

To examine the specificity of face-responsive regions for face processing, we used fMRI to measure the response of the fusiform gyrus and the superior temporal sulcus (STS) to pictures of human faces, animals, faceless animals, and houses. Results indicate that faces, animals, and faceless animals all elicited greater activity than houses, and had identical peaks of activation in the lateral fusiform gyrus, bilaterally, and in the right posterior STS. Moreover, within the lateral fusiform gyrus the responses to faces, animals and faceless animals were all greater than the responses to these stimuli in the medial aspect of the fusiform gyrus, a region that responds more strongly to other objects (e.g. houses). These findings suggest that the neural representation of animals in the fusiform gyrus and the posterior STS relies strongly on the same neural substrates that represent faces. *NeuroReport* 10:2945–2950 © 1999 Lippincott Williams & Wilkins.

Key words: Animals; Face perception; Fusiform gyrus; fMRI; Superior temporal sulcus

Are face-responsive regions selective only for faces?

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Introduction

Neuroimaging studies in humans have consistently found that a region in the lateral portion of the fusiform gyrus responds more to faces than to other objects [1–7]. Some investigators have even suggested that this region may be a face-specific module [5,6]. Recently we reported that processing pictures of animals and human faces both elicit similar patterns of activity in the lateral fusiform gyrus and the posterior STS [8]. However, because it has been shown that animal faces can elicit a strong response in the face-responsive region of the lateral fusiform gyrus [9], it is possible that the response to animals we previously observed was elicited by the presence of the animals' faces. The aim of the current study is to address this issue by examining the response of these face-responsive regions to pictures of animals, animals with obscured faces (or faceless animals), and human faces. If pictures of faceless animals also elicit a strong response in the face-responsive regions, then it would suggest that these regions mediate the recognition of another object category in addition to faces, arguing against the notion of a face-specific module. A preliminary report of these results has been presented previously [10].

Materials and Methods

Subjects: Six subjects (one female, age (mean \pm s.d.) 26 ± 3.2 years) took part in the fMRI study and 20 subjects (eight female, mean age 28 ± 5 years) took

part in the behavioral study. All subjects were right-handed and neurologically normal, and gave written informed consent.

Experimental procedure: The stimuli were black-and-white photographs of animals, animals with white circles completely obscuring their faces (faceless animals), human faces and houses (see Fig. 1). To ensure that the animal and faceless animal stimuli were matched for difficulty, 20 subjects were tested on a naming task with pictures of animals and faceless animals outside of the scanner. The stimuli were presented at fixation, one picture every 2 s, with an ISI of 0.5 s. Voice onset time and naming responses were recorded as subjects named each picture aloud.

Six different subjects were tested on a delayed match-to-sample task with pictures of animals, faceless animals, human faces, and houses while fMRI images were acquired. In this task, a sample stimulus was presented at fixation for 1 s. Following a 0.5 s delay, two choice stimuli (different exemplars of the same object) were presented side by side for 2 s. Subjects indicated which object was identical to the sample stimulus with a button press. For the sensorimotor control, phase-scrambled images of the same pictures were used as stimuli, and the sample and choice stimuli were identical. Subjects responded by pressing both buttons simultaneously.

Imaging procedure: Eighteen contiguous, coronal, 5 mm slices were obtained during six runs of 91

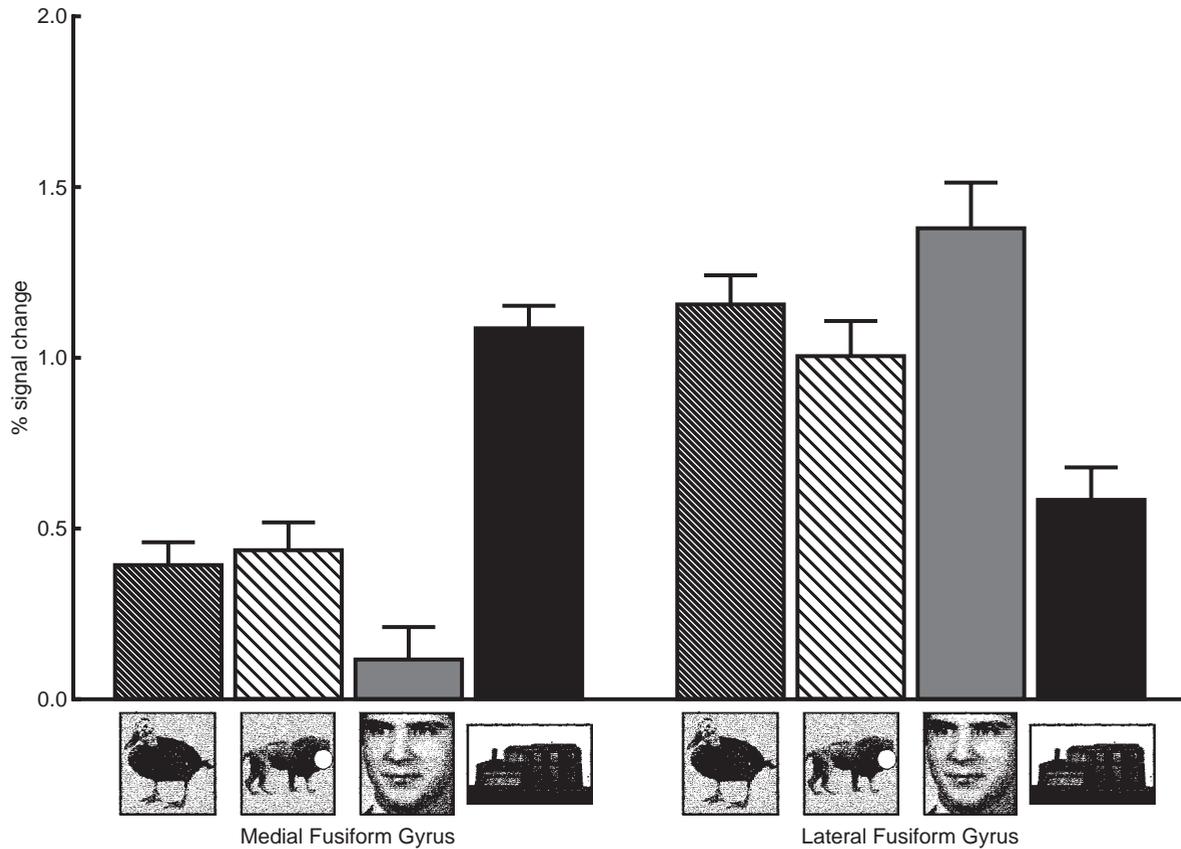


FIG. 1. Examples of the four different stimulus categories and the average per cent signal change (\pm s.e.) in the medial and lateral fusiform gyrus.

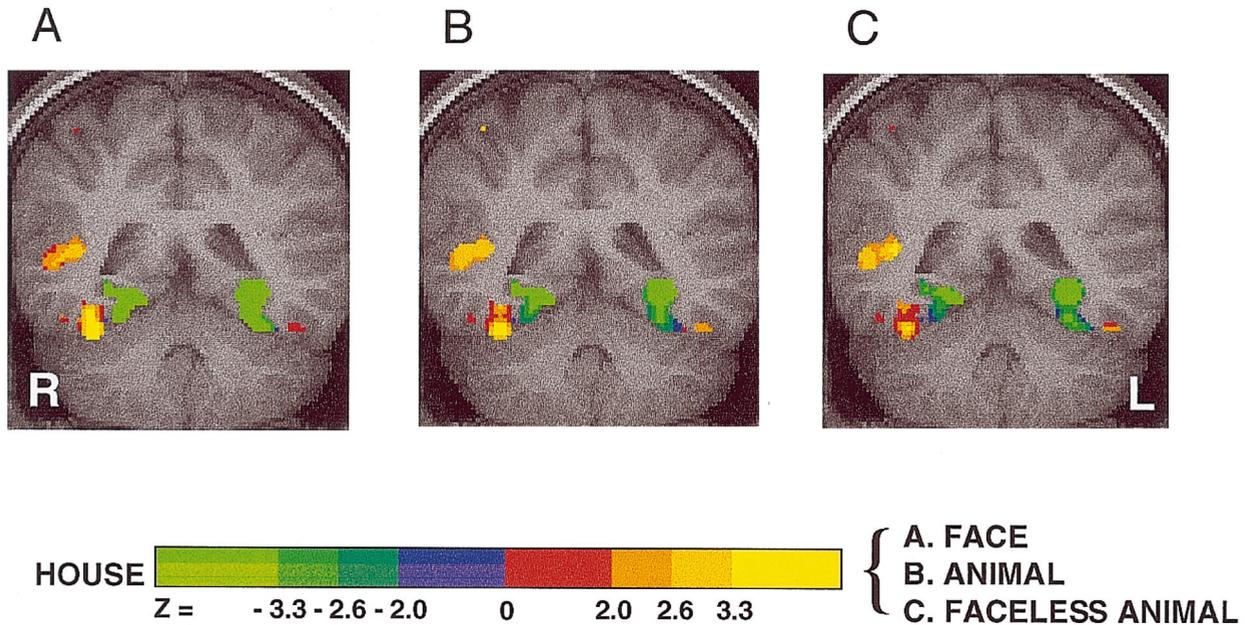


FIG. 2. Category-related activations associated with (a) faces, (b) animals and (c) faceless animals relative to houses in a representative subject. The color in which each voxel is displayed reflects an independent test of the significance of the contrast between faces, animals, faceless animals, and houses. Face-, animal- and faceless animal-responsive regions are shown in the red–yellow color spectrum; house-responsive regions are shown in the blue–green color spectrum.

scans each (repeat time 3 s). Gradient echo, echo-planar imaging was used (TE = 40 ms, flip angle = 90°, FOV = 20 cm, 64 × 64 matrix, voxel size = 3.125 × 3.125 × 5 mm) on a GE Signa 1.5 T MRI scanner.

Statistics: Individual subject data were analyzed with multiple regression [11,12] (see [7] for complete details). In order to obtain estimates of the magnitude of the response that were not biased by the method of voxel selection, separate regressors for even and odd numbered runs identified voxels that showed a significant difference between the response to faces and houses. Different regions were identified for even and odd numbered runs that had at least seven contiguous voxels with a significant overall experimental effect ($Z > 3.09$ for an omnibus test of the combined effect of the regressors of interest) and a difference between the responses to faces and houses ($Z > 1.95$, $p < 0.05$, two-tailed, uncorrected). A mean time series for the odd-numbered runs was calculated for each region that was defined based on even-numbered runs, and vice versa. Thus, there were two independent data sets, and any difference between the response to faces, houses, animals and faceless animals was not contaminated by a voxel selection bias. The average per cent signal changes in the face- and house-responsive regions were calculated for each subject and each stimulus category using the average signal intensity during the sensorimotor control epochs as a baseline. The means of the two estimates of response strength for each region were then analyzed with a three-factor (stimulus × region × hemisphere) ANOVA across subjects.

Multiple regression analyses were also used to identify regions that showed significantly different responses for faces, animals and faceless animals when compared with houses, and stereotaxic coordinates [13] were obtained for each of these regions (see [7] for complete details).

Results

Behavioral response: Performance measures on the naming task with pictures of animals and faceless animals revealed no significant differences in voice onset time (mean ± s.e.: 1038 ± 15 ms; 1020 ± 25 ms) or accuracy (percentage correct: 95 ± 0.6%; 93 ± 0.8%) for animals and faceless animals. Similarly, there were no significant differences in reaction time (731 ± 25 ms; 718 ± 22 ms; 759 ± 24 ms; 711 ± 23 ms) or accuracy (96 ± 0.6%; 96 ± 0.7%; 96 ± 0.6%; 95 ± 1.2%) for animals, faceless animals, human faces and houses in the delayed match-to-sample task.

fMRI response: Consistent with previous reports [1–7], a region in the lateral fusiform gyrus and occipitotemporal sulcus responded more strongly to pictures of human faces than to pictures of houses (faces 1.4%; houses 0.6%, $p < 0.0005$, see Table 1). Additional contrasts revealed that pictures of animals (1.1%) and faceless animals (1.0%) also produced a significantly greater response in this region than pictures of houses (animals *vs* houses: $p < 0.005$, faceless animals *vs* houses: $p < 0.05$, see Fig. 1). There were no significant differences between animals and faces or between animals and faceless animals in this region, although human faces elicited a larger response in this area than pictures of faceless animals ($p < 0.05$). It is important to note that within the fusiform gyrus, the centers-of-gravity associated with human faces, animals and faceless animals were essentially identical (Fig. 2; Table 2). When a more stringent criterion for defining the face-responsive region of the lateral fusiform gyrus was used (differential category effect with $Z > 3.3$, $p < 0.001$, two-tailed, minimum region size = 5 voxels), the region was reduced from a mean volume of $2.2 \pm 1.2 \text{ cm}^3$ to $0.7 \pm 0.7 \text{ cm}^3$. The per cent signal change for faces in this more stringently defined region increased from 1.4% to 1.5%. Nevertheless, this area still responded significantly more to pictures of animals (1.1%) and faceless animals (0.9%) than to pictures of houses (0.3%; animals *vs* houses $p < 0.005$; faceless animals *vs* houses $p < 0.05$). Again, there were no significant differences between animals and faces and between animals and faceless animals, and the response to faceless animals was smaller than the response to human faces ($p < 0.05$).

Consistent with previous reports [7,14,15], a region in the more medial aspect of the fusiform gyrus, including the lingual gyrus and collateral sulcus, responded more strongly to pictures of houses than to pictures of faces (houses 1.1%; faces 0.1%; Fig. 1; Fig. 2). This region also responded more to pictures of houses than to pictures of animals (0.4%) and faceless animals (0.4%; $p < 0.001$). Within this house-responsive region of the medial fusiform gyrus, pictures of animals and faceless animals both elicited greater responses than pictures of human faces (animals *vs* faces $p < 0.05$; faceless animals *vs* faces $p < 0.05$, Fig. 1).

The response to animals and faceless animals in the face-responsive lateral fusiform region was more than twice the response to these same stimuli in the house-responsive medial fusiform region ($p < 0.001$, Fig. 1). Moreover, the direct comparison of animals and faceless animals to houses identified animal-responsive and faceless animal-responsive regions in the lateral fusiform gyrus that had essentially the same center of gravity as the face-responsive region

Table 1. Contrasts between different stimulus categories in the lateral and medial fusiform gyrus (LFG and MFG, respectively). The difference in the average percent signal change (PSC) and the significance of that difference are also given

Comparison	Region	PSC difference	Significance
Animals vs faceless animals	LFG	0.1	n.s.
	MFG	0	n.s.
Animals vs faces	LFG	0.3	n.s.
	MFG	0.3	$p < 0.05$
Animals vs houses	LFG	0.5	$p < 0.005$
	MFG	0.7	$p < 0.0005$
Faceless animals vs faces	LFG	0.4	$p < 0.05$
	MFG	0.3	$p < 0.05$
Faceless animals vs houses	LFG	0.4	$p < 0.05$
	MFG	0.7	$p < 0.0005$
Faces vs houses	LFG	0.8	$p < 0.0005$
	MFG	1.0	$p < 0.0005$

Table 2. Regions showing differential responses to human faces, animals, faceless animals, and houses

Region	Selectivity	Hemisphere (N)	Talairach coordinates		
			X	Y	Z
Medial fusiform gyrus	Houses	R (6)	28 ± 7	-42 ± 6	-13 ± 8
		L (6)	-26 ± 3	-46 ± 9	-10 ± 8
Lateral fusiform gyrus	Human faces	R (6)	39 ± 3	-50 ± 7	-19 ± 3
		L (5)	-38 ± 1	-51 ± 3	-15 ± 1
	Animals	R (6)	41 ± 1	-50 ± 4	-19 ± 5
		L (5)	-41 ± 3	-49 ± 5	-18 ± 3
	Faceless animals	R (4)	41 ± 1	-50 ± 4	-16 ± 4
		L (4)	-42 ± 4	-48 ± 5	-17 ± 3
Superior temporal sulcus	Human faces	R (3)	53 ± 4	-57 ± 6	14 ± 10
		L (0)	-	-	-
	Animals	R (3)	52 ± 3	-57 ± 3	15 ± 6
		L (0)	-	-	-
	Faceless animals	R (3)	51 ± 3	-56 ± 5	12 ± 6
		L (0)	-	-	-

N=number of subjects (out of 6) who showed significant category-related activation ($p < 0.05$).

(Fig. 2; Table 2). These results indicate that the maximal response to animals and faceless animals was in the same cortical region that showed a maximal response to human faces.

Finally, in three of the six subjects, pictures of human faces elicited a stronger response in the posterior region of the superior temporal sulcus (STS) than did pictures of houses (faces 0.5%; houses -0.1%, see Fig. 2). In these same subjects, pictures of animals and faceless animals also elicited a stronger response in the STS than pictures of houses (animals 0.3%; faceless animals 0.2%; $p < 0.0001$ for animals vs houses and faceless animals vs houses; Fig. 2). As in the fusiform gyrus, direct comparison of animals and faceless animals to houses identified animal-responsive and faceless animal-responsive regions in the posterior STS that had essentially the same center of gravity as the face-responsive region (Table 2).

Discussion

Pictures of animals, faceless animals, and human faces all elicited a maximal response in the same region of the lateral fusiform gyrus. This region has been implicated in previous neuroimaging studies as an area specialized for the perception and recognition of faces [5,6]. However, results from the current study call into question the specificity of this region for face processing for the following reasons. First, the response to animals and faceless animals in this region was nearly as strong as the response to human faces, even though the region was identified based on its response to human faces. Second, the response to human faces and animals did not differ significantly. Third, the responses to animals and faceless animals also did not differ significantly. Only the difference between human faces and animals with obscured faces achieved statistical signifi-

cance. Fourth, even when a more stringent criterion was used to define the face-responsive region, the relative strengths of the response to human faces, animals, and faceless animals remained largely unchanged. This change in criterion selected voxels that were less responsive to houses but not more selective for faces as compared to animals. Thus, results from the current study appear to extend the stimuli processed in the face-responsive region of the lateral fusiform gyrus to another object category, namely animals.

It is not surprising that the face-selective lateral fusiform region also responds to other objects. Even in the most face-selective regions of monkey temporal cortex (TPO, TEa, TEm), only 20% of cells are face selective [16]. Moreover, these face-selective cells respond significantly to some non-face objects or scenes [17]. What is surprising is that the pattern of response to animals, even without faces, does not just extend to the face-selective lateral fusiform region, but its peak is also there. This suggests that this piece of cortex plays a central role in the representation of both faces and animals.

Although the centers of gravity of the activations in the lateral fusiform gyrus associated with animals, faceless animals, and human faces were essentially identical, it is important to note that the pattern of activation for animals, faceless animals, and human faces across the entire fusiform gyrus was not identical. Specifically, pictures of animals and faceless animals also elicited significantly greater responses in the medial aspect of the fusiform gyrus compared to pictures of human faces. This finding suggests that human faces may be processed by a more discretely organized system than other objects. If animal and face recognition were dependent, at least in part, on a common neural substrate then that may explain why prosopagnosia (the inability to recognize faces) sometimes occurs as an isolated disorder [18], and also why difficulty identifying four-legged animals is a common, perhaps the most common, co-occurring symptom in prosopagnosic patients [19].

A recent neuroimaging study suggested that face imagery can elicit a response in the so-called fusiform face area [20]. Because we cannot rule out the possibility that the subjects in the current study imagined or filled in the animals' faces when they saw pictures of faceless animals, this is an alternative that needs to be addressed in future experiments. Nevertheless, the fact that pictures of animals with obscured faces elicited a robust response in the face-responsive regions of the lateral fusiform gyrus and the posterior STS suggests that the animal-selective

response that we previously reported in these regions was not due solely to the presence of the animals' faces.

Citing the preliminary report of these results [10] as one of the rationales for their experiment, Kanwisher *et al.* [21] recently reported that the human fusiform face area does not respond more to pictures of animal bodies without heads than to other objects. In the current study, we find that pictures of faceless animals do elicit a significantly greater response than another category of object (i.e. houses) in the face-responsive region of the lateral fusiform gyrus.

It is unclear which of the methodological differences between the current study and that of Kanwisher *et al.* accounts for the different findings; however, the differences in speed and duration of stimulus presentation between the two studies may be a factor. During the delayed match-to-sample task in the current study, the sample stimulus was presented for 1 s and the choice stimuli were presented for 2 s. Behavioral data from the naming experiment (stimulus duration 2 s) indicate that our subjects were able to recognize and name both the animal and faceless animal stimuli with equivalently high degrees of accuracy (>90%). In contrast, in the study by Kanwisher *et al.*, the stimuli were presented briefly in rapid succession (300 ms with 500 ms ISI). Consequently, subjects may have been able to recognize fewer headless animals than the subjects in our study. Even though subjects in the Kanwisher *et al.* study performed the one-back task above chance, they may have done so by a form-matching strategy rather than by identifying the stimuli. Therefore, it is possible that the headless animals elicited less activity in the face-responsive region of the fusiform gyrus in Kanwisher *et al.*'s study because their subjects could not adequately recognize or identify the headless animal stimuli as a specific animal.

Another difference between our study and that of Kanwisher *et al.* is the manner in which the animals' faces were obscured. In the current study, the faceless animal stimuli were created by obscuring the animals' faces with white circles, thus the outline of the animals' heads could still be seen. Kanwisher *et al.* obscured the animals' faces by removing the entire head. It may be that the response in the face-responsive regions to our faceless animal stimuli was driven, in part, by the perception of the outline of the animals' heads.

Finally, in the current study, pictures of animals, faceless animals and human faces all elicited similar patterns of activity in posterior STS. Because previous studies with human [22,23] and non-human

primates [24,25] have demonstrated that a region in posterior STS responds to biological motion (e.g. mouth and eye movements), it is possible that the animal- and face-related activity in this region is associated with stored information about biological motion.

Conclusion

The present study found that relative to another class of objects (houses), pictures of human faces, animals and faceless animals all elicited robust activity in the lateral fusiform gyrus, bilaterally, and in the right posterior STS. This suggests that these regions are not solely dedicated to face perception but rather may respond to other object categories as well. Our results further indicate that as visual stimuli, human faces may be special and appear to be processed by a more discretely organized system than other object categories. This may be due, in part, to our expertise with faces, and may reflect a finer tuning of the cortical region that responds to a broad category of objects.

References

1. Puce A, Allison T, Gore JC and McCarthy G. *J Neurophysiol* **74**, 1192–1199 (1995).
2. Puce A, Allison T, Asgari M *et al.* *J Neurosci* **16**, 5205–5215 (1996).
3. Clark VP, Kiel K, Maisog JM *et al.* *Neuroimage* **4**, 1–15 (1996).
4. Kanwisher NG, Chun MM and McDermott J. *Cogn Brain Res* **5**, 55–67 (1996).
5. Kanwisher N, McDermott J and Chun MM. *J Neurosci* **17**, 4302–4311 (1997).
6. McCarthy G, Puce A, Gore JC and Allison T. *J Cogn Neurosci* **9**, 605–610 (1997).
7. Haxby JV, Ungerleider LG, Clark VP *et al.* *Neuron* **22**, 189–199 (1999).
8. Chao LL, Haxby JV and Martin A. *Nature Neurosci* (in press).
9. Tong F, Nakayama K, Moscovitch M *et al.* *Cogn Neuropsychol* (in press).
10. Chao LL, Martin A, Lalonde FM *et al.* *Neuroimage* **7**, S350 (1997).
11. Friston KJ, Holmes AP, Poline JB *et al.* *Neuroimage* **2**, 45–53 (1995).
12. Haxby JV, Maisson JM and Courtney SM. Multiple regression analysis of effects of interest in fMRI time series. In: Lancaster J, Fox P and Friston K eds. *Mapping and Modeling the Human Brain*. Wiley, New York, (in press).
13. Talairach J and Tournoux P. *Co-planar Stereotaxic Atlas of the Human Brain*. Thieme, New York, 1988.
14. Epstein R and Kanwisher N. *Nature* **392**, 598–601 (1998).
15. Aguirre GK, Zarahn E and D'Esposito M. *Neuron* **21**, 373–383 (1998).
16. Baylis GC, Rolls ET and Leonard CM. *J Neurosci* **7**, 330–342 (1987).
17. Rolls ET and Tovee MJ. *J Neurophysiol* **73**, 713–726 (1995).
18. McNeil JE and Warrington EK. *Q J Exp Psychol A, Human Exp Psychol*. **46A**, 1–10 (1993).
19. Farah MJ. *Cogn Neuropsychol* **3**, 25–41 (1991).
20. Kanwisher N and O'Craven KM. *Soc Neurosci Abstr* **24**, 213.9 (1998).
21. Kanwisher N, Stanley D and Harris A. *Neuroreport* **10**, 183–187 (1999).
22. Bonda E, Petrides M, Ostry D and Evans A. *J Neurosci* **16**, 3737–3744 (1996).
23. Puce A, Allison T, Bentin S *et al.* *J Neurosci* **18**, 2188–2199 (1998).
24. Perrett DI, Harries MH, Mistlin AJ *et al.* *Int J Comp Psychol* **4**, 25–54 (1990).
25. Oram MW and Perrett DI. *J Cogn Neurosci* **6**, 99–116 (1994).

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