the stimuli, again with no differentiation between the stimulus categories. In contrast, the fMRI response in PF (in a region defined from the fMRI response to alternating blocks of faces and randomized controls) was much greater to faces as compared to objects or cars. The selectivity of PF for faces in this task is striking given that the sensory characteristics of the face photographs are clearly more similar to those of the car photographs than to those of the face sketches, whereas the face-selective responses are to faces regardless of whether they are photographs or sketches. These results confirm the high degree of face-selectivity that others have reported for PF in fMRI [Puce et al., 1995; Clark et al., 1996; Kanwisher et al., 1996], PET [Sergent, 1993; Haxby et al., 1994] and MEG [Halgren et al., submitted] studies.

An area similar in shape and size to PF but more responsive to *non*face objects and cars was identified medial to PF, in the collateral sulcus between the fusiform and parahippocampal gyri (Fig. 3). We term this area PC (posterior collateral). This finding is consistent with other recent reports of preferential responses to nonface objects in this general region [Kanwisher et al., 1996; Ishai et al., 1997]. In these reports, the gap between the face-responsive and the object-responsive areas seen in our study is filled-in. These studies used different stimuli, suggesting that the entire medio-lateral width of the fusiform gyrus at this antero-posterior level may be occupied by cortical strips that are differentially responsive to several different categories of visual objects. This in turn would imply that PF and PC are parts of the same cortical area, involved in the categorical encoding of complex visual stimuli. This inference is supported by

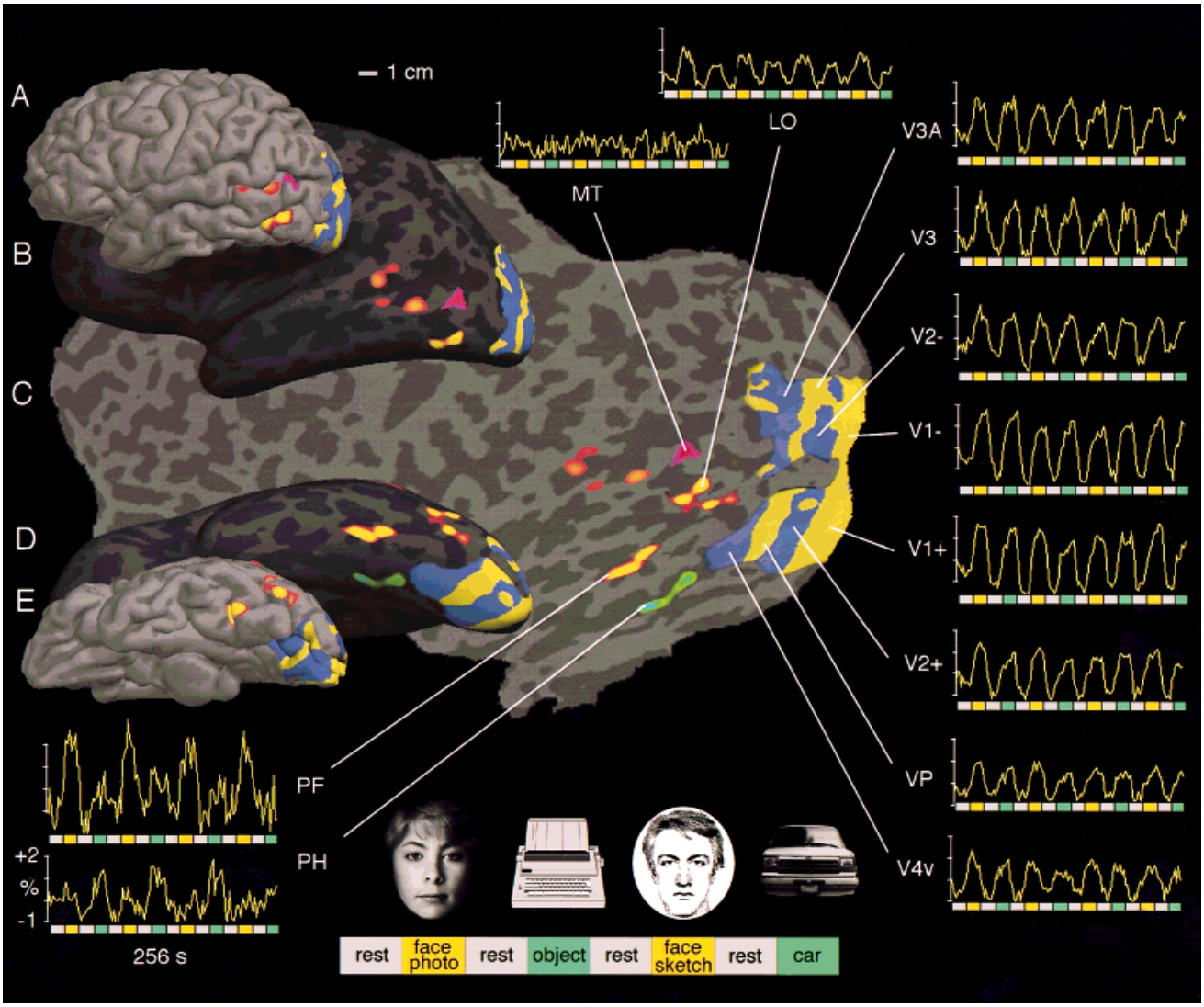

Figure 3.

fMRI responses of different visual areas to faces vs objects in a single subject. Face-selective areas (in orange-red) were identified as in Figure 1. These areas are labelled PF (posterior fusiform), LO (lateral occipito-temporal), and PST (in the posterior superior temporal sulcus). Retinotopic areas mapping the inferior (V1−, V2−, V3, V3A) and superior (V1+, V2+, VP, V4v) visual fields are shown with the visual field sign indicated in yellow (mirror-image) and blue (non-mirror image). The visual motion area MT (in hot pink) was identified using low contrast moving versus stationary rings. These areas are painted onto that subject's left hemisphere, in normal lateral (A) and ventral (E) views, in inflated lateral (B) and ventral (D) views, and in a flattened view (C). The time-course of fMRI activations are shown for the entire 256 s run consisting of 16 periods alternating between visual stimuli (green or orange bars) and resting fixation (gray bars). Stimulus categories were grayscale face photographs, black-and-white face sketches, grayscale drawings of a variety of inanimate objects, or grayscale photographs of the fronts of cars (see examples of stimuli at the bottom of the figure). All retinotopic visual areas responded approximately equally to the different stimulus categories (see the right-hand column of time-courses), with the strongest activation noted in primary visual cortex (V1). Area MT did not respond differentially to any stimulus category. Activation was also seen in non-retinotopic areas of the ventral visual stream. Large and highly face-selective responses are seen in PF, and to a much smaller degree in LO. The *opposite* profile is seen in PC, which responded much more to objects and cars than to faces.

the cytoarchitectonic studies indicating that the posterior fusiform region encompassing PC, PF and the intervening cortex on the crown of the gyrus has a distinct and uniform cellular architecture [von Economo and Koskinas, 1925; Braak, 1978].

Like the medial part of TF in macaques, PC lies just anterior to the part of V4v that maps the most dorsal part of the visual field [Felleman and VanEssen, 1991]. Also like medial TF in macaques, PC is just lateral to the subicular complex in the posterior parahippocampal gyrus, a limbic area with very distinctive cellular architecture in the medial part of the parahippocampal g. There is a small gap between PC and the subicular complex, and this can be inferred to correspond to area TH, which is in the corresponding position in macaques. TH does not receive visual input, but rather input from auditory association cortex [Suzuki, 1996]. Thus, human PC could not be homologous to macaque area TH. All of the above considerations support a clear homology between human PC and macaque medial TF. If, as suggested above, PC and PF are medial and lateral subfields within the same high-order visual association area, then the apparent homology of PC with medial TF provides further support for the suggested homology of PF with lateral TF. If PC and PF mark the medial and lateral boundaries of TF, respectively, then human TF would have an area of about 10 cm^2, about as big as upper field V2. This suggests that some higher visual areas concerned with object processing may be expanded relative to retinotopic areas in the human.

In macaques, TF's main inputs arise in V4v and PIT, the major initial stages in the ventral object-processing stream [Felleman and VanEssen, 1991]. Cells in these areas usually have large receptive fields that often include the fovea, and they respond to visual stimuli of varying complexity [Gross, 1992]. TF projects heavily to more anteromedial temporal areas including entorhinal and perirhinal cortices, which in turn provide the major inputs to the hippocampal formation, amygdala and ventrolateral prefrontal cortex [Felleman and VanEssen, 1991; Suzuki, 1996]. In humans, the former areas constitute the critical anatomical substrate for forming new declarative memories of faces [Corkin, 1984; Suzuki, 1996], and the later areas are crucial for the emotional interpretation of faces [Adolphs et al., 1994; Halgren and Marinkovic, 1995; Marinkovic et al., 1997]. The ventral and anterior temporal areas are implicated in naming familiar faces and recalling information about the person portrayed [Eslinger et al., 1996; Damasio et al., 1996]. Direct feedback connections also course from TF to V4v, PITv and even V1, allowing top-down influences on basic perceptual processes [Rockland and Van Hoesen, 1994; Felleman and VanEssen, 1991].

A second face-selective fMRI response was noted superior and anterior to the visual motion area MT, in the middle temporal gyrus (Figure 3). These responses were weaker than in PF, and occurred mainly in the right hemisphere. This area could not be studied in all subjects because it was not always sampled by our slice selection, and it was located at the limits of sensitivity of the surface coil. The location of these responses relative to MT suggests that they are homologous to the responsive cells previously noted in the macaque STS [Perrett et al., 1992], and to intracranially recorded EEG responses to faces in this region [Halgren et al., 1994].

A third face-responsive area was also noted, centered anterior to the more foveal part of V4v (Fig. 3). This area was rather extensive, and in some subjects it extended posteriorly into foveal VP and V3A. This activation does not appear to correspond directly to the area most often lesioned in prosopagnosia, nor to that most often activated in other PET, fMRI or intracranial EEG studies. This area can be distinguished from PF through its weaker and less face-specific response, in comparison to objects and cars (Fig. 3). Thus, this area corresponds to that termed LO which has been shown using fMRI to be activated by objects and beings of all kinds, familiar and unfamiliar, without any clear selectivity for the type of item [Tootell et al., 1996; Malach et al., 1995]. If these putative homologies are correct, then LO may provide substantial afferents to PF, and face-selectivity in PF may result from convergence of less-specific inputs from LO.

CONCLUSIONS

The current results identify three face-responsive areas. The most responsive and selective area (PF) is in the posterior fusform g., and may be homologous to lateral TF, a gateway for high-level visual information in the object-processing stream to reach multimodal mnestic and emotional areas. Medial to PF in the posterior parahippocampal gyrus is an area that selectively responds to nonface objects, and may be homologous to medial TF. The second face-selective area is in the middle temporal gyrus, and appears to correspond to the face-responsiveness often noted in the macaque superior temporal sulcus, implicated in attention. The third face-selective area is selective for objects and animals as well as faces, and lies in the cortex that projects to PF. Overall, these results suggest that in the evolution of the human brain from our common

ancestor with the old world monkeys, the high order visual processing areas have shifted postero-ventrally and differentiated, while maintaining their topographical relations and general functional specializations. Regardless of the validity or usefulness of these possible homologies, the current results clearly place the fusiform face area in a nonretinotopic region of the ventral visual processing stream.

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REFERENCES

Adolphs R, Tranel D, Damasio H, Damasio A (1994): Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. Nature 372:669–672.

Allison T, Ginter H, McCarthy G, Nobre AC, Puce A, Luby M, Spencer DD (1994): Face recognition in human extrastriate cortex. J Neurophysiol 71:821–825.

Boussaoud D, Desimone R, Ungerleider LG (1991): Visual topography of area TEO in the macaque. J Comp Neurol 306:554–575.

Braak H (1978): The pigment architecture of the human temporal lobe. Anat Embryol 154:213–240.

Clark VP, Keil K, Maisog JM, Courtney S, Ungerleider LG, Haxby JV (1996): Functional magnetic resonance imaging of human visual cortex during face matching: a comparison with positron emission tomography. NeuroImage 4:1–15.

Corkin S (1984): Lasting consequences of bilateral medial temporal lobectomy: clinical course and experimental findings in H.M. Semin Neurol 4:249–259.

Dale AM, Sereno MI (1993): Improved localization of cortical activity by combining EEG and MEG with MRI cortical surface reconstruction: A linear approach. J Cogn Neurosci 5:162–176.

Damasio AR, Damasio H, Tranel D (1990): Face agnosia and the neural substrates of memory. Ann Rev Neurosci 13:89–109.

Damasio H, Grabowski TJ, Tranel D, Hichwa RD, Damasio AR (1996): A neural basis of lexical retrieval. Nature 380:499–505.

Eslinger PJ, Easton A, Grattan LM, Van Hoesen GW (1996): Distinctive forms of partial retrograde amnesia after asymmetric temporal lobe lesions: Possible role of the occipitotemporal gyri in memory. Cereb Cortex 6:530–539.

Felleman DJ, VanEssen DC (1991): Distributed hierarchical processing in the primate cerebral cortex. Cereb Cortex 1:1–47.

Gross CG (1992): Representation of visual stimuli in inferior temporal cortex. Phil Trans R Soc Lond B [Biol] 335:3–10.

Halgren E, Marinkovic K (1995): Neurophysiological networks integrating human emotions. In: Gazzaniga M (ed) The Cognitive Neurosciences. Cambridge, Mass.: MIT Press, pp. 1137–1151.

Halgren E, Baudena P, Heit G, Clarke JM, Marinkovic K (1994): Spatio-temporal stages in face and word processing. 1. Depth-recorded potentials in the human occipital, temporal and parietal lobes. J Physiol (Paris) 88:1–50.

Halgren E, Marinkovic K, Baudena P, Devaux B, Broglin D, Heit G, Chauvel P (1991): Human intracranial potentials evoked by faces. Soc Neurosci Abst 17:656.

Haxby JV, Horwitz B, Ungerleider LG, Maisog JM, Pietrini P, Grady CL (1994): The functional organization of human extrastriate cortex: A PET-rCBF study of selective attention to faces and locations. J Neurosci 14:6336–6353.

Heywood CA, Cowey A (1993): Colour and face perception in man and monkey: the missing link. In: Gulyas B, Ottoson D, Roland PE (eds) Functional Organisation of the Human Visual Cortex. Oxford, New York, Seoul, Tokyo: Pergamon Press, pp. 195–210.

Ishai A, Ungerleider LG, Martin A, Maisog JM, Haxby JV (1997): fMRI reveals differential activation in the ventral vision pathway during perception of faces, houses, and chairs. NeuroImage 5:S149.

Kanwisher N, Chun MM, McDermott J, Hamilton R (1996): fMRI reveals distinct extrastriate loci selective for faces and objects. Soc Neurosci Abst 22:1937.

Malach R, Reppas JB, Benson RR, Kwong KK, Jiang H, Kennedy WA, Ledden PJ, Brady TJ, Rosen BR, Tootell RBH (1995): Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc Natl Acad Sci USA 8135:8139.

Marinkovic K, Trebon P, Halgren E, Chauvel P (1997): Effects of temporal and frontal cortectomies on emotional judgements of facial expressions and memory for emotional words. Soc Neurosci Abst 23:1317.

McKeefry DJ, Zeki S (1997): Mapping and topographic organization of the visual field in human area V4 as revealed by fMRI. NeuroImage 5:81.

Meadows JC (1974): The anatomical basis of prosopagnosia. J Neurol Neurosurg Psychiat 37:489–501.

Northcutt RG, Kaas JH (1995): The emergence and evolution of mammalian neocortex. TINS 18:373–379.

Perrett DI, Hietanen JK, Oram MW, Benson PJ (1992): Organization and functions of cells responsive to faces in the temporal cortex. Phil Trans R Soc Lond B [Biol] 335:23–30.

Puce A, Allison T, Gore JC, McCarthy G (1995): Face-sensitive regions in human extrastriate cortex studied by functional MRI. J Neurophysiol 74:1192–1199.

Rockland KS, Van Hoesen GW (1994): Direct temporal-occipital feedback connections to striate cortex (V1) in the macaque monkey. Cereb Cortex 4:300–313.

Sams M, Hietanen JK, Hari R, Ilmoniemi RJ, Lounasmaa OV (1997): Face-specific responses from the human inferior occipito-temporal cortex. Neuroscience 77:49–55.

Schneider W, Noll DC, Cohen JD (1993): Functional topographic mapping of the cortical ribbon in human vision with conventional MRI scanners. Nature 365:150–153.

Sereno MI, Allman JM (1991): Cortical visual areas in mammals. In Leventhal AG (ed): The Neural Basis of Visual Function. London: Macmillan, pp. 160–172.

Sereno MI, McDonald CT, Allman JM (1994): Analysis of retinotopic maps in extrastriate cortex. Cereb Cortex 4:601–620.

Sereno MI, Dale AM, Reppas JB, Kwong KK, Belliveau JW, Brady TL, Rosen BR, Tootell RBH (1995): Borders of multiple visual areas in human revealed by functional magnetic resonance imaging. Science 268:889–893.

Sergent J (1993): The processing of faces in the cerebral cortex. In Gulyas B, Ottoson D, Roland PE (eds): Functional Organisation of the Human Visual Cortex. Oxford, New York, Seoul, Tokyo: Pergamon Press, pp. 359–372.

Suzuki WA (1996): The anatomy, physiology and functions of the perirhinal cortex. Curr Opin Neurobiol 6:179–186.

Talairach J, Tournoux P (1988): Co-Planar Stereotaxic Atlas of the Human Brain. New York: Thieme.

Tootell RBH, Reppas JB, Kwong KK, Malach R, Born RT, Brady TJ, Rosen BR, Belliveau JW (1995): Functional analysis of human MT and related visual areas using magnetic resonance imaging. J Neurosci 15:3215–3230.

Tootell RBH, Dale AM, Sereno MI, Malach R (1996): New images from human visual cortex. TINS 19:481–489.

Tootell RBH, Mendola JM, Hadjikhani NK, Ledden PJ, Liu AK, Reppas JB, Sereno MI, Dale AM (1997): Functional analysis of V3A and related areas in human visual cortex. J Neurosci 17:7060–7078.

Ungerleider LG, Mishkin M (1982): Two cortical visual systems. In: Ingle DJ, Goodale MA, Mansfield RJW (eds) Analysis of visual behaviour. Cambridge, Massachusetts: MIT press, pp. 549–586.

VanEssen DC, Drury HA (1997): Structural and functional analyses of human cerebral cortex using a surface-based atlas. J Neurosci 15:7079–7102.

von Bonin G, Bailey P (1947): The Neocortex of *Macaca mulatta.* Urbana, IL: University of Illinois Press.

von Economo C, Koskinas GN (1925): Die Cytoarchitektonik der Hirnrinde des erwashsenen Menschen. Berlin: Springer-Verlag.

Zilles K (1990): Cortex. In Paxinos G (ed): The Human Nervous System. San Diego: Academic Press, pp. 757–802.