

# Are faces of different species perceived categorically by human observers?

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## SUMMARY

What are the species boundaries of face processing? Using a face-feature morphing algorithm, image series intermediate between human, monkey (macaque), and bovine faces were constructed. Forced-choice judgement of these images showed sharply bounded categories for upright face images of each species. These predicted the perceptual discrimination boundaries for upright monkey–cow and cow–human images, but not human–monkey images. Species categories were also well-judged for inverted face images, but these did not give sharpened discrimination (categorical perception) at the category boundaries. While categorical species judgements are made reliably, only the distinction between primate faces and cow faces appears to be categorically perceived, and only in upright faces. One inference is that humans may judge monkey faces in terms of human characteristics, albeit distinctive ones.

## 1. INTRODUCTION

Adult humans are extremely good at identifying adult human faces. In one study, error-free recognition was reported for over 2000 different portraits in an old–new recognition task (Standing *et al.* 1970). We can also recognize individual monkey faces, and we are sensitive to the vertical orientation of the portrait, whether it is of a monkey or a human face (Wright & Roberts 1996). This and like findings beg the question ‘What is the nature of the human ability to recognize individual faces across species boundaries?’ One possibility is that a single template serves face perception across different species. It would use the general architecture and image properties of the upright face, including the vertical bilateral symmetry of the spatial arrangement of two eyes above a nose and a mouth (Johnson & Morton 1991). Face expertise may then generalize to all faces, whatever the species, as long as they share some of the requisite image characteristics.

An alternative idea is that face templates are species-specific. There is some support for this notion from neuropsychological reports. Brain lesions can selectively disrupt recognition for human and for animal faces in patients such as livestock farmers who have experience of individual animals as well as people (MacNeil & Warrington 1993; Assal *et al.* 1984). If face recognition by humans is species-based, then there may be categorical perception (CP) for face images from different

species. CP occurs when members of a class of stimuli which vary in their sensory characteristics are nevertheless processed as if they are equivalent. If separate categories exist for different species’ faces, then the identification and the discrimination of artificial face images intermediate between faces of each species should be discrete, and the identification contour should predict the discrimination boundary. That is, the function that describes the discrimination of items in the series should be discontinuous: at the categorical boundary, discrimination should be enhanced with respect to the actual physical difference between the stimuli. But if a single categorical prototype informs processing of faces of all species, there should be no such systematic sharpening between species’ faces. Furthermore, if CP is related to expertise with faces, then where it occurs it should be evident for upright but not for inverted faces. There is strong developmental, experimental and neuropsychological evidence that in experts such as adult human observers, face processing is engaged automatically only when faces are upright (Yin 1969; Goldstein 1975; Diamond & Carey 1977, 1986; Farah *et al.* 1995).

This experiment tests these predictions directly, using full-face images of humans, cows and macaque monkeys, systematically warped to generate controlled images (morphs) physically intermediate between those of each true species member. Image morphing allows complete control of the physical blending of stimulus properties. If there is CP for each species’ face, then efficiency in discriminating between pairs of neighbouring images

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should be predicted by the boundaries of categorization of the species. The rationale is as follows: assume, for example, that a 50% monkey–50% cow face is judged to be the boundary image for the cow–monkey morph series. That is, this image is unreliably chosen as ‘cow’ or ‘monkey’, whereas images containing a greater or lesser proportion of monkey face are reliably chosen as monkey or cow. With CP, the perception of difference is driven by the underlying categorical structure. Therefore, a simple discrimination task should be more efficient for items that straddle the boundary than for those that lie within it. In this example, the prediction is that image pairs (40% cow–60% monkey) and (60% cow–40% monkey) should be distinguished more accurately than image pairs (80% cow–20% monkey) and (60% cow–40% monkey). Only CP would explain discrimination efficiency peaks aligned to the judgement boundary.

Demonstrations of CP thus require two-phase testing: identification and perceptual discrimination over the same stimulus sets for all subjects. Where a categorical boundary is indicated in a judgement task, CP can be inferred if that boundary correlates with a peak in discrimination efficiency (fewest errors) in a discrimination task that requires the subject to distinguish pairs of tokens from a series where the physical distance between items is identical throughout the series.

## 2. METHOD

### (a) Subjects

These comprised 14 volunteer adult students from Goldsmiths College, University of London, whose ages ranged from 22 to 41 years (mean age 28 years). None was familiar with individual macaque monkeys or cows.

### (b) Image manipulation

Full-face photographic images of four adult humans, four adult rhesus monkeys (*Macaca mulatta*) and four cows (Friesian) were computer-scanned. These were source images for constructing four series of human–monkey–cow morphs, with a different individual face used as the source for each series.

For each face image (eight bit greyscale), 224 face-feature landmarks were taken, following the procedure described by Benson & Perrett (1991). Using these landmark points, the morphing algorithm (Benson 1994) produced 12 intermediate images between each of the endpoints, human (H), monkey (M), and cow (C), as follows: 80%H–20%M, 60%H–40%M, 40%H–60%M, 20%H–80%M, 80%M–20%C, 60%M–40%C, 40%M–60%C, 20%M–80%C, 80%C–20%H, 60%C–40%H, 40%C–60%H, 20%C–80%H. Excluding endpoint images (100% H, M, C), a 12-image, three-way continuum was produced for each of the sets of three original images of a human, a monkey and a cow. The use of a three-way series reduces the likelihood of anchor effects related to multiple exposure of endpoint images in different combinations. The elimination of 100% endpoint images from the tested series further reduces the possibility that ‘real’ face images might be used as memorial anchors. These images were cropped, normalized for size, and ghosting reduced with image-processing software (Adobe Photoshop<sup>®</sup>). Figure 1 shows one such series.

### (c) Design and procedure

All subjects performed two discrimination tasks, one on a series of upright faces, the other on a different series of inverted faces. The other two series served for practice for each of the tasks. The stimulus series for practice and for experiment, their orientation, and the order of orientation were counterbalanced across subjects. The discrimination tasks were always performed first. The experiment lasted approximately 40 min, with a break between the discrimination and identification parts.

### (d) Discrimination: visual ABX

Sequential choice discrimination (ABX discrimination; Liberman *et al.* 1957; Harnad 1987), within each 12-image series, was the discrimination task of choice. First one (A), then another (B) stimulus image from the series is presented, followed immediately by a target stimulus (X) which is identical to either the first or second image seen ( $X = A$  or  $X = B$ ). The subject made a manual response indicating whether the first or the second stimulus was the correct match. For each subject, every paired combination of neighbouring stimulus images (12, i.e. positions 1–2; 2–3; 3–4, etc. to 12–1) was presented four times (AB–A, BA–A, AB–B, AB–B). In addition, every combination of ‘gap pairs’ (i.e. 1–3, 2–4) was also presented. If CP occurs, discrimination should be most efficient in category boundary position as indicated by the identification task (below). Only neighbouring pair results (1–2 to 12–1) are reported here, since these comprise the finest test of boundary discrimination.

The image was shown on a mid-grey field on the 18 inch (14 cm) computer monitor. The image size was  $9 \times 7$  cm at a viewing distance of 50 cm. Superlab software controlled the display and responses. When no image appeared on the screen, the unstructured background field was seen. Stimulus duration was 750 ms for stimuli A and B, while stimulus X remained on screen until the response was made. The inter-stimulus interval was 1500 ms between each presentation. Time-out between trials was set at 4.00 s.

Each subject performed two discrimination tasks; one for upright and one for inverted faces. Each complete set of 120 possible trials within each task was sampled randomly without replacement and was preceded by 30 trials from the practice series. Instructions, which appeared on screen before the experiment, and on paper by the side of the equipment during the practice phase, stressed that speed and accuracy would be measured, and subjects used the ‘Z’ and ‘M’ (leftmost and rightmost) keyboard keys for response to the first or the second stimulus. These were colour coded to aid response. After practice, subjects were asked to comment on the task, and some feedback was given. Accuracy and reaction time (RT) were logged for each trial, including practice trials.

### (e) Identification task

Following the discrimination tasks, subjects classified the images seen previously. Single face images from the experimental series appeared unpredictably in either orientation, for keyed responses (M, B or Z for human, cow or monkey; these were relabelled ‘H’, ‘C’, ‘M’ to help responses). Each face image appeared centrally and in an identical form (contrast, size) to the discrimination task. Each image remained on screen until the response was made, with an interval of 1 s between a response and a new stimulus. In this, as in the discrimination task, a practice session preceded the experiment proper.



Figure 1. A human-cow-monkey 12-step morph series. The steps are the same as those labelled in figure 2 (below).

### 3. RESULTS

#### (a) Identification—forced-choice categories

Figure 2 shows the identification functions (categories chosen) for upright and for inverted faces, respectively. Analysis of variance (ANOVA) in which the factors were series (image set 1, 2, 3 or 4), orientation (upright or inverted), category (human, monkey or cow), and position, showed no significant main effect, but a highly significant interaction of category and position ( $p < 0.001$ ). This was the sole significant effect. The between subject factor of face series failed to affect this or other findings, and the following analyses report effects collapsed over this variable.

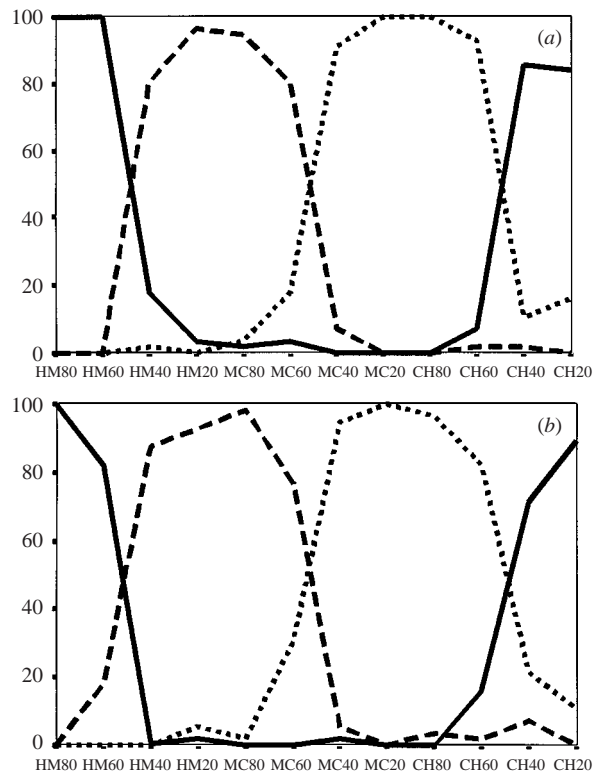
As Figure 2 shows, boundaries were in essentially the same position whether inverted or upright faces were viewed. Category boundaries were between positions 40–60 and 60–40 for each of the three series, HM, MC and CH.

#### (b) Identification RTs

Inverted faces should be slower to categorize than upright images and mid-range images and mid-series images may take longer to identify than those closer to the category endpoints. ANOVA, with factors orientation (upright–inverted), category (man–monkey, monkey–cow, and cow–human) and position (80%, 60%, 40% and 20%), upheld these predictions. Upright faces were categorized faster than inverted ( $F_{13,1} = 5.96$ ,  $p = 0.03$ ). Mid-positions were slower than end positions ( $F_{39,3} = 10.83$ ) (40% and 60% slowest). There was also a significant interaction of orientation and position ( $F_{39,3} = 4.76$ ,  $p < 0.01$ ): mid-range items showed the greatest inversion decrement.

#### (c) ABX discrimination: accuracy

Inspection of figure 3 suggests that errors dipped at two of the three identification boundary positions



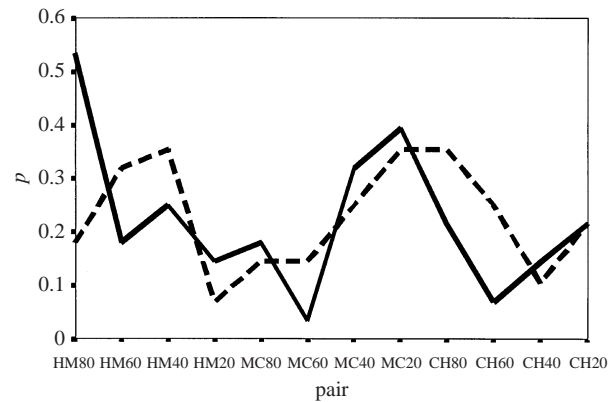
item label	% human	% monkey	% cow
HM80	80	20	—
HM60	60	40	—
HM40	40	60	—
HM20	20	80	—
MC80	—	80	20
MC60	—	60	40
MC40	—	40	60
MC20	—	20	80
CH80	20	—	80
CH60	40	—	60
CH40	60	—	40
CH20	80	—	20

Figure 2. Forced-choice identification for human-cow-monkey series. (a) Upright, (b) inverted. Solid line, human; dashed line, monkey; stippled line, cow.

(MC60 and CH60), but only for upright and not for inverted faces. Does statistical analysis support this? The first ANOVA analysed orientation (upright-inverted), category (HM, MC or CH), and pair position (8020/6040; 6040/4060; 4060/2080; 2080/8020) as factors. The interaction between category and pair position was significant ( $F_{78,6} = 4.59, p < 0.001$ ). The orientation-position interaction approached significance ( $F_{39,3} = 3.48, p = 0.06$ ).

(d) *Testing boundary discrimination*

The prediction from the identification functions is that discrimination will be most accurate at position 40:60/60:40 (i.e. at positions HM60, MC60, and CH60) within each condition. The position factor was transformed directly to contrast this: (40:60 versus the



pair label	pairs shown	
HM80	HM80-HM60	
HM60	HM60-HM40	category boundary
HM40	HM40-HM20	
HM20	HM20-MC80	
MC80	MC80-MC60	
MC60	MC60-MC40	category boundary
MC40	MC40-MC20	
MC20	MC20-CH80	
CH80	CH80-CH60	
CH60	CH60-CH40	category boundary
CH40	CH40-CH20	
CH20	CH20-HM80	

Figure 3. Mean probability of error (p) in the ABX discrimination task. Solid line, upright; dashed line, inverted.

mean of (20:40, 60:80 and 80:20) and a three-way ANOVA (orientation, condition and position (two levels)) performed. This gave a main effect of position ( $F_{13,1} = 7.02, p = 0.02$ ) and an orientation-position interaction ( $F_{13,1} = 8.09, p = 0.01$ ). Separate ANOVAs (condition position) for upright and for inverted images confirmed that the efficiency peak at the 40:60/60:40 position held for upright but not for inverted faces. For upright faces, position  $F_{13,1} = 31.26, p < 0.001$ ; for inverted faces  $F = 0.05$  (all probabilities are Bonferroni corrected). For upright faces there was a category effect ( $F_{26,2} = 4.06, p < 0.05$ ) which did not interact with position. Human-monkey images were significantly worse than either mancow or cowhuman images ( $p < 0.02$  for least difference analysis). Moreover, post hoc analysis showed that the upright human-monkey images, alone of the upright images, did not show an advantage for the 40:60 pair over the mean of the other positions ( $t = 0.8, p > 0.2$ ).

(e) *ABX RTs*

Reaction times were also tested. No significant effects occurred except for the three-way interaction ( $F_{78,6} = 2.55, p = 0.026$ ) between condition, pair and orientation. One condition (inverted MC60) was significantly slower than all others. Importantly, correlations between individual error and RT scores for each stimulus pairing were not significant. There

was no trade-off between accuracy and RT in the discrimination task.

#### 4. DISCUSSION

Participants reliably categorized upright and inverted face image morphs intermediate between different species, and category judgement under these forced-choice conditions was clearly bounded. We have shown categorical identification for these images. Did the categorical boundaries in forced-choice judgement predict ABX discrimination performance (CP)?

The answer to this is in three parts. First, categorical sharpening was reliably obtained only for upright, not for inverted images. Secondly, for upright images, pairs that straddled the category boundary (MC60/MC40 and HC60/HC40) were more accurately judged than those that fell within it. Thirdly, for the human–monkey series, this effect was not significant. In addition, the upright human–monkey series was less accurate than either of the other two series. While separate categories inform the discrimination of primate from cow faces, for primates including monkey and man, a single prototype may serve face discrimination. These data add to the growing evidence that CP can be demonstrated in the domain of face images. Photographic warping procedures similar to those used here have shown CP for facial expressions (Calder *et al.* 1996; de Gelder *et al.* 1997) and for facial identity (Beale & Keil 1995).

##### (a) *Effects of inversion on categorical perception*

Upright, but not inverted, faces of humans, monkeys and cows generate categorical perception in the ABX discrimination task. Faces are thought to be particularly sensitive to this manipulation, and sensitivity to facial inversion is considered a hallmark of face identification expertise. It should be noted that sensitivity to facial inversion is not confined to human face experts. Sheep are good at recognizing individual sheep faces, and show orientation sensitivity for sheep from their herd (Kendrick *et al.* 1995, 1996).

In the present study, forced-choice judgement of inverted face type was good, with boundaries indistinguishable from those for upright faces. Inverted faces may be compared with species prototypes after rotation to the canonical (upright) orientation. This process is time-consuming (inverted faces took longer to classify) and may interact with attentional and other processes. Under the time and accuracy constraints of the ABX task, the orientation-specific face prototype may take too long or be too hard to engage, so other matching mechanisms for inverted faces come into play which are not dependent on facial prototypes. These could include matching on the basis of specific features such as size, tone, and external contour of the image.

##### (b) *Categorical judgement but not categorical perception: men and monkeys*

The failure to find CP for the man–monkey series, which was nevertheless categorized appropriately in the judgement task, may be similarly explained.

Forced-choice decisions on human–monkey faces may use a slow, task-specific procedure: while this shows that such accurate judgements are possible, they may not use sufficiently reliable processing mechanisms to support the discrimination task which was speed-stressed and required immediate memory. That is, the dissociations observed in this study between forced-choice category identification (good in all conditions) and perceptual discrimination (sharp-bounded for upright primate versus cow) lend weight to the power of the CP paradigm: they show that perceptual categorical discrimination need not always follow good classification. Classification is necessary, but not sufficient for CP.

##### (c) *How many face prototypes? Evidence from neuropsychology*

Some neuropsychological evidence also suggests that knowledge of faces of different species may use distinct processing schemes. Prosopagnosia is the term given to the acquired loss of face recognition (Bodamer 1947). The farmer WJ, who became prosopagnosic following an ischaemic incident, was significantly more impaired in recognizing individual familiar human faces than at recognizing the individual sheep in his flock by face alone (MacNeil & Warrington 1993). He was also better at old–new discrimination of unfamiliar sheep than at old–new discrimination of unfamiliar male faces. Thus, the specificity of the face-processing problem was unlikely to have been due to a loss in knowledge of particular people, but rather to the specific loss of the ability to distinguish human faces. Bruyer *et al.* (1983), following Bornstein *et al.* (1969), report a farmer whose prosopagnosia was also limited to human faces and spared the identification of cows and of dogs. It is unlikely that this dissociation comes about because animal faces are more resistant to the effects of neurological insult. Assal *et al.* (1984) report that MX, another livestock farmer, recovered from prosopagnosia differentially: human faces were relearned, but animal faces were not. These data suggest that distinct cortical systems may serve the identification of human (including primate) faces than those of other beasts.

##### (d) *Theoretical implications*

Various models propose that face recognition is based on a vector description of face feature sets (where features are construed widely to include image properties). Neural networks can perform principal component analyses on such images, which capture these properties (O'Toole *et al.* 1991, 1994; Valentin *et al.* 1994). Neurobiological findings also suggest that localized neural networks are responsible for the analysis and identification of faces in primates (Young & Yamane 1992; Tovée & Cohen-Tovée (1993) for a review). The facial prototype tends to be located in densely populated face-space (typical faces differ least from each other), and the denser area can serve as an attractor basin for a neural net learning to classify or remember the face. In line with this, typical faces generate more false alarms in recognition than do

distinctive ones (Valentine & Bruce 1986a; Vokey & Read 1992; Bruce *et al.* 1994), and are perceived faster as faces in face–non-face categorization experiments (Valentine & Bruce 1996b). The present experiment suggests that for most human viewers, monkey faces can be judged by human face criteria. They may even function as a particularly distinctive type of face. This is a readily testable idea. They should take longer to distinguish from non-faces than human faces, and they may be individually more memorable than human faces. Monkey faces may also be judged uglier than human faces, since distinctive human faces are judged less attractive than typical ones (Ellis *et al.* 1988), and be somewhat less susceptible than human faces to the effects of inversion, since distinctive faces show a reduced inversion effect (Valentine 1991). By contrast, cow faces appear to be judged in relation to a different prototype, and the memorability and perceptibility—let alone the attractiveness or expressiveness—of cow faces cannot be predicted from knowledge of human ones.

### (e) Directions

These findings leave open a number of intriguing questions: do macaque monkeys, like humans, use a single category for their own and human faces? To what extent can these findings generalize to other primate species? Does (human) practice with monkey faces change the pattern of discrimination and the categorical structure of primate face-space? To what extent might the tendency to individuate primate faces be 'built-in' to the human face-processing system as a feature of long evolutionary standing? Further research may help to answer these questions.

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### REFERENCES

- Assal, G., Favre, C. & Anderes, J. P. 1984 Non-reconnaissance d'animaux familiers chez un paysan: zooagnosie ou prosopagnosie pour les animaux. *Revue Neurologique* **140**, 580–584.
- Beale, J. M. & Keil, F. C. 1995 Categorical effects in the perception of faces. *Cognition* **57**, 217–239.
- Benson, P. J. & Perrett, D. I. 1991 Computer averaging and manipulations of faces. In *Photovideo: photography in the age of the computer* (ed. P. Wombell), pp. 32–38. London: Rivers Oram Press.
- Benson, P. J. 1994 Morph transformation of the facial image. *Image Vision Comput.* **12**, 691–696.
- Bodamer, J. 1947 Die Prosopagnosie. *Archiv für Psychiatrie und Nervenkrankheiten* **179**, 6–53.
- Bornstein, B., Sroka, H. & Munitz, H. 1969 Prosopagnosia with animal face agnosia. *Cortex* **5**, 164–169.
- Bruce, V., Burton, A. M. & Dench, N. 1994 What's distinctive about a distinctive face? *Q. J. Exp. Psychol.* **47A**, 119–141.
- Bruyer, R., Laterre, C., Seron, X., Feyereisen, P., Strypstein, E., Pierrard, E. & Rectem D. 1983 A case of prosopagnosia with some preserved covert remembrance of familiar faces. *Brain Cognit.* **2**, 257–284.
- Calder, A. J., Young, A. W., Perrett, D. I., Ectoff, N. L. & Rowland, D. 1996 Categorical perception of morphed facial expressions. *Visual Cognit.* **3**, 81–117.
- de Gelder, B., Teunisse, J.-P. & Benson, P. J. 1997 Categorical perception of facial expressions. *Cognit. Emotion* **11**, 1–23.
- Diamond, R. & Carey, S. 1977 Developmental changes in the representation of faces. *J. Exp. Child Psychol.* **23**, 1–22.
- Diamond, R. & Carey, S. 1986 Why faces are and are not special. *J. Exp. Psychol. General* **115**, 107–117.
- Ellis, H. D., Shepherd, J. W., Gibling, F. & Shepherd, J. 1988 Stimulus factors in face learning. In *Practical aspects of memory: current research and issues. I.* (eds M. M. Gruneberg, P. E. Morris & R. N. Sykes), pp. 136–143. Chichester, UK: Wiley.
- Farah, M. J., Tanaka, J. W. & Drain, H. M. 1995 What causes the face inversion effect? *J. Exp. Psychol.: Human Perception Performance* **21**, 628–634.
- Goldstein, A. G. 1975 Recognition of inverted photographs of faces by children and adults. *J. Genetic Psychol.* **127**, 109–123.
- Harnad, S. 1987 Category induction and representation. In *Categorical perception: the groundwork of cognition* (ed. S. Harnad). New York: Cambridge University Press.
- Johnson, M. H. & Morton, J. 1991 *Biology and cognitive development: the case of face recognition*. Oxford, UK: Blackwell.
- Kendrick, K. M., Atkins, K., Hinton, M. R., Broad, K. D., Fabrenys, C. & Keverne, B. 1995 Facial and vocal discrimination in sheep. *Anim. Behav.* **49**, 1665–1676.
- Kendrick, K. M., Atkins, K., Hinton, M. R., Heavens, P. & Keverne, B. 1996 Are faces special for sheep? Evidence from facial and object discrimination-learning tests showing effects of inversion and social familiarity. *Behav. Processes* **38**, 19–35.
- Lieberman, A. L., Harris, K. S., Hoffman, H. S. & Griffith, B. C. 1957 The discrimination of speech sounds within and across phoneme boundaries. *J. Exp. Psychol.* **53**, 358–368.
- MacNeil, J. E. & Warrington, E. K. 1993 Prosopagnosia: a face-specific disorder. *Q. J. Exp. Psychol.* **46A**, 1–10.
- O'Toole, A., Deffenbacher, K. A., Abdi, H. & Bartlett, J. C. 1991 Simulating the other race effect as a problem in perceptual learning. *Connexionist Sci.* **3**, 163–178.
- O'Toole, A., Deffenbacher, K. A., Valentin, D. & Abdi, H. 1994 Structural aspects of face recognition and the other-race effect. *Memory Cognit.* **22**, 208–224.
- Standing, L., Conezio, J. & Haber, R. 1970 Perception and memory for single trial learning of 2560 visual stimuli. *Psychon. Sci.* **19**, 73–74.
- Tovée, M. J. & Cohen-Tovée, E. M. 1993 The neural substrates of face-processing models: a review. *Cognitive Neuropsychol.* **10**, 505–528.
- Valentin, D., Abdi, H., O'Toole, A. J. & Cottrell, G. W. 1994 Connectionist models of face processing: a survey. *Pattern Recognit.* **27**, 1209–1230.
- Valentine, T. 1991 A unified account of the effects of distinctiveness, inversion and race in face recognition. *Q. J. Exp. Psychol.* **43**, 161–204.
- Valentine, T. & Bruce, V. 1986a Recognising familiar faces: the role of distinctiveness and familiarity. *Canadian J. Psychol.* **300**–305.
- Valentine, T. & Bruce, V. 1986b The effects of distinctiveness in recognising and classifying faces. *Perception* **15**, 525–535.
- Vokey, J. R. & Read, J. D. 1992 Familiarity, memorability and the effect of typicality on the recognition of faces. *Memory Cognit.* **20**, 291–302.
- Wright, A. A. & Roberts, W. A. 1996 Monkey and human face perception: inversion effects for human faces but not for monkey scenes or faces. *J. Cognit. Neurosci.* **8**, 278–290.
- Yin, R. K. 1969 Looking at upside-down faces. *J. Exp. Psychol.* **81**, 141–145.
- Young, M. & Yamane, S. 1992 Sparse population coding of faces in the inferotemporal cortex. *Science* **256**, 1327–1331.

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