

# Koinophilia revisited: the evolutionary link between mate selection and face recognition

M. K. Unnikrishnan\*

*Previous reports suggest that average faces are attractive, and that humans innately recognize and appreciate the attractiveness in the average face. The exception report model of face recognition employs the koinophilic fittest (modal) face for efficient and rapid recognition of conspecifics. The closeness of a face to the modal face is a measure of its attractiveness, whereas the departures from it are a measure of its ugliness and individuality. The 'fusiform face area' on the inferior surface of the temporal lobes of the brain might evaluate both the beauty and individuality of a face in a single, efficient and an evolutionarily well-honed operation.*

**Keywords:** Evolution, face fusiform area, face recognition, Koinophilia, mate selection, sexual selection.

ABILITY to judge the potential fitness of a mate and the highly specialized cognitive skills that help us identify individuals in the community appear to have little in common. While both are critical for survival, there is no recorded literature on any explicit connection between the two. This article aims to highlight an evolutionary link connecting mate selection and face recognition. Before trying to explain how the cognitive skills that guided mate selection improved the recognition between conspecifics (members of the same species), it is important to set the stage for understanding the context that invokes the connection between two seemingly independent cognitive domains. In the following pages, I propose to outline the body of research that suggests a strong evolutionary connection between the two phenomena.

## Historical precedents

Francis Galton, a half cousin of Charles Darwin, was a polymath who dabbled in a diverse array of topics such as eugenics, statistical correlation, synesthesia and the inheritance of intelligence, to name but a few. When photography was still in its infancy, Galton devised a technique called composite photography, where multiple images were captured sequentially on the same photographic plate, generating a composite image. Using this technique, he created composite portraits of a number of subjects, hoping to generate prototypical faces of a vegetarian and a criminal. The exercise proved futile; but to his utter amazement, the composite portraits became more and more attractive with the addition of each new face. Galton published this rather inexplicable finding in

1878, concluding that average facial dimensions combine to create a good-looking face<sup>1</sup>.

That average features should appear attractive was unexpected, because attractive faces are anything but common or ordinary in appearance. In spite of the novelty of the paper, Galton's observations lay buried between the pages of history for a century. Much later, Langlois and Roggman, from the University of Texas, Austin, USA, conducted a series of experiments that supported the 'beauty is average' hypothesis. Creating composite images on computer screens, a technique superior to Galton's composite photography, they asked students to rate the attractiveness of several composite portraits<sup>2</sup>. They found that attractiveness increased in proportion to the number of faces that went into creating the composite. The average of multiple faces was consistently more attractive than the individual faces that created the composite. Attractiveness could not be increased significantly beyond the 32-image composite, suggesting that facial proportions stabilize rather quickly within the normal population (Figure 1). Moreover, different 32-face composites looked similar, even when the constituent faces were different for each set. Indeed, many studies have repeatedly shown that computer-generated prototypical faces are more attractive than the faces which were used to generate them<sup>3-10</sup>.

The Hazda tribe, an isolated hunter-gatherer society of Tanzania, Africa, rated average Hazda faces as more attractive than the actual faces in the tribe<sup>9</sup>. While Europeans also rated average Hazda faces as more attractive, the Hazda people did not express any preference for average European faces. The authors attribute this difference to the visual experiences of the Europeans and the Hazda tribes. While the Hazda had never been exposed to human races outside their immediate environment, the Europeans had been exposed to both Western and African faces. The

M. K. Unnikrishnan is in the Manipal College of Pharmaceutical Sciences, Manipal University, Manipal 576 104, India.

\*e-mail: mkunnikrishnan@gmail.com

authors suggest that the indifference of the Hazda tribes towards average European faces could have been the result of lacking the European 'norm' in their visual experience. These results suggest that the rules for extracting attractive faces are culture-independent and innate, but the results of applying the rules depend on the environment and cultural experience<sup>11</sup>.

That the preference for the average is biological rather than cultural has been supported by a number of studies on infants and children. Neonates and infants of varying ages, for instance, gaze longer at attractive faces than at unattractive faces<sup>8,12-16</sup>. Strauss reported that 10-month-old children responded to average faces in the same way as they responded to attractive faces. They also reacted to them as if they were familiar (though never seen before), the way adults do<sup>17</sup>. Furthermore, Strauss was able to demonstrate that these infants were able to extract the average from simply drawn faces consisting of only four features of independently varying sizes.

Rubenstein *et al.*<sup>8</sup> showed that already at six months of age, children not only treated average faces the same as they treated attractive faces, but they were also able to extract the central tendency from a set of complex, naturalistic faces presented to them (i.e. not just the very simple schematic faces consisting of only the four dimensions used by Strauss). Thus the ability to extract the average from a set of realistic facial images operates from an early age, and is therefore almost certainly instinctive.

The body of research cited above has established two vitally important facts: (1) average faces are attractive and (2) the human mind is tuned to recognize and appreciate the attractiveness in the average face from a very

early age, and is therefore probably innate. Why are average proportions so important? What makes the average face so stunning and captivating? What could be the purpose of such a mathematical convenience in the construction of the living body?

In an effort to answer these questions, Langlois<sup>13</sup> notes that evolutionary pressure operates against phenotypic extremes causing the population mean to carry a majority of traits associated with fitness. Symons<sup>18</sup> argued that stabilizing pressure compels a convergence towards the average because mutations are the major cause of extreme phenotypes in the population. Since the vast majority of these mutations are harmful, they are eliminated by natural selection, leaving the fit features to characterize the modal phenotype in any given population. Many evolutionary biologists have tried to explain the intrinsic survival advantage of the average, but none of them appear as persuasive and meticulous as Johan Koeslag, the proponent of 'koinophilia'. In a series of articles in the *Journal of Theoretical Biology*, Koeslag has provided the most comprehensive and convincing arguments that espouse the fitness value of average features<sup>19-24</sup>.

### Koinophilia

Sexual selection and mate choice are critical components of fitness, because an organism passes on only 50% of its genome to its offspring, the other half coming from its sexual mate. A poor choice of mate could reduce an individual's fitness to zero, regardless of his or her own intrinsic fitness. However, as the real, current fitness of the mate can only be judged in retrospect (as it is measured in the number of offspring, grand-offspring and great grand-offspring relative to that of the rest of the population), the best and possibly only alternative indication of fitness is the possession of a plethora of common phenotypic features. (Phenotype, in this context, includes the physical, behavioural, auditory and olfactory attributes noticed by conspecifics.) These common features would indicate, at the very least, that they have been the fittest features up until now. Therefore, the development of sensory mechanisms for identifying the most common phenotypes would almost certainly have been a priority soon after the evolution of sex, 3 billion years ago<sup>25</sup>. Stated differently, since it is impossible to predict the fitness of a new mutation (and therefore of any novel or unusual phenotype), except statistically, all mutations are best regarded as deleterious. Therefore, the only way of avoiding them in a potential mate would be by sensitizing the cognitive systems towards all forms of phenotypic novelty.

Koeslag calls this avoidance of phenotypic novelty in potential mates as 'koinophilia'<sup>19</sup>. The term is derived from 'koinos' in Greek meaning 'usual', or 'common', and 'philos' meaning 'love', i.e. an affinity or love for



Figure 1. Beautiful faces are average.

common or usual phenotypic features in potential mates. Koinophilia operates on the entire phenotype. Any feature, such as body morphology, colouration, odour, song, motor functions and social behaviour, which does not escape the notice of conspecifics is therefore subjected to koinophilic evaluation.

Koinophilia has several important evolutionary consequences, or effects. For instance, the existence of several closely related sympatric species such as cheetahs, lions and leopards in the face of a complete absence of intermediate phenotypes, presents a nagging problem in evolution. What evolutionary force drives any lion that slightly resembles a leopard to extinction, keeping lion and leopard morphologies distinct? In fact, all the individuals of a species are remarkably similar, to such an extent that field guides, encyclopaedias and museums can generally describe, in minute detail, all the members of a given species with the use of a single illustration or specimen (or, if there is significant sexual dimorphism, a pair of illustrations or specimens). These problems are resolved if sexual creatures consistently choose mates with the least number of unusual features. Thus the lion that has developed leopard-like features cannot reproduce; it looks unusual and cannot find a mate. This eventually causes individual variation to diminish to the extent that it is difficult to discern as an outside<sup>19</sup>. Every individual looks like every other individual, very often even to the keenest observer (look for instance at the flamingoes in Figure 2). Scientists intent on studying individual behaviour in a natural population, therefore, almost always have to resort to individually tagging the animals in question.

This might seem in stark contrast to our experience of our fellow humans. We are exquisitely sensitive to the



**Figure 2.** Members of a sexual species look alike.

differences between individuals, each having a face that is unique and unmistakably distinct from all the other faces on earth. However, this only applies to individuals belonging to our own race. The individuals belonging to a foreign race look the same (the so-called ‘other race effect’), emphasizing that humans also look remarkably alike, just like in any other species.

When a new species arises, it seems to do so abruptly on a geological timescale, very often, but not exclusively, after a mass extinction or isolation event (e.g. on an island, or the break-up of a continent). However, once the transition to a new species has occurred, there is resistance to further phenotypic changes. This sudden ‘freezing’ of the phenotype, is easily explained by a koinophilic mating strategy, as that is, in fact, its major effect on a breeding population<sup>24</sup>. Koinophilia, therefore, not only provides an explanation for the absence of intermediate forms between species (e.g. between lions and leopards), but it also explains the long periods of ‘stasis’ or ‘evolutionary stagnation’ between speciation events (i.e. the ‘punctuated equilibrium’ hypothesis of Eldredge and Gould<sup>26</sup>). Thus, the cockroach spans 300 million years of phylogenetic stasis, while many genera and families of other sexual animals are as old as their classes.

There is abundant evidence from the published literature to support koinophilia. Forced random mating in fruit flies was shown to reduce the vigour of the offspring<sup>27</sup>. *Drosophila* with visible mutations mates less often than wild-types<sup>28</sup>. The same has been observed in the wasp, *Mormoniella vitripennis*<sup>29</sup>. Sexual isolation is often rigorous for both sympatric and allopatric races (i.e. races sharing the same, or geographically slightly separated habitats) within a given species, even when there are no anatomical or physiological barriers to hybridization. Checkerspot butterflies, for instance, on the Jasper Ridge of the Stanford University campus were found to exist as three sexually isolated groups, despite abundant opportunity for panmixis (random mating)<sup>30</sup>. Contrast this with the dramatic phenotypic differences between various breeds of dogs, created by selective breeding over a very brief period of history. This amply illustrates how rapidly new phenotypes, and therefore species, can arise in the absence of koinophilia. Likewise, the enhanced rate of mutation observed in laboratory mice could be the result of human intervention baulking koinophilic mate selection<sup>31</sup>.

More interestingly, since koinophilia is restricted to sexually reproducing creatures, it is not surprising to see asexual plants displaying phenomenal phenotypic variation. Thus the asexual dandelions, hawkweeds and blackberries present a taxonomic nightmare, as it is almost impossible to group them into anything resembling ‘species’ (i.e. collections of individuals who all look alike)<sup>32</sup>.

Koinophilia being concerned with the external phenotype, mutations which do not alter the appearance or

behaviour of creatures (i.e. cryptic mutations), would be expected to accumulate with time, thereby allowing molecular evolution to proceed without hindrance. The high rate of mitochondrial mutation, relative to genomic DNA, could be, at least partly, on account of the cryptic nature of mitochondrial mutations<sup>33</sup>.

Using a stochastic computer model, it has been demonstrated that koinophilia can contribute to the resistance of bi-gender sexually reproducing creatures against replacement by asexuals, despite the inherent twofold fitness advantage that asexuals have over sexual creatures who produce males<sup>24</sup>. Employing another stochastic computer model, it was shown that koinophilia replaces random mating within a population subject to random mutations<sup>20</sup>. The advantage was greatest when the mean fitness of the mutations was nearly neutral (i.e. they were on average only mildly deleterious). This is because when mutations are lethal, no special aids are needed to eliminate them – natural selection removes them almost as quickly as they arise. But when mutations are only mildly disadvantageous, natural selection allows them to linger and therefore accumulate over many generations. Koinophilia however prevents this accumulation, and drastically reduces the mutational load in the population – an advantage that a randomly mating population does not enjoy.

The most remarkable achievement of koinophilia-driven sexual selection is in being able to explain cooperation<sup>22,23</sup>. Cooperation is clearly highly advantageous to any group of creatures. But, surprisingly, it presents a major evolutionary problem, because selfish individuals are bound to arise by mutation. These selfish mutants enjoy all the advantages of the cooperative endeavours of their fellows, while they avoid the inevitable costs of that cooperative behaviour. A pack of wolves can, for instance, bring down a bison, but not without a certain amount of danger to some members of the pack. The selfish individual does not run this risk, and therefore has a selective advantage over his cooperative counterparts. His selfishness will therefore be passed on, on average, to more offspring than are produced by each cooperative member of the pack. This will happen in successive generations causing the entire pack to eventually consist of selfish individuals. Cooperation is therefore inherently 'evolutionarily unstable'. Yet examples of cooperative behaviour abound throughout the animal kingdom. The problem could be solved by koinophilia. If the selfish behaviour is noticed by the group, and is regarded as deviant, then the selfish individual will probably not easily find a mate, and thus not reproduce. If it cannot reproduce its fitness falls to zero, whatever advantages it might extract from the group while it is alive.

The most striking aspect of koinophilia is its parsimony. The Occam's razor principle asserts that amongst competing theories, the simplest theory postulating the least number of assumptions, and solving the largest

number of problems, is the most acceptable. It follows that koinophilia should be the most likely explanation for a suite of evolutionary paradigms, including cooperation. Why then has koinophilia failed to win widespread acceptance?

The 'beauty is average' hypothesis should have strengthened the notion of koinophilia. But Perrett and co-workers<sup>7</sup> appear to have found evidence that the average face is not the most attractive face. They found that they could create a face that was more attractive than the average face by averaging the faces of only the most beautiful individuals. If they then mildly exaggerated the very slight differences between the two average faces (the average of the general population, and the average of only the beautiful faces), they were able to create a face that seemed more attractive still. It is difficult, however, from a glance at the three faces obtained by Perrett *et al.*<sup>7</sup>, to notice any differences between them at all. The three faces are remarkably similar. This indicates that Perrett *et al.*<sup>7</sup> have not found any evidence to contradict, in any meaningful manner, the 'beauty is average' hypothesis. Despite this, their findings have been widely quoted as suggesting that the preferred sexual mate is not one with average features, but one with exaggerated, and therefore unusual features<sup>7</sup>. After all, intuitively, beauty does appear to be exceptional.

The problem arises from the fact that the 'average' is equated with 'common'. This is a misconception on two counts. No individual has an exactly average height (unless that height is expressed crudely to only three significant figures). Individuals might have heights close to the average height, but the 'average height' itself is a theoretical concept, and, like many mathematical abstractions, is never attained in real life. Secondly, 'an average face' consists of many averages (average distance between the eyes, average length of the nose, average protrusion of the nose, average width of the upper lip, thickness of the lips, etc.). Even if one accepts a definition of 'average' as all the values within one standard deviation on either side of the mean, and assumes that a face can be faithfully reproduced using only 100 independent measurements, then an 'entirely average' face (as defined earlier in this sentence) would occur only once in  $10^{18}$  faces ( $P = 0.66^{100} = 9.0 \times 10^{-19}$ , or 1 in approximately  $10^{18}$ ). In other words, it would be an extremely rare face, likely to occur only once in almost one billion generations of a population as large as the world's present human population. This, in turn, means that every human has an 'unusual' or 'non-average' face of one sort or another, making each face unique.

Another common objection raised about the 'beauty is average' hypothesis is that the average faces are symmetrical and free of skin blemishes, two features that have been shown to correlate strongly with sexual attractiveness<sup>6,11,34-36</sup>. This, however, does not bring into question the validity of the 'beauty is average' hypothesis, since

both are genuine results of the averaging process. The observation merely suggests that some of the features averaged in an average face might be more important than others, or, that they are more easily tested for their attractiveness than others. However, that these two considerations are not the complete explanation for the beauty of the average face has been demonstrated by Rhodes and Tremewan<sup>10</sup>, who used line drawings of faces (obviously free of skin tones and skin blemishes). The average of these line drawings was consistently more attractive than the faces used to calculate the average. Thus the average of many facial features contribute to the attractiveness of the average face, as demonstrated by Langlois *et al.*<sup>37</sup>, who managed to specifically rule out symmetry, blur and other artefacts of the averaging process as explanations for the 'beauty is average' hypothesis<sup>37</sup>.

Thus, in a thorough, wide-ranging review of sexual selection and the biology of beauty, Grammer and co-workers<sup>11</sup> conclude that the human obsession with beauty is no different from similar obsessions in other organisms; that the basic feature of human beauty in faces and bodies is gender-specific averageness; and that those averages can be different in different settings and cultures. Thus while there is no innate beauty detector, the basic rules on how to look for beauty are innate.

### From mate selection to face recognition

The high degree of intraspecific morphological, behavioural, vocal and olfactory uniformity allows even the minutest deviation from the species norm to be easily noticed by conspecifics. This will have two effects. First, it greatly improves and sharpens the mate selection process, thus preventing the genome from accumulating mutations that would otherwise be removed only slowly by natural selection. Secondly, since no individual is 'average' in every respect (as defined above), the combination of 'non-average' features that conspecifics consequently notice in their fellows allows them to recognize individuality. As will be explained below each combination of just a few unusual features will, within the context of real populations, be unique, just as each car of the same make and colour taken off the street has a unique set of blemishes (scratches, dents and rust patches) which advertise its individuality.

An infatuation with the norm can only exist if that norm can be distinguished from the deviations from it. In other words, an infatuation with the norm requires an equal fascination with the abnormal. The evolution of koinophilia is therefore also the evolution of the recognition of individuality. The closeness of a face to the modal face is a measure of its attractiveness (and therefore its fitness), whereas the departures from it are a measure of its ugliness and individuality. Consequently, face recognition and mate selection are two sides of the same coin.

This is therefore where face recognition and koinophilic mate selection meet. It is a notion derived from an earlier paper on face recognition<sup>38</sup>, which employs the koinophilic fittest face as the gold standard for all comparisons, allowing exception reporting to form the basis of a simple, fast and accurate face identification process.

### The exception reporting model of face recognition

The widely recognized Bruce and Young model of face recognition suggests that the age, gender and facial expressions are evaluated before the face is identified as belonging to a certain individual<sup>39</sup>. The 'fusiform face area' (FFA) on the inferior surface of the temporal lobe of the brain is specially dedicated to this latter task<sup>40</sup>.

Two models of face recognition have been proposed. Both assume that faces are encoded as vectors in a multi-dimensional 'face-space' volume<sup>41</sup>, with the prototypical face located at its centre. Each measurement which contributes to the construction of a realistic and recognizable face is plotted on a different 'dimension'. Thus interpupillary distance can be plotted on a two-dimensional graph against nose length. If mouth width is added, a third dimension is created, and so on. Most computer artists require 250 points or more to construct a good-quality line drawing of a recognizable face<sup>7</sup>. So the proposed 'face-space' has at least 250 dimensions, each of which has to be remembered precisely to correctly place a given face in this mental multidimensional volume. The 'norm-based model' compares individual faces with the prototypical norm at the centre of the face-space volume, whereas the 'exemplar-based model' assumes that a norm is not abstracted, but that specific faces are stored and remembered only in relation to their nearest neighbours in the multidimensional face-space<sup>41-43</sup>. Both models are uneconomical because they involve neural processes that have to execute 250 feature-by-feature comparisons of the index face with a standard (either the prototypic norm, or a face that serves as the standard in a certain region of face-space to which the index face seems to belong). The rapidity and ease of face recognition do not seem to be compatible with either model.

The exception reporting model of face recognition postulates a modified norm-based model, in which attention is focused exclusively on features that differ significantly from the koinophilic fittest face (modal face)<sup>38</sup>. In this paper<sup>38</sup> the norm was defined as all values between the 5th and 95th percentile, regardless of the distribution of the metric (i.e. Gaussian or not). Each unusual feature therefore occurs in 5% of the population (e.g. an unusually short nose has a probability of 0.05, as does an unusually long nose). The exception reporting (ER) model of face recognition therefore requires remembering only 10 unusual features in a face to make it a 1 in 10<sup>13</sup> face



**Figure 3.** Even the slightest error destroys the portrait. Caricatures are instantly recognized despite gross distortions. (Portraits and caricature reproduced with permission from Vivek Vilasini, and Aswini and Abani respectively.)

( $P = 0.05^{10} = 9.77 \times 10^{14} = 1$  in  $10^{13}$ ). Note that the present human population comprises just less than  $7 \times 10^9$  individuals, who are divided approximately 50 : 50 between males and females, of which, in turn, 30% or more are children. Thus remembering only ten unusual, gender-specific features is more than adequate to provide every human we meet with a unique face. This is clearly far more economical than memorizing 250 or more detailed measurements in every face we encounter. Furthermore, the ER model proposes that it is not necessary to know how long the unusually long nose is. It is sufficient simply to know that it is longer than usual. This therefore allows caricatures to be drawn of faces, where long noses are made longer still. These caricatures occupy positions in face-space very different from their target faces, but our face recognition machinery readily links the caricature to the person it is supposed to depict. In fact, Rodriguez *et al.*<sup>44</sup> have shown that face identification is more accurate when persons are presented with caricatures instead of veridical images of the faces, from which subjects are then asked to recognize the real persons, while Nejadi and Sims<sup>45</sup> conclude from their studies of sketches that non-artists produce of faces, that the faces are probably stored as caricatures in the mind.

Caricatures are effective *only* when the unusual features *alone* are exaggerated. The slightest distortion of the modal features can destroy the identity of a portrait. The four portraits on the left of Figure 3 are painstaking attempts at realistically depicting Gandhi, but, evidently, none of them succeed. None of them captures or exagger-

ates the deviant features that made Gandhi's face unique. Not only do the four portraits fail to resemble Gandhi, they actually look like very different individuals! On the other hand, the caricature of Mother Theresa on the right (Figure 3) is instantly recognizable, despite the extravagant distortions! The 'errors' in the caricature are gross in relation to the poor portraits of Gandhi. Yet the human mind does not notice any 'error' in the caricature. Taken together, the contrasting results from the failed 'portraits' and the elegant caricature amply demonstrate that feature-by-feature comparisons are unnecessary for face recognition. Simple ER, despite gross exaggerations, is amazingly accurate.

The ER model explains the 'other race effect', in which people from an unfamiliar race all seem to look alike. When the modal facial features of the alien race differ significantly from one's own, those features which would have rendered a face unique in the familiar population now apply to everyone belonging to the unfamiliar race, making them all look alike.

Strauss<sup>17</sup> and Langlois *et al.*<sup>37</sup> have reported that computer-generated composite faces appear familiar. This could be because face recognition depends on the entrenchment in memory of a cluster of modal features which serve as the 'golden standard', with which other faces are compared. On the other hand, it has been reported that attractive faces, which are close to the modal face, are difficult to distinguish from one another<sup>46,47</sup>. This is easily explained by the ER model, as these faces possess few exceptional features.

When people look for family resemblances, some see strong resemblances to the mother's side, while others see the father's influence, or that of some other relative. Such differences in perception are possible because recognition requires only a limited number of unusual features. Different people could be using different sets of features to identify a given face.

The economy of the ER model has been demonstrated in computer face recognition programs. Hansen and Atkinson<sup>48</sup> (University of the West of England, Bristol), have demonstrated that when the data in a facial portrait which is shared by 90% of the other portraits are eliminated from a face, the ability of the computer face recognition program to correctly identify that face dropped by only 24%, suggesting that outlier features play a disproportionate role in determining the individuality of a face. So, a 90% reduction in data caused only a 24% reduction in performance, even though the data concerned involved only the grey scale of each pixel in the portrait, and not the features a human would notice in a face (e.g. nose length, etc.). Hansen and Atkinson<sup>48</sup> conclude that the relatively high rate of success in face recognition after obliterating the common features provides strong empirical support for the ER model of face recognition, which could probably be efficiently exploited by the computer face recognition industry.

## Conclusion

It may thus be argued that face recognition is an automatic by-product of sexual selection. There can be no doubt about the critical importance of a fundamentally reliable fitness meter for sexual creatures seeking a mate. If that meter is indeed koinophilia, then it is almost inevitable that creatures became grouped into species soon after the evolution of sex 3 billion years ago<sup>25</sup>, and that at a later date some of these species evolved cooperation. Cooperation creates communities, and in such communities it is vital that each individuals can be recognized for who they are, and where they fit into that community. I therefore posit that the evolution of koinophilia was eventually driven by two strong evolutionary forces: reliable mate selection and individual recognition.

The existence in the brain of an area exclusively devoted to face recognition attests to the evolutionary significance of this ability. Since face recognition by ER is merely a by-product of the assessment of beauty, it is indeed possible that the neural networks that enable face recognition are also employed in the assessment of beauty. Therefore, it is not surprising that Iaria *et al.*<sup>49</sup> found that the FFA might also be involved in the processing of facial attractiveness. In conclusion, the FFA might well evaluate both the beauty and individuality of a face in a single, efficient and an evolutionarily well-honed operation.

- Galton, F., Composite portraits, made by combining those of many different persons in a single resultant figure. *J. Anthropol. Inst.*, 1878, **8**, 132–144.
- Langlois, J. H. and Roggman, L., Attractive faces are only average. *Psychol. Sci.*, 1990, **1**, 115–121.
- Rhodes, G., Brennan, S. and Carey, S., Identification and ratings of caricatures: implications for mental representations of faces. *Cognit. Psychol.*, 1987, **19**(4), 473–497.
- Kalkofen, H., Müller, A. and Strack, M., Kant's facial aesthetics and Galton's composite portraiture – are prototypes more beautiful? In Proceedings of the 11th International Congress on Empirical Aesthetics (ed. Halasz, L.), International Association for Empirical Aesthetics, Budapest, 1990, pp. 151–154.
- Müller, A., Visuelle prototypen und die physikalischen dimensionen von attraktivität. In *Physische Attraktivität* (eds Hassebrauck, M. and Niketta, R.), Hogrefe, Göttingen, 1993, pp. 123–162.
- Grammer, K. and Thornhill, R., Human (*Homo sapiens*) facial attractiveness and sexual selection: the role of symmetry and averageness. *J. Comp. Psychol.*, 1994, **108**(3), 233–242.
- Perrett, D. I., May, K. A. and Yoshikawa, S., Facial shape and judgements of female attractiveness. *Nature*, 1994, **368**(6468), 239–242.
- Rubenstein, A. J., Kalakanis, L. and Langlois, J. H., Infant preferences for attractive faces: a cognitive explanation. *Dev. Psychol.*, 1999, **35**(3), 848–855.
- Apicella, C. L., Little, A. C. and Marlowe, F. W., Facial averageness and attractiveness in an isolated population of hunter-gatherers. *Perception*, 2007, **36**(12), 1813–1820.
- Rhodes, G. and Tremewan, T., Averageness, exaggeration, and facial attractiveness. *Psychol. Sci.*, 1996, **7**, 105–110.
- Grammer, K., Fink, B., Moller, A. P. and Thornhill, R., Darwinian aesthetics: sexual selection and the biology of beauty. *Biol. Rev. Cambridge Philos. Soc.*, 2003, **78**(3), 385–407.
- Langlois, J. H., Roggman, L. A., Casey, R. J., Ritter, J. M., Rieser-Danner, L. A. and Jenkins, V. Y., Infant preferences for attractive faces: rudiments of a stereotype? *Dev. Psychol.*, 1987, **23**, 363–369.
- Langlois, J. H., Ritter, J. M., Roggman, L. A. and Vaughn, L. S., Facial diversity and infant preferences for attractive faces. *Dev. Psychol.*, 1991, **27**, 79–84.
- Slater, A. M. *et al.*, Newborn infants prefer attractive faces. *Infant Behav. Dev.*, 1998, **21**, 345–354.
- Samuels, C. A. and Ewy, R., Aesthetic perception of faces during infancy. *Br. J. Dev. Psychol.*, 1985, **3**, 221–228.
- Kramer, S., Zebrowitz, L. A., San Giovanni, J. P. and Sherak, B., Infants' preferences for attractiveness and babyfacedness. In *Studies in Perception and Action III* (eds Bardy, B. G., Bootsma, R. J. and Guiard, Y.), Erlbaum Associates, Hillsdale, NJ, 1995, pp. 389–392.
- Strauss, M. S., Abstraction of prototypical information by adults and 10-month-old infants. *J. Exp. Psychol.: Hum. Learn. Mem.*, 1979, **5**(6), 618–632.
- Symons, D., *The Evolution of Human Sexuality*, Oxford University Press, Oxford, 1979.
- Koeslag, J. H., Koinophilia groups sexual creatures into species, promotes stasis, and stabilizes social behaviour. *J. Theor. Biol.* 1990, **144**(1), 15–35.
- Koeslag, J. H., Koinophilia replaces random mating in populations subject to mutations with randomly varying fitnesses. *J. Theor. Biol.*, 1994, **171**(3), 341–345.
- Koeslag, J. H., On the engine of speciation. *J. Theor. Biol.*, 1995, **177**, 401–409.
- Koeslag, J. H., Sex, the Prisoner's Dilemma Game, and the evolutionary inevitability of cooperation. *J. Theor. Biol.*, 1997, **189**(1), 53–61.

## GENERAL ARTICLES

---

23. Koeslag, J. H. and Terblanche, E., Evolution of cooperation: cooperation defeats defection in the cornfield model. *J. Theor. Biol.*, 2003, **224**(3), 399–410.
24. Koeslag, P. D. and Koeslag, J. H., Koinophilia stabilizes bi-gender sexual reproduction against asex in an unchanging environment. *J. Theor. Biol.*, 1994, **166**(3), 251–260.
25. Margulis, L. and Sagan, D., *Origins of Sex: Three Billion Years of Genetic Recombination*, Yale University Press, New Haven, 1986.
26. Eldredge, N. and Gould, S. J., Punctuated equilibria: an alternative to phyletic gradualism. In *Models in Paleobiology* (ed. Schopf, T. J. M.), Freeman, Cooper and Co, San Francisco, CA, 1972, pp. 82–115.
27. Partridge, L., Mate choice increases a component of offspring fitness in fruit flies. *Nature*, 1980, **283**, 290–291.
28. Reed, S. C. and Reed, E. W., Natural selection in laboratory population of *Drosophila* II competition between white eye gene and its allele. *Evolution*, 1950, **4**, 34–42.
29. Grant, D., Snyder, G. A. and Glessner, S. F., Frequency dependent mate selection in *Mormoniella vitripennis*. *Evolution*, 1974, **28**, 259–264.
30. Ehrlich, P. R., White, R. R., Singer, M. C., Mckenzie, S. W. and Gilbert, I. R., Checker-spot butterflies: a historical perspective. *Science*, 1975, **188**(4185), 221–228.
31. Fitch, W. M. and Atley, W. R., Evolution in inbred strains of mice appears rapid. *Science*, 1985, **228**, 1169–1175.
32. Clapham, A. R., Tutin, T. G. and Warburg, E. F., *Flora of the British Isles*, Cambridge University Press, Cambridge, 1952.
33. Vawter, L. and Brown, W. M., Nuclear and mitochondrial DNA comparisons reveal extreme rates variation in the molecular clock. *Science*, 1986, **234**, 194–196.
34. Thornhill, R. and Gangstead, S. W., Human facial beauty. *Hum. Nat.*, 1993, **4**, 237–263.
35. Thornhill, R. and Gangestad, S. W., Human fluctuating asymmetry and sexual behavior. *Psychol. Sci.*, 1994, **5**, 297–302.
36. Gangestad, S. W., Thornhill, R. and Yeo, R. A., Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethol. Sociobiol.*, 1994, **15**, 73–85.
37. Langlois, J. H., Roggman, L. A. and Musselman, L., What is average and what is not average about attractive faces? *Psychol. Sci.*, 1994, **5**, 214–220.
38. Unnikrishnan, M. K., How is the individuality of a face recognized? *J. Theor. Biol.*, 2009, **261**(3), 469–474.
39. Bruce, V. and Young, A., Understanding face recognition. *Br. J. Psychol.*, 1986, **77**, 305–327.
40. Kanwisher, N. G., McDermott, J. and Chun, M. M., The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.*, 1997, **17**, 4302–4311.
41. Valentine, T., A unified account of the effects of distinctiveness, inversion, and race in face recognition. *Q. J. Exp. Psychol. A.*, 1991, **43**(2), 161–204.
42. Leopold, D. A., O’Toole, A. J., Vetter, T. and Blanz, V., Prototype-referenced shape encoding revealed by high-level aftereffects. *Nature Neurosci.*, 2001, **4**(1), 89–94.
43. Leopold, D. A., Bondar, I. V. and Giese, M. A., Norm-based face encoding by single neurons in the monkey inferotemporal cortex. *Nature*, 2006, **442**(7102), 572–575.
44. Rodriguez, J., Bortfeld, H., Rudomin, I., Hernandez, B. and Gutierrez-Osuna, R., The reverse caricature effect revisited: familiarization with frontal facial caricatures improves veridical face recognition. *Appl. Cognit. Psychol.*, 2008, **23**, 733–742.
45. Nejadi, H. and Sim, T., A study on recognizing non-artistic face sketches. Applications of Computer Vision (WACV), 2011 IEEE Workshop, 2011, pp. 240–247.
46. Bruce, V., *Recognizing Faces*, Lawrence Erlbaum Associates Ltd, London, 1988.
47. Wickham, L. H. and Morris, P. E., Attractiveness, distinctiveness, and recognition of faces: attractive faces can be typical or distinctive but are not better recognized. *Am. J. Psychol.*, 2003, **116**(3), 455–468.
48. Hansen, M. F. and Atkinson, G. A., Biologically inspired 3D face recognition from surface normals. *Proc. Comput. Sci.*, 2010, **2**, 26–34.
49. Iaria, G., Fox, C. J., Waite, C. T., Aharon, I. and Barton, J. J., The contribution of the fusiform gyrus and superior temporal sulcus in processing facial attractiveness: neuropsychological and neuro-imaging evidence. *Neuroscience*, 2008, **155**(2), 409–422.

ACKNOWLEDGEMENTS. I thank Dr Raghavendra Gadagkar, Chairman, Centre for Contemporary Studies, Indian Institute of Science, Bangalore, for providing the resources and facilities for preparing the groundwork for this paper during my tenure as visiting scientist in June 2010. I also thank Ms Piya Paul for helping me with the manuscript.

Received 16 June 2011; revised accepted 4 January 2012