

Box 4 The effects of the conspicuousness dependence in memory retention

For condition (10) of aposematic evolution to hold, the derivative on its left-hand side must be positive, that is, the following inequality must hold:

$$\frac{1}{c(x,u)} \left[\frac{\partial a(y,x,u)}{\partial y} \right]_{y=x} + \frac{1}{c(x,u)^2} a(x,x,u) (-c_x(x,u)) > 0 \quad (11)$$

Thus, either $[\partial a(y,x,u)/\partial y]_{y=x} > 0$ or $c_x(x,u) < 0$ must hold. Whereas the first inequality implies peak shift, the second inequality implies that the more conspicuous a type of prey is, the more memorable it is^{18,23}. It is apparent from condition (11) that the greater the predator's memory retention ($1/c(x,u)$) and associative memory acquisition ($a(x,x,u)$) are, the more likely it is for aposematism to evolve. We note that the evolutionary dynamics in the case of increasing memory-retention toward greater conspicuousness are qualitatively the same as those in the case of peak shift (shown in Fig. 2).

be written as

$$N > p'(x)/[p(x)^2 \partial a(y,x,u)/\partial y]_{y=x} \quad (3)$$

and this relation between N and x is represented by the region above the curve line in Fig. 2 (Box 3). In this region, the conspicuousness x of the prey population should increase, whereas it should decrease outside the region (arrows in Fig. 2). Starting with the original conspicuousness value $x_0 (> 0)$ of the cryptic wild type (Box 3), conspicuousness x will evolve and lead to a higher level (indicated in Fig. 2 by the thick part of the curve line) once N exceeds a threshold value N_0 (determined by the intersection between the curve line and the line $x = x_0$ in Fig. 2). Thus, although the evolution of aposematism proceeds in a gradual manner, a great discontinuity in the degree of conspicuousness is created as a result of the evolution. This discontinuity predicted by the model can explain the unambiguous distinction in appearance between many aposematic species and their closely related cryptic species, which is observed in nature.

We have shown that a predator's generalization with peak shift, which creates a substantial associative learning of a rare mutant by the predator solely experiencing an abundant wild type, may overcome the two barriers to the initial evolution of aposematism pointed out by Guilford^{1,2}, helping the initial evolution of aposematism to occur.

It has been suggested that aposematism may evolve by gradual change²¹. Our model provides a mechanism for, and thus supports, this idea. Peak shift has been shown to be a stabilizing force once aposematism has evolved^{3,13}; our model reveals that peak shift can also be a driving force for the initial evolution of aposematism.

We have assumed that $c = 1$, but if $c = c(x,u)$, our model indicates that not only peak shift, but also increasing memory retention toward greater conspicuousness ($c_x(x,u) < 0$), can give rise to the evolution of aposematism (Box 4). □

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Effects of sexual dimorphism on facial attractiveness

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Testosterone-dependent secondary sexual characteristics in males may signal immunological competence¹ and are sexually selected for in several species^{2,3}. In humans, oestrogen-dependent characteristics of the female body correlate with health and reproductive fitness and are found attractive^{4–6}. Enhancing the sexual dimorphism of human faces should raise attractiveness by enhancing sex-hormone-related cues to youth and fertility in females^{5,7–11}, and to dominance and immunocompetence in males^{5,12,13}. Here we report the results of asking subjects to choose the most attractive faces from continua that enhanced or diminished differences between the average shape of female and male faces. As predicted, subjects preferred feminized to average shapes of a female face. This preference applied across UK and Japanese populations but was stronger for within-population judgements, which indicates that attractiveness cues are learned. Subjects preferred feminized to average or masculinized shapes of a male face. Enhancing masculine facial characteristics increased both perceived dominance and negative attributions (for example, coldness or dishonesty) relevant to relationships and paternal investment. These results indicate a selection pressure that limits sexual dimorphism and encourages neoteny in humans.

Computer-graphic techniques can be used to construct 'average' male and female faces by digitally blending photographs of individuals of the same sex¹⁴ (Fig. 1). Sexual dimorphism in face shape can then be enhanced or diminished^{14,15} (Fig. 2). We presented such manipulations of both Japanese and Caucasian face stimuli to

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Japanese subjects in Japan and Caucasian subjects in Scotland.

The amount of transformation (that is, masculinization or feminization) that was applied by subjects to obtain the most attractive face shape was compared with a mean of 0% predicted by the null hypothesis (that altering sex-related characteristics would not affect attractiveness) and predicted by the hypothesis that attractiveness is averageness¹⁶. The face shape selected by Caucasian subjects as most attractive (from the shape range available) was significantly feminized for both the Caucasian female face (mean level of feminization was 24.2%; $t_{49} = 7.6$, $P < 0.001$) and the Japanese female face continua (mean 10.2%; $t_{49} = 2.3$, $P = 0.027$). Japanese subjects also selected significantly feminized versions of the female stimuli for both the

Japanese (mean 22.9%; $t_{41} = 7.6$, $P = 0.001$) and the Caucasian (mean 15.3%; $t_{41} = 4.5$, $P = 0.001$) female face continua.

Three-way analysis of variance (ANOVA) of the level of transform applied by subjects to define attractive face shapes revealed no main effect of subject sex ($F_{1,88} = 1.58$, $P = 0.21$), population of subjects ($F_{1,88} = 0.32$, $P = 0.57$) or type of stimulus face (Japanese/Caucasian; $F_{1,88} = 1.42$, $P = 0.24$). The only significant interaction between main effects was that between subject population and type of stimulus face ($F_{1,88} = 17.06$, $P < 0.001$), which was attributable to the greater degree of feminization preferred for stimulus faces of the subject's own population (Fig. 3a).

Previous studies show cross-population consistency in judgements of attractiveness^{9,11,14,17}. Our study shows cross-cultural (between-population) agreement in the preference for feminized to average face shapes, which refutes the averageness hypothesis^{14,16}. The study also indicates effects of experience on judgements of female attractiveness as a greater degree of feminization was preferred for faces from the subject's own population than for faces from a different population. Both generalization and cultural specificity of judgements of attractiveness may result from learning. We find cues to female attractiveness relate to the way that female faces differ from males. Sensitivity to the consistent sex differences in faces (and hence female attractiveness) could be learned through exposure to male and female exemplars. Most differences learned this way will generalize between populations as they reflect the common action of sex hormones during growth. Subjects, however, may become more sensitive to the sexual dimorphism of faces within the subject's own population because of increased exposure to population-specific male–female variations.

For the male face stimuli, the shape selected by Caucasian subjects as most attractive (from the shape range available) was significantly feminized for both the Caucasian male face (mean level of feminization was 15%; $t_{49} = 4.22$, $P < 0.001$) and the Japanese male face continua (mean 9%; $t_{49} = 2.2$, $P = 0.03$). Japanese subjects also selected significantly feminized versions of the male stimuli for both the Japanese (mean 20%; $t_{41} = 6.5$, $P < 0.001$) and the Caucasian (mean 17%; $t_{41} = 4.8$, $P < 0.001$) male face continua. For the male stimuli, three-way ANOVA revealed there was no main effect of subject sex ($F_{1,88} = 0.18$, $P = 0.67$), subject population ($F_{1,88} = 2.94$, $P = 0.09$) or type of stimulus face ($F_{1,88} = 0.02$, $P < 0.89$) and no significant interactions between effects.

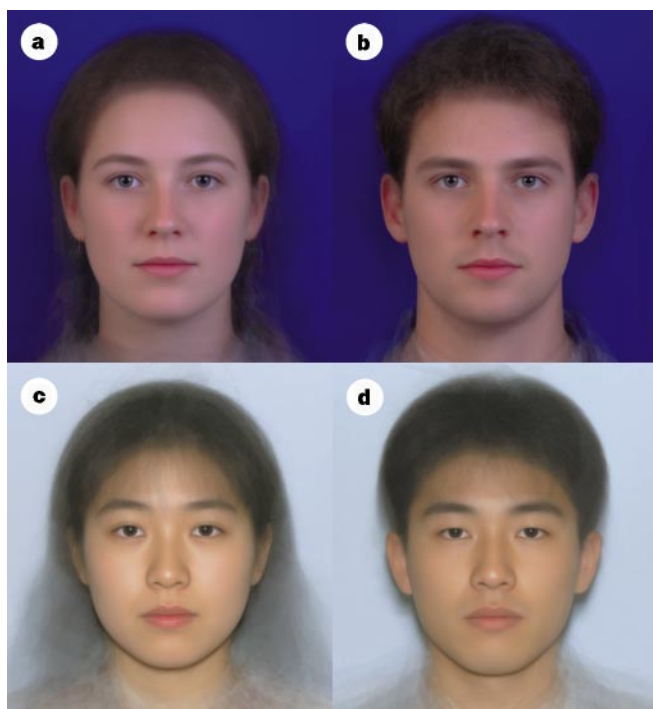


Figure 1 Composite 'average' facial images. **a**, 'Caucasian' female face; **b**, 'Caucasian' male face; **c**, 'Japanese' female face; **d**, 'Japanese' male face.



Figure 2 Facial images of Caucasian and Japanese females and males that were 'feminized' and 'masculinized' 50% in shape. **a**, Caucasian female, feminized; **b**, Caucasian female, masculinized. **c**, Caucasian male, feminized; **d**, Caucasian

male, masculinized. **e**, Japanese female, feminized; **f**, Japanese female, masculinized. **g**, Japanese male, feminized; **h**, Japanese male, masculinized.

Asymmetries in the facial outline (from the hairline), which remain after cropping, could contribute to judgements. With a different set of Caucasian faces (19 male, 17 female, 30–35 years old), symmetrical composites were made by averaging component faces and their mirror reflections. Caucasian subjects ($n = 67$, age range 15–40, 23 female) made forced-choice judgements of attractiveness of symmetrical average stimuli that were 50% masculinized or feminized. Masculinization of face shape decreased attractiveness of male (87% of subjects; Binomial test $P = 0.001$) and female faces (78%; $P < 0.001$), whereas feminization increased attractiveness of male (64%; $P < 0.05$) and female faces (53%; $P < 0.05$).

Males have larger faces than females. However, standardizing the distance between pupils removes this size difference. We prepared composite images from a new set of Caucasian faces (26 male, 17 female, 18–21 years old) without standardizing the inter-pupil separation. Manipulation of these composites maintained sexual dimorphism in face shape and size. Caucasian subjects ($n = 135$, age range 15–71, 65 female) ranked average images that were masculinized and feminized by 50% for attractiveness. Masculinization of the average shape decreased attractiveness of male (74% of subjects; $P < 0.000005$) and female (76%; $P < 0.000005$) faces, whereas feminization increased attractiveness rankings for male (58%; $P = 0.029$) and female (60%; $P < 0.013$) faces.

Thus, preference for feminized face shapes over average male and female face shapes was found with interactive and forced-choice methods using different face sets, even when the potential contributions by symmetry and size dimorphism were controlled.

To interpret preferences, 50% masculinized, 50% feminized and cropped average images (Fig. 2) were rated for perceived characteristics by a new set of subjects. Twenty Caucasian subjects (age range

18–50, 10 female) were presented with four sets of three images that represented the end points of each continuum and the average. Subjects were asked to rank stimuli from one set on seven characteristics (masculinity, dominance, warmth, emotionality, honesty, intelligence and age). The order of testing of characteristics and image sets was randomized. An additional 20 subjects (age range 19–61, 10 female) ranked the stimuli on three further characteristics (cooperativeness, assertiveness and 'good parent').

For Caucasian and Japanese male faces, increasing the masculinity of face shape across the three set members increased ranking of perceived dominance, masculinity and age but decreased ranking of perceived warmth, emotionality, honesty, cooperativeness and quality as a parent (Friedman's $\chi^2 \geq 15.6$, degrees of freedom (d.f.) = 2, $P < 0.0005$, for each rated dimension). Increasing masculinity affected the Japanese and Caucasian female face sets in the same way for all characteristics ($\chi^2 \geq 8.1$, d.f. = 2, $P < 0.017$, each dimension), except for 'good parent' with the Caucasian female faces, where the rank order was average, feminized and masculinized ($\chi^2 \geq 6.7$, d.f. = 2, $P < 0.035$). Increasing masculinity did not consistently decrease apparent intelligence (Caucasian male and female faces, $P > 0.5$; Japanese female face, $P = 0.07$; Japanese male face, $P = 0.02$) or increase attributions of assertiveness (Japanese and Caucasian female faces, $P > 0.5$; Japanese male face, $P = 0.058$; Caucasian male face, $P = 0.157$).

The preference for male face shapes that are slightly feminized may reflect the effects of masculinity on perceived age. Whereas status and height are valued in males^{9,18}, youth benefits judgements of attractiveness for both female^{9,11,19} and male¹⁹ faces. For both males and females, enhancing sexual dimorphism in face shape develops cues to characteristics which, from a biological perspective, appear beneficial (that is, youth and fertility in females^{7–11} and dominance in males^{12,13,18}). For males, however, enhancing masculinity in face shape also predisposes some negative personality attributions. Such attributions, although stereotypic, may predict behaviour; ratings of perceived dishonesty from facial appearance correlate with the face owner's willingness to participate in deceptive behaviour²⁰. Indeed, increasing testosterone level in males is associated with more troubled relationships (including increased infidelity, violence and divorce)²¹. Feminization of male face shape may increase attractiveness because it 'softens' particular features^{10,22} that are perceived to be associated with negative personality traits.

Together, the results indicate that judgements of male attractiveness reflect multiple motives²². Females may adopt different strategies, giving preference to characteristics that are associated with dominance and an effective immune system^{12,13}, or to characteristics that are related to paternal investment.

Sexual dimorphism in any species reflects compromises among diverse selection pressures. In humans, the greater upper body musculature and more rugged skeletal anatomy of males relative to females may reflect advantages in male–male competition and hunting. Because male attractiveness is an important determinant of relationships and sexual partnerships²³, the reduction in attractiveness of male face shape with masculinization represents a further selection pressure. This would act against 'run away' fisherian sexual selection for extreme male characteristics¹, and is consistent with the relative lack of sexual dimorphism in humans²⁴.

The preferences found here indicate a selection pressure on the evolution of face shape that acts against pronounced differences between males and females and, as more-feminine face shapes are perceived as younger, the preferences would encourage a youthful, neotinous appearance in the species generally. □

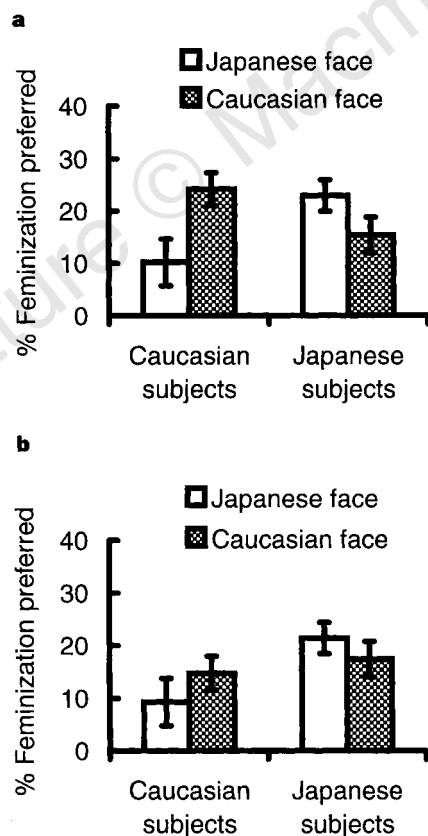


Figure 3 The effect of feminization of face shape on judgements of female and male attractiveness. **a**, Female stimuli; **b**, male stimuli. Overall, subjects preferred a feminine face shape to an average shape both within and between populations. The degree of feminization preferred was greater within than between populations for female faces.

Methods

Preparation of composite facial images. Japanese faces (students at Ottemon-Gakuin University; 28 male, age 20–23 years, mean 21.6 years; 28 female, age 20–22 years, mean 21.4 years) were photographed under standard lighting conditions with neutral facial expression. Similar photographs were

prepared for Caucasian faces (students at St Andrews University, 25 male, age 19–23 years, mean 21.0 years; 30 female, age 19–22 years, mean 20.6 years). Photographs were converted to digital format (Kodak Photo-CD) and 174 feature points on salient facial landmarks (for example, nose-tip) were defined manually for each face^{14,15}. The average face shapes of the male and female Japanese and Caucasian face subsets were calculated from the feature points. The position of eye centres was standardized for corresponding average male and female face shapes. Each original face image was then warped to the shape of the corresponding average face and the resultant reshaped face images were blended together by averaging colour and intensity values of pixels at corresponding image locations^{14,15} (Fig. 1). The vector difference between corresponding feature points on the male and female averages was increased or decreased by 50% to create feminized and masculinized shapes. The image of the composite face was then warped into these new face shapes to create image pairs with identical texture but enhanced or diminished sexually dimorphic differences in face shape. The size of all male and female face images was matched by standardization of inter-pupil distance. The resulting composite images were cropped around the face and faded into a black background (Fig. 2). Cropping removed the hair, ears and neck, which were not consistent in shape or visibility in component images because of differing hairstyles and clothing.

Procedure. A Silicon Graphics Indigo² Maximum Impact (4 MB TRAM) was used to create smooth continua between 50% masculinized and 50% feminized face pairs (Fig. 2) as the end points, and the cropped average as the midpoint. The point along a shape continuum was controlled interactively by the position of the computer mouse. The appropriate image was calculated in real-time using texture mapping hardware. Stimuli were presented in 24-bit colour at the centre of an 800 × 800 pixel window. Fifty Caucasian subjects (research staff and students from St Andrews University; age 19–31 years, 25 female) and 42 Japanese subjects (research staff and students from ATR and Doshisha University; age 18–44 years, 19 female) were instructed to select the most attractive face from the continuum. Each continuum was presented twice to allow left/right counterbalancing of the end points, making a total of eight trials in randomized order.

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Separate body- and world-referenced representations of visual space in parietal cortex

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In order to direct a movement towards a visual stimulus, visual spatial information must be combined with postural information¹. For example, directing gaze (eye plus head) towards a visible target requires the combination of retinal image location with eye and head position to determine the location of the target relative to the body. Similarly, world-referenced postural information is required to determine where something lies in the world. Posterior parietal neurons recorded in monkeys combine

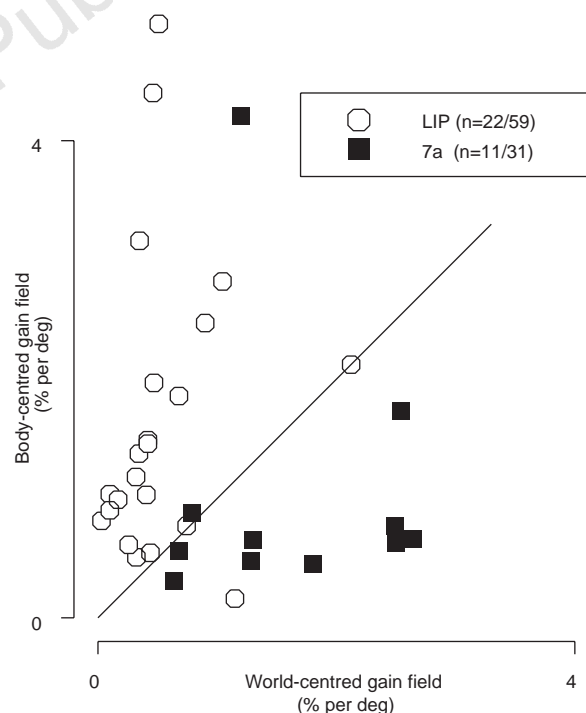


Figure 1 LIP responses (open circles) were modulated by body- but not world-referenced target location; 7a responses (filled squares) were modulated by world- but not body-referenced location. Visually evoked or delayed saccades were made after combined head-and-body rotation in the dark (world-referenced modulation), or after an equal counter-rotation of the body under a stable head. The absolute value of the gain field is shown for cells whose responses during and immediately after visual cue presentation depended on either body- or world-referenced head position (Student's *t*-test, $P < 0.05$; 33 of 90 cells). Cells above the diagonal line had stronger body-referenced modulation; cells below the line had stronger world-referenced modulation. Only two 7a cells fell above the line, and only two LIP cells fell below the line, indicating that body- and world-referenced modulation were well segregated by area (see Table 1).

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