The Riddle of Attractiveness: Looking for an 'Aesthetic Sense' Within the Hedonic Mind of the Beholders

Michel Kreutzer, Verena Aebischer

Chapter 12
The Riddle of Attractiveness: Looking for an 'Aesthetic Sense' Within the Hedonic Mind of the Beholders

Michel Kreutzer and Verena Aebischer

> *Beauty, my dear Sir, is not so much a quality of the object beheld, as an effect in him who beholds it.*
> Spinoza, 1674 (1901), Letter to Hugo Boxel

Abstract Darwin conceived the theory of sexual selection in order to explain beauty in animal Kingdom. He hypothesised that most of the male ornaments had been developed to correspond to a female 'sense of beauty'. His successors developed a theory of mate choice in which the aesthetic sense was left out. The male sexual ornaments were considered as salient cues that evolved because they are indicators of males' fitness, which stimulate the female to mate. As a consequence "good genes" would spread to future generations. Such a perspective left no place for the males' appearance and displays as a source of pleasure for females. More recently, authors have considered that male traits might evolve because they make discrimination, stimulus recognition, memorability and learning easier. The winner is the most attractive not necessarily the 'strongest' male. Moreover, male traits might be favoured because they happen to fit an already existing bias in the female sensory system. Such a sensory exploitation determines the direction of a "runaway process".

Today, the "aesthetic sense" is back, the neurosciences study the chemistry and circuitry that support pleasure in the brains of humans and animals; social psychology and animal cognition focus on emotions, categorisation and prototype used for mate choice. Animals and humans in order to make a decision, have to evaluate both

M. Kreutzer (✉)
Laboratoire d'Ethologie, Cognition et Développement (EA 3456), University Paris Ouest, Nanterre—La Défense, 92000 Nanterre, France
e-mail: Michel.Kreutzer@u-paris10.fr

V. Aebischer
Laboratoire Parisien de Psychologie Sociale (EA 4386), University Paris Ouest, Nanterre—La Défense, 92000 Nanterre, France
e-mail: Verena.Aebischer@u-paris10.fr

the sensation and the goal directed action. For this a salient hedonic value has to be built by the mind. Here are the processes involved in the 'aesthetic judgement'.

Keywords Animal aesthetics · Attractiveness in humans · Brain reward circuitry and aesthetics · Evolution of beauty · Hedonic mind

12.1 Introduction

"The sense of beauty" is a basic process in the theory of sexual selection that Darwin introduced in the second part of the ninteenth century. Since its publication in 1871 it has met widespread criticism, scepticism and recast of the theory. The idea that female animals are capable of aesthetic choice was not well received among evolutionists. As shown in Sect. 2 and 3, over the past 150 years, many controversies and reformulations have taken place about the function of aesthetic choice. In behavioural studies, until today, much more research has been conducted on the male anatomy and displays supposed to 'stimulate' or to 'charm' the females than studies on female emotions or 'feelings' in front of good looking males. There might be two reasons to that: Either because male behaviour is easier to study than female subjectivity or because authors found it more interesting to study males who are traditionally said to be more 'active' in mate choice. Interestingly, as Sect. 4 illustrates, aesthetic choice has also been absent in the investigation of mate choice in humans explored by social scientists, obsessed as they were by the fitness model of their natural science colleagues. However, as evidenced in the last paragraphs of Sect. 3 and 4 aesthetic choice based on the sense of beauty is coming back with numerous studies on the brain and mind of the receiver, the 'choosy' female. Section 5 illustrates that the sense of beauty or aesthetic sense is much more a process in the mind of the individuals who perceive a signal than a property of the signal per se. Recent work in social psychology, animal cognition and neurosciences reserves an important place to the study of what makes a partner attractive in the eyes of the beholder. The expression "aesthetic judgement" has been used by numerous authors in the context of pair formation and mate choice, and aesthetic choices are explored in humans and animals. Social psychology and animal cognition, for instance, take especially in consideration emotions, categorisation and prototypes related to mate choice. Section 6 is on 'hedonic reward', and 'pleasure', which are prerequisites to "aesthetic judgment" in animals and humans especially when choosing sexual partners. When testing the 'sense of beauty', the neurosciences study the hedonic circuitry that supports the pleasure in the brain of humans and animals opening up new avenues for the understanding of "aesthetic choices".

12.2 A Theory for the Origin of Natural Beauty

12.2.1 To Whom Beauty is Addressed?

When considering nature and especially living species, humans may experience the beauty of some of them. From our admiration for flowers and ornaments in animals or vocalisations emerges the question: to whom this beauty is addressed?

Darwin (1859) had this question in mind when he observed plants and animals. To him the existence of beauty in low animals like coral or sea anemones is the direct result of the structure and the chemical nature of their tissues. Their aesthetic properties fulfil no function at all. They may have something to do with what Portman (1952) called the "unaddressed appearance". Beauty also exists to attract animals; this is the case when it serves the purpose of plants that need animals for their pollination. Then beauty is addressed to pollinating animals who are rewarded with nectar and odour. There is coevolution because beautiful things on one side fit the sensibility of the receiver on the other side.

However, Darwin was most aware of beauty addressed by males to females of their species. As Hoquet (2009) underlines, if, for Darwin, beauty is not useful then it does not serve natural selection. For instance, the evolution of the male bowerbirds' elaborate courtship displays and complex nest decoration presented a problem to Charles Darwin's theory of natural selection, because in no way did such behaviour help the bird to survive in its environment. Both appeared to be colourful and complex elaborations produced by and for an aesthetic sensibility. How could these elaborations during the course of evolution be otherwise explained than by the animals' "taste for the beautiful", their "sense of beauty" or "aesthetic faculty"?

The theory of evolution was first centred on natural selection, which explains variation among species. Natural selection is based on differential survival that depends on the interactions between individuals and their environment. It is a theory of "adaptation", where only traits with life preserving value could evolve. Its crucial point is the survival of the fittest. Darwin was not convinced, contrary to Wallace (1858), co-discoverer of the theory of natural selection, that the 'struggle for life' was the right explanation for all the transformations in animals and especially for their beauty. When he established the concept of natural selection in his 'origin of species' (1859), sexual selection was only slightly mentioned. It left the question of the causation of beauty unsolved. For that reason, Darwin, later (1871), wrote another book, devoted mostly to sexual selection, a theory to explain beauty in animal kingdom.

12.2.2 Sexual Selection and the Female Aesthetic Sense

Sexual selection is a strategy that is complementary and different from natural selection, as it makes bodies, most often the males' bodies, more beautiful and at the same time enhances the aesthetic sense of the receivers, most often the females' aesthetic sense. Milam (2010) summarised Darwin's ideas and the discussion they raised in the following way:

In sexual selection two mechanisms:

> … explained why males and females differed in appearance and behaviour: one was female choice, the other was male-male competition. In female choice, females compared the mating displays of reproductively mature males and chose the most appealing male with which to mate. In male-male competition, males fought to determine which male would have access to the reproductively available female(s) in the area. Both mechanisms, Darwin argued, would result in exaggerated male traits. Over evolutionary time, female choice would lead to aesthetically pleasing male traits (long tails and brightly coloured plumage), and male-male competition to armour or weapons (bony plates or antlers)…. In this way '… female choice presupposed both a sense of aesthetic appreciation and an ability to choose rationally based on this aesthetic sensibility'. (Milam 2010, pp. 1–2)

Sexual selection provided Darwin with an answer to the question: How was it that females and males of the same species differed so significantly in their appearance and behaviour, especially with regard to mating display? Sexual selection does not depend on struggle for life, as natural selection does, but on competition between males for the possession of the females; the result is few or no offspring for the loser. Most of the time fighting between males was replaced by male competition for female attention through courtship displays. Females, on the other hand, actively use their attention and their 'taste for the beautiful' to select the most attractive partners.

Darwin (1871) was very clear on these points, when referring to the male features he said:

> … these organs will have been perfected through sexual selection, that is by the advantage acquired by certain males over their rivals. (Darwin 1871, I, p. 257)

And he said that in birds:

> … those males, which are best able by their various charms to please or excite the female, are under ordinary circumstances accepted. (Darwin 1871, II, p. 124)

The continuity between animals and humans is presented in the following way:

> Sense of Beauty.—This sense has been declared to be peculiar to man. But when we behold male birds elaborately displaying their plumes and splendid colours before the females, whilst other birds not thus decorated make no such display, it is impossible to doubt that the females admire the beauty of their male partners. (Darwin 1871, I, p. 63)

> Why certain bright colours and certain sounds should excite pleasure, when in harmony, cannot, I presume, be explained any more than why certain flavours and scents are agreeable; but assuredly the same colours and the same sounds are admired by us and by many of the lower animals. (Darwin 1871, I, p. 64)

> No doubt the perceptive powers of man and the lower animals are so constituted that brilliant colours and certain forms, as well as harmonious and rhythmical sounds, give pleasure and are called beautiful…. (Darwin 1871, II, p. 353)

Darwin also developed a modern point of view on the coevolution between signal, attractiveness, and brain capacities:

> Everyone who admits the principle of evolution, and yet feels great difficulty in admitting that female mammals, birds, reptiles, and fish, could have acquired the high standard of taste which is implied by the beauty of the males, and which generally coincides with our own standard, should reflect that in each member of the vertebrate series the nerve-cells of the brain are the direct offshoots of those possessed by the common progenitor of the whole

> group. It thus becomes intelligible that the brain and mental faculties should be capable under similar conditions of nearly the same course of development, and consequently of performing nearly the same functions. (Darwin 1871, II, p. 401)
>
> He who admits the principle of sexual selection will be led to the remarkable conclusion that the cerebral system not only regulates most of the existing functions of the body, but has indirectly influenced the progressive development of various bodily structures and of certain mental qualities. …/… musical organs, both vocal and instrumental, bright colours, stripes and marks, and ornamental appendages, have all been indirectly gained by one sex or the other, through the influence of love and jealousy, through the appreciation of the beautiful in sound, colour or form, and through the exertion of a choice; and these powers of the mind manifestly depend on the development of the cerebral system. (Darwin 1871, II, p. 402)

So it appears that male beauty has been developed for the purpose of being appreciated by the corresponding female sense of beauty. Females will go for the most beautiful males, whose beauty provides the most pleasure. In Darwin's theory of sexual selection females do not appreciate beauty as a signal of fitness; their 'aesthetic judgment' is their only guide. His theory is a theory of the female psychology, not of evolutionary "ultimate" causes.

12.3 Fall and Rise of the Idea of Aesthetic Choices

12.3.1 Who has the Capacity to Appreciate Beauty?

For Darwin different species share the same sense of beauty, which is the reason why humans find bright colours and songs beautiful in birds. As a reverse Watanabe (2012) demonstrated how some visual and auditory dimensions of human art productions have a reinforcing property for non-human animals. Thus Darwin believed in the anatomical, physiological, intellectual and behavioural continuity of humans with other animals; he applied the theory of natural selection and sexual selection in a similar way to both humans and animals. This was far from convincing to his naturalist colleagues, then as it is today. Wallace (1864) preferred to draw a clear line, with humans on one side and animals on the other, and contrary to Darwin, argued that animals did not possess the capacity to reason, therefore they could not choose (see Slotten 2004 for details). Wallace believed that female animals were not capable of evaluating the aesthetic appeal of males' courtship displays and of choosing a mate based on such effects. Romanes (1881) was of a different opinion; he agreed with Darwin's point of view that animals are able to make decisions and to feel the stimuli that determine their choices. Romanes attributed aesthetic 'emotions of the beautiful' to animals exhibiting colourful secondary sexual features and extended such capacities even to the arthropods. Huxley (1914), a famous defender of evolutionary theories, did not agree with the idea that females evaluated the aesthetic of the males. His idea was that of emotional excitement. Looking at the displays of the great crested grebe he noted that both sexes participated in courtship dances; sexual selection could, therefore, not be involved in male beauty.

12.3.2 Genetic Fitness is Declared as the Eternal Winner, the Fall of Beauty

During the course of the twentieth century the importance of the female aesthetic sense fell in disrepute and with it the theory of sexual selection. They were replaced by a theory of mate choice that some authors included in the natural selection processes. One may find a complete analysis of this in Milam (2010). The rise of Mendelian genetics focused evolutionary biology on the genetic change in a single population over time with natural selection depending on the total number and quality of an individual's offspring. Sexual selection was thus eclipsed and evolution redefined as a process of natural selection merely changing gene frequencies along generations (Haldane 1932). The gradual accumulation of micro modifications could drive large modifications and directional evolution over the time.

With the emergence of a synthesis constituting a new evolutionary theory, called neo-Darwinism, biologists investigated evolution as a process of speciation (Mayr 1942). Instead of sexual selection and aesthetic choices, authors began to investigate what happened if some females in a population only preferred to mate with a specific kind of males. Thus, female choice could drive the creation of a reproductively isolated population and potentially lead to speciation. Fisher (1930) provided an explanation for the evolution of secondary sex ornaments by mate choice. If females have a sexual preference for a particular kind of male trait, so he argued, this confers a selective advantage. The trait will became a salient cue and will spread to future generations in a "runaway process". In no way does this theory imply that females perceive beauty, they only "appreciate" secondary sexual ornaments, which, when associated with a slight survival advantage, could became an indicator of fitness.

For most of these authors, the history of mate choice is distinct from the history of sexual selection, the latter being only considered as the Darwinian explanation of beauty in animal kingdom. From their perspective, mind and aesthetic sensibilities ought to be considered as discontinuous elements demarcating animals from humans, thus sharing Wallace's ideas about the differences between humans and animals.

The interest for female sensibility to male traits gained momentum with the discovery of the "rare male effect" Bösiger (1974), Petit (1958). Both authors' intent was to explain why females preferred to mate with male types that were the least frequently found in a population. One held the view that females act to maintain genetic diversity, whereas the other interpreted it in terms of female sensitivity to males' stimulatory courtship behaviours.

12.4 Signal Design: Sexual Selection is Back, but Where is Beauty?

Darwin's theory was forcefully resisted by scientists for over a century, in part because the active choosing of mates seemed to grant too much power to females, who were thought to remain passive in the mating process. It was also resisted

because it seemed to blur the animal-human boundary. That those females should go for the beautiful, and for the most beautiful male, because of their sense of beauty, stirred up controversy among communities of biologists who preferred to subsume sexual selection under natural selection. They would rather explain female preferences for males' courtship display in terms of reaction to signals advertising fitness. In other words, what would appear to be a choice of "beauty" should ultimately be understood as a preference for utility.

12.4.1 Selective Female and Male Honest Signalling

Bateman (1948) and Trivers (1972) opened a new line of interest in sexual selection by providing arguments for female choice. Bateman demonstrated that in Drosophila the reproductive success during lifetime is constrained for both male and female; for a male by the number of mates an individual is able to obtain and for the female by the number of births or hatchings. The female does not have as many opportunities to reproduce as the male does. Because of her greater reproductive refractoriness she is supposed to be more attentive to the success of her reproduction by showing greater selectivity when choosing her partners than her male counterparts. Trivers, in a similar way, developed the "theory of parental investment" in which he compared male and female cost to reproduce: gametes, pregnancies, broodings, taking care of the young, etc. According to his theory, the sex that exhibits more costly parental investments (most often the female in birds and mammals) will be the chooser. The sex that exhibits less investment will compete for mating opportunities; as a consequence it is the females that will most often choose the males in higher vertebrates.

The term 'choice' in animal behaviour was used in "behavioural ecology", during the sixties and seventies, to describe the ultimate causes that are causes considered efficient from the evolutionary point of view to explain natural and sexual selection. That does not mean that animals are aware of their determinisms. Game theory (Maynard Smith 1989) applied to animal behaviour has considered individuals as rational agents who try to enhance benefits and to minimise costs. From such a perspective it was hypothesised that the choosy sex will mate with individuals who possess traits that signify overall genetic quality. Females are, therefore, seeking good genes in order to gain an evolutionary advantage for their offspring. Thus the theory of sexual selection is not looking for a female 'taste for the beautiful' but explains that females are looking for indicators of males' fitness. Anderson (1994, p. 22) summarises this as follows:

> There is now much evidence that females often choose their mate, and that such choice favours conspicuous male traits. The exact ways in which female choice selects for such traits are still debated, and so are the ways in which female preferences evolve, which remain a main controversial issue in the theory of sexual selection.

Among the potentially salient traits for females' choice, bilateral symmetry and its deviations (fluctuating asymmetry) as well as pigmentation were examined. Hamilton and Zuk (1982) hypothesised that sexual ornaments are indicators of disease resistance to parasites, and also an index for good health and fertility. In

birds, plumage colour, pigment and ornaments symmetry support this hypothesis (Swaddle 1996; Møller 1992, 1996; Hill et al. 1999). Because symmetry is said to reveal disease resistance and the ability of a genotype to undergo stable development of a phenotype under given environmental conditions, this feature was also tested positively in humans (Tovée et al. 2000). Many authors designated as beauty such symmetry and conspicuous ornamentations or colours.

The theory of the handicap principle (Zahavi 1975, 1977) explains how female preferences for males' signals have evolved. The handicap principle describes how evolution may lead to honest signalling. It suggests that to avoid animals' cheating for advantages over conspecifics about their state, capacity or intention, reliable signals must be costly to the signaller. They indicate to the receiver the sexual quality of the emitter; because inferior quality signallers cannot afford to produce such extravagant signals. Males exhibiting the most costly features must also be the most vigorous ones. Sexual ornaments such as bird songs, peacock tails, courtship displays, or bowerbirds' bower, are costly signals, and therefore salient indicators of the male quality. However, the theory does not include a description of the females' feeling when looking at these ornaments.
As Anderson (1994, p. 17) explains:

> The idea that conspicuous male display, colours feather plume, and other secondary sex ornaments evolve through female choice met much early scepticism. Darwin seemed to assume similar sense of beauty in other higher vertebrates as in man. But this assumption, right or wrong, is not necessary for female choice: discrimination among males in relation to size, shape colour or others should suffice.

12.4.2 Sensory Bias, Receiver Psychology and the Design of Animal Signals

For Ryan (1990) a new male trait might be favoured because it happens to fit an already existing bias in the female sensory system. Such a sensory exploitation determines the direction of a "runaway process". Males might evolve traits that exploit pre-existing sensory biases of the female. The theory states that the sensory bias evolves in a non-mating context; for instance the foraging ecology of a species may lead to high sensitivity to certain colours. This bias might favour the evolution of male ornaments with such colours and the female preferences for these traits. Females leave males with poorly developed courtship signals for males that provide more effective stimulation. Ryan concludes (1990, p. 186):

> Such an approach can only increase our understanding of the fascinating process of sexual selection by showing how properties of the receivers exert selection on male traits, and how they are responsible for some of the most bizarre morphologies and behaviours in the animal kingdom. It certainly will inform us about how evolution operates and thus can contribute to hypotheses of the evolution of female preferences.

Female preference may have evolved for reasons not related to fitness advantages for males with the most far-reaching signals. Other factors, such as an initial sensory bias, or selection for species recognition, might help explain mate choice. Some

male traits may have evolved simply because they make it easier for females to find the male. Sexual selection would favour males who most effectively stimulate the recipients, that is, with intense, persistent, or otherwise conspicuous signals. These ideas were particularly well developed in the "receiver psychology" approach of Guilford and Dawkins (1991, 1993). They underline the role played by sensory systems of the receiver's brain in constraining the design of the signals emitted by the sender. The receiver's capacity of signal detection (reaction time and detection against background noise), discrimination, stimulus recognition, memory and learning, must be taken into account. In addition Rowe (1999) mentioned the advantage of the multimodal components of a signal, because redundancy facilitates its detection.

Receiver psychology only takes into account some aspects of the theory of signal transmission, detection and recognition, but not cognition, emotion and feeling of the receiver. As in the studies of the male emitter, there is no place for "a taste for the beautiful" in the receiver psychology. The receiver is considered like an automaton.

12.4.3 Beauty is Back

The female "sense of beauty" has been brought back with Burley and Symanski (1998) in their seminal paper: "A taste for the beautiful": Latent aesthetic mate preferences for white crests in two species of Australian Grassfinches. By experimental means they demonstrated that two avian species from a lineage devoid of crested species have mate preferences for opposite sex conspecifics wearing artificial white crests. Other colours of crests that have been studied were not preferred. One may interpret such results as a confirmation of the sensory bias hypothesis. But the fact that in the lineage there was no crest at all does not fit very well with sensory bias For Burley and Symanski these results give "powerful evidence for highly structured aesthetic mate preferences in estrilidae finches and suggest that the preference for such a "structure" is influenced by the central nervous system". In conclusion they hypothesise that aesthetic preferences are a potent force in the early evolution of sexually selected traits, and that "indicator" traits evolve secondarily from traits initially favoured by aesthetic preferences. From this a new question arises: sender or receiver, who is the first during the course of evolution? It may well be the receiver and her need for hedonic rewards.

12.5 From Sexual Selection to Seduction in Humans

The breakthrough in applying sexual selection to humans came in the late 1970s and 1980s in the form of theoretical advances initiated by Buss and colleagues in the fields of psychology and anthropology (Buss 1989, 1994; Buss and Barnes 1986) and what was to become evolutionary psychology[1]. Evolutionary psychologists

[1] In his 1989 study on "Sex differences in human mate preferences: Evolutionary Hypotheses Tested in 37 Cultures," Buss asked 10,047 people in 37 different cultures located in 33 countries to

have found sexual selection theories to be most helpful to account for widespread gendered behaviours among humans. Theories in the field of sexual selection seemed to shed light on human sex differences and hence those pertaining to "human mating" and reproduction.

12.5.1 The Fitness Model Applied to Humans

Interestingly, like his counterparts in biology, Buss developed a series of hypotheses, all of them related to the fitness model. And from the beginning evolutionary psychology was entangled in social and stereotypical conceptions of masculinity and femininity, with Buss wanting to verify a few of the most obvious evolutionary predictions about sex differences in mating preferences; for example, whether men desire youth and physical attractiveness in a mate and whether women desire status and economic security. He found support for greater male than female use of resource display and for greater female use of enhancing physical appearance. Most sexually selected traits or behaviours in humans were explained as proxies for fitness. Thus, he contented (Buss 1998; cited by Haufe 2007, p. 116) that women had a preference for a "reliable man willing to commit to her" and that "the resources, aid, and protection" which those men provided caused her to have "children who survived and thrived". Buss offered no data on reproductive success of women either with a preference for reliable men or without a preference for reliable men. In place of the necessary data, Buss offers the "discovery" that women "place a premium on a man's social status, his ambition and industriousness, and his older age—qualities known to be linked with resource acquisition," (Buss 1998; cited by Haufe 2007, p. 117). The evolutionary approach generates only "after the fact" explanations, relying on models from ethology and experiments conducted with animals combined with observations and findings in psychology, psychiatry, behavioural genetics and neurobiology. There is no demonstration of differences in reproductive success in humans resulting from the valuable resource or the preference for reliable men.

The female preference for reliable, resource-giving men is supposed to have evolved sometime during the Pleistocene. Indeed, as underlined by some of the most influential proponents of evolutionary psychology, Cosmides and Tooby (1997) "our modern skulls house a stone age mind". Behaviour in the present is generated by information-processing mechanisms that exist because they solved adaptive problems in the past, which our hunter-gatherer ancestors faced during our species' evolutionary history. For this reason, evolutionary psychology is past-oriented. However, to Cosmides, contrary to Buss, because these mechanisms solved problems efficiently in the past does not mean that they necessarily generate adaptive behavior in the present (also see Symons (1989) and Tooby and Cosmides (1990).

---

provide information about features which according to Buss have been shown to be theoretically important to human mating preferences.

12.5.2 Sex Roles Without Aesthetics

A different explanation for sex differences in behaviour has been suggested by social structural theory (Eagly and Wood 1999). Rather than to attribute sex differences in contemporary society to sex-typed evolved mechanisms, social structuralists maintain that because men and women tend to occupy different social roles, they become psychologically different in ways that adjust them to these roles. Physical sex differences, in interaction with social and ecological conditions, influence the roles held by men and women because certain activities are more efficiently accomplished by one sex. The benefits of this greater efficiency can be realise when women and men are allied in cooperative relationships and establish a division of labour. The particular character of the activities that each sex performs then determines its placement in the social structure (Wood and Eagly 2000).

Evolutionary theory values and validates as a natural given stereotypical conceptions of masculinity (philandering, social status and strength) and feminity (passivity, valuing of their body and youth). Social structuralists focus on the sexes' efficient cooperation in life tasks given women's capacity for gestation and lactation and men's greater speed and physical strength (Wood and Eagly 2000). Both theories have in common that they have never ever considered the role aesthetics could play in mate choice.

12.5.3 Seduction in Humans

A more complete picture of mate choice is offered by Moore (1985), who has observed nonverbal facial expressions and gestures, exhibited by human females that are commonly labelled "flirting" behaviours. Moore has identified 52 nonverbal solicitations such as giggling, laughing, smiling, head tossing, hair flipping, caressing ones arm or leg. Indeed, men seem to have little chances to seduce a woman if she has not taken notice of them before, and if she has not signalled interest via nonverbal cues. Glancing behaviours are important in signalling interest, glancing at and then away from the male. Glancing behaviour appears to be a significant part of the female role (Cary 1978). Males are generally hesitant to approach without some indication of interest, and repeated eye contact seems to demonstrate a woman's interest (Crook 1972a, b). Women reject suitors by failing to recognise their presence through eye contact. Moore observed, then, head tossing, with the head flipped backwards so that the face was briefly tilted upwards often combined with pushing her fingers through her hair or running her palm along the surface of her hair, but also pouting, eyebrow flashing and, above all, smiling. Smiling is among the most prevalent behaviours and consists of the corners of the mouth being turned upward, in partial or sometimes full exposure of the teeth. The "coy" smile combines a half-smile with a downward gaze or very brief eye contact. These expressions and gestures appear to function as attractants and advertisers of female interest.

According to Moore, nonverbal solicitation is only one of the first steps in the sequence of behaviours beginning with mate attraction and culminating with mate selection. Women who signal often are also those who are most often approached by men. They can elicit a high number of male approaches, allowing them to choose from a number of available men. Or they may direct solicitations at a particular male. Behaviours such as nodding, leaning close to the man, smiling and laughing are in higher frequencies after the man has made contact with the woman. Conversation is initiated and the participants appear highly animated. Women, while talking to men appear excited, laughing, smiling, and gesticulating frequently. In the sexual arousal phase, touching gestures are exchanged.

Not only does the woman first signal her interest in a potential candidate, the actual choice and final decision is also hers and rests on what the man says to the woman in addition to his behaviour towards her and others. However, little is known as to which men are chosen for further interaction, which are rejected, and on what grounds. More investigation on that level of female choice could open up new vistas as to aesthetical considerations involved in that choice.

Another example of female choice and signal sending was offered by Zanna and Pack (1975). Young women were asked to characterise themselves to a male partner who was either attractive or unattractive and whose ideal of a woman conformed either very closely to the traditional female stereotype or to its opposite. When the male partner was attractive and favoured the traditional female stereotype, the young women portrayed themselves as significantly more conventional and traditional than when, a few weeks before, they had been asked to make an objective description of themselves. When he was attractive, but favoured a modern type of woman, they portrayed themselves as more modern, unconventional and independent than before. However, when the partner was unattractive, they did not change their self-description. Nobody knows how the story would have evolved, had these young women really met the attractive or the unattractive partner. However, the experiment shows quite clearly that these young women have first appreciated the partner's attractiveness, before signalling that there could be some commonalities and mutual understanding between them.

12.6 The Mind of the Beholder

Receivers are not simple signal analysers passively waiting to be stimulated. The receptors experience emotions, build representations of their relationships with peers and may feel social pleasure in the presence of some of them. These aspects must be taken into account if we want to understand the aesthetic value that females attribute to some males. However, the study of animals' subjectivity is more complicated than the study of their behaviour. Anthropomorphism, which consists of transposing human emotions or rationality onto animal actions, tended to make animals look more like humans. Most researchers, therefore, prefer to choose the paradigm of parsimony. In doing so, they seem, however, to neglect that the receiver psychology is much more complex than that of an automaton, even a sophisticated one.

12.6.1 Cognition, Categorisation and Prototype

The world is not just a source of isolated stimuli, which act independently from each other, as behaviourists first thought. A substantial amount of studies on animal cognition show that birds and mammals have representations of their world as categories of objects and events. Herrnstein (1984) was one of the first to demonstrate natural concept discrimination in pigeons. Subjects were trained to classify photographs that exemplify categories as trees, individual persons, fish and others … As stated by Roitblat (1985, p. 306):

> …these results support the hypothesis that pigeons form abstract representations of the discriminated concepts…

Cognition in animals (Thompson 1995) got further understanding when the theory of prototype (Rosch and Mervis 1975) was extended to them. Similar objects are members of the same category. The categories may have clear or fuzzy boundaries depending on their properties, graduated colour, or not, like an animal. But the important point is that some members are better exemplars than others. For instance, for most people some dogs are better than others to represent the category dog. These central exemplars are prototypes.

Categorisation in animals is an important step towards "aesthetic values" in animals, because if some males are better than others to be chosen as sexual partners, they can be considered to be prototypes. Moreover, if emotions and pleasure are experienced at the sight of these prototypes, then we are at the heart of the category "beautiful partners". The "sense for beauty" could work.

Surprisingly, when it comes to humans, attractiveness based on physical characteristics has captivated researchers' interest mainly from a male perspective. In an overview of recent research, Swami and Furnham (2006), both social psychologists, showed that there are physical characteristics that are attractive across cultures. In most cultures men will rate women with a 0.7 waist to hip ratio WHR as more attractive than a woman with a higher WHR. For faces averageness, symmetry, and sexual dimorphism (masculinity in males, femininity in females) are also preferred across cultures (for reviews, see Fink and Penton-Voak 2002; Thornhill and Gangestad 1999).

Attractiveness is most salient in people's reactions to faces (Olson and Marshuetz 2005). Recent studies have uncovered some of the factors involved in the perception of attractiveness that seem to be universal. When people were asked to rate the attractiveness of computer-composite images of faces (female and male) they perceived attractiveness increases the more different faces of the same sex were averaged and went into each image (composites created by averaging 4 vs. 8 vs. 16 vs. 32 faces). The more images were used, the more idiosyncrasies of particular faces, which may be unusual, become ironed out. Moving a facial image closer to the average increases its attractiveness (Langlois and Roggman 1990). This "beauty-in-averageness effect" only works, however, when the features of the faces are average of the group to which a face belongs (Potter and Corneille 2008).

The beauty in averageness effect is often theoretically explained as reflecting a biological predisposition to interpret prototypes as salient cues for mate choices (Symons 1979).

Referring to the honest signalling theory Thornhill and Gangestad (1993) consider that if facial composites made by combining individual faces are judged to be more attractive than the majority of individual faces it is because the composites possess both symmetry and averageness of features. Facial averageness may reflect high individual protein heterozygosis and thus an array of proteins to which parasites must adapt. As we know heterozygote are better than homozygote in defence against parasites. Facial averageness reflects, therefore, resistance to parasites whereas symmetry certifies overall phenotypic quality and developmental health (Thornhill and Gangestad 1993).

A rather different explanation has been suggested by Zajonc (1980). In humans particular cerebral areas are related to appreciation of beauty (Kawabata and Zeki 2004). The basis for the relation of attractiveness and averageness might be our preference for things that are familiar to us. It is intimately linked to affective reactions, which are often the very first reactions of the organism and are dominant reaction for many species. This form of preference without inference may contribute to perceived attractiveness. In other words, emotions may come to play without our being aware of it. The closeness to the faces people may have seen creates a preference based on a comforting sense of ease. Such prototypes are attractive because they are easy on the mind (Langlois and Roggman 1990; Rhodes and Tremewan 1996; Winkielman et al. 2006). The pleasing prototypes respond to principles of economy.

12.6.2 What is Attractive in Humans?

People who are judged to be physically attractive make generally more favourable impressions on others than do people with lesser looks. There is an important list of qualities that attractive people are supposedly blessed with. They are assumed to have more agreeable personalities, to be more sociable, healthy, intelligent, better students, and teachers than less attractive people (Eagly et al. 1991). And both men and women desire as romantic partners the most attractive women or men they are able to win (Walster et al. 1966). But what makes a person attractive? Some general characteristics are universally considered to be attractive such as symmetry and averageness of faces and a narrow waist-to-hip ratio (Marcus and Miller 2003). However, there are also some specific features of the face and of the body that seem to attract one or both sexes.

According to Jones and Hill (1993), there is more to facial attractiveness than averageness. Although Langlois and her colleagues found that composite faces are more attractive than most of the faces that go into making the composites, few individual faces are consistently rated more attractive than any composite (Alley and Cunningham 1991). Cunningham (1986) showed that photographs of female faces

rated attractive in the United States have unusually large eyes, high cheekbones, thin cheeks, and small noses, chins, and jaws. Appealing female faces have a more neotenous "babyface" appearance combining features such as large eyes and a small nose (Jones 1995; Perrett et al. 1998). The ideal male face is closer to the average male face. However, male faces undergo a more thorough remodeling during adolescence than female faces, with a great expansion of the nose, mid-face, brows, chin, and jaw, which reduces the apparent prominence of the eyes and cheekbones (Jones and Hill 1993).

In one recent study, Li and Kenrick (2006, p. 479) found that young psychology male and female undergraduates who had or were considering having casual sex were physically attracted to the person and thought it would feel good. But the male students, far more than the female students, thought that it would allow them to get a sense of their value in the mate market.

Why does physical attractiveness lead to attraction? Aesthetic appeal seems to be desirable, and leads to positive affect (Kenrick et al. 1993). People like to look not only at people, but also at things that they find visually appealing. Even infants show a preference for attractive compared to unattractive people (Langlois et al. 1991). Research also suggests that when men see photos of very attractive women, a particular part of the brain is more strongly activated than when they concentrate on photos of average-looking women (Aharon et al. 2001). The part of these men's brains that is activated in response to beautiful faces is also activated in response to rewarding behaviours such as money and drugs (Sanderson 2010, p. 416).

12.6.3 Emotions in Humans and Animals

Darwin was particularly aware of what animals felt, because in his theory of evolution it was a proof of the continuity between animals and humans, which was the subject of his book, *The expression of the emotions in man and animals* (1872). The following two passages show his awareness that animal like humans experience emotion and pleasure.

> The sexes of many animals incessantly call for each other during the breeding-season; and in not a few cases, the male endeavours thus to charm or excite the female. This, indeed, seems to have been the primeval use and means of development of the voice…. Thus the use of the vocal organs will have become associated with the anticipation of the strongest pleasure which animals are capable of feeling. Animals which live in society often call to each other when separated, and evidently feel much joy at meeting. (Darwin 1872, p. 84)

> When male animals utter sounds in order to please the females, they would naturally employ those which are sweet to the ears of the species; and it appears that the same sounds are often pleasing to widely different animals, owing to the similarity of their nervous systems, as we ourselves perceive in the singing of birds and even in the chirping of certain tree-frogs giving us pleasure. On the other hand, sounds produced in order to strike terror into an enemy, would naturally be harsh or displeasing. (Darwin 1872, p. 91)

Later in a paragraph on "Pleasure, joy, affection" Darwin comments the pleasure and satisfaction that animals experience by referring to an observation made by the French psychiatrist Duchenne:

> Dr Duchenne—and I cannot quote a better authority—informs me that he kept a very tame monkey in his house for a year; and when he gave it during meal-times some choice delicacy, he observed that the corners of its mouth were slightly raised; thus an expression of satisfaction, partaking of the nature of an incipient smile, and resembling that often seen on the face of man, could be plainly perceived in this animal. (Darwin 1872, p. 132)

More recently Bekoff (2007, p. 14) referred to the importance of emotions to understand animals' life as follows:

> Of course there are differences among species. We would expect variations based on social, ecological, and physical factors. However there are compelling similarities despite sometimes extreme differences…. The brain of mice, dogs, elephants, and human differ greatly in size, but all of these species display joy and empathy.

Communication and sending a signal can be considered as a means to manipulate the mental state of the receiver. Music is a good candidate for such a job in humans. Miller published an article, in 2000, reaffirming Darwin's suggestion that human music is manipulative and was shaped by sexual selection to function as a courtship display:

> The vocalizations and gestures do not appear to be telling another individual about the world in the same way as we refer to objects, events and ideas when talking to another individual. Monkeys and apes probably simply do not appreciate that other individuals lack the knowledge and intentions that they themselves possess. Rather than being referential, theirs calls and gestures are manipulative: they are trying to generate some form of desired behaviour in other individual. The multimodal communication, the use of rhythm and melody, enhance synchronisation and the share of emotional state. (Miller 2000, p. 121)

Miller insisted that the function of such aesthetic selection criteria is to enhance selective mate preference in order to improve the outcome of sexual recombination that maintains genetic diversity, promotes speciation, and facilitates evolutionary search through optimal outbreeding.

Mithen (2006, p. 96) looking for "The origins of music in the singing Neanderthals", title of his book, went a step further in the understanding of the feeling of the receiver. Music affects emotion and mood:

> Mood is slightly different from an emotion; the former is a prolonged feeling that lasts over minutes, hours or even days, while the latter may be a very short feeling. The success of music therapy further demonstrates how music can be used both to express and to arouse a wide range of emotions, and also lead to substantial improvements in mental and physical health.

The idea that music importantly modifies the inner state of the listener—receiver has gained support over the past couple of decades since we now know a lot more about centres and circuitry, on one side, and social or behavioural situations implicating receiver's satisfaction, on the other side.

12.7 The Hedonic Receiver

12.7.1 Reward, Dopamine and the Mesocorticolimbic Circuitry

Olds and Milner (1954) introduced a seminal research by demonstrating that rats produced positive reinforcement until exhaustion by electrical stimulation of their septal area and other regions of their brain, especially their lateral hypothalamus (LH). Demonstration was also produced in humans that LH is a key centre of the brain reward function. Indeed Bishop et al. (1963) using intracranial self-stimulation in man obtained results similar to those of the rat experiments. Electrode stimulation evoked desire to stimulate again and strong sexual arousal, while never producing orgasm. What it did was to make humans press the button more.

A considerable body of literature followed these discoveries on the neurobiology of reward, based largely on studies of addiction or substance abuse. The circuitry involved in addiction is most often described as the 'dopamine mesocorticolimbic system'. Relevant circuitry in such studies has included dopamine cell bodies in the ventral tegmental area (VTA) that project to nucleus accumbens (NAcc, especially the core shell) that project via ventral pallidum to thalamus. There is a broad thalamic projection to prefrontal and cingulate cortex. The cortex completes the loop by projecting to VTA. Moreover the VTA projects directly to cortex and amygdala in addition to the nucleus accumbens.

In spite of the fact that addictive drugs act on the brain reward systems, one may consider that the brain had evolved not simply to respond to drugs but to natural rewards, such as food and sex. Appropriate responses to natural rewards were evolutionary important for survival, reproduction, and fitness Kelley and Berridge (2002). Many studies have effectively demonstrated the close correlation between dopamine release and behaviours that are sustained by drive and motivation (as taking food, water search and looking for a sexual partner). Today authors are in accordance when considering that neural circuits using dopamine confer to given stimuli particularities, which elicit them to be relevant to sensory, emotional or affective systems. Wise (2004) gave evidence of the role of such a system in learning. Today for many neuroscientists the primary role of the mesocorticolimbic dopamine circuitry in reward is to facilitate arousal, attention, motivation, memory consolidation, goal directed behaviour, and decision making (Schultz 2006).

Whatever the species, the pleasure of the brain is a central theme in cognitive neurosciences. Animals and humans in order to make a decision, have to evaluate both the sensation and the goal directed action. For this a salient hedonic value has to be built by the brain circuitry (Dickinson and Balleine 2009). Thus the reward processes in humans and animals have led to comparative studies. For Berridge and Kringelbach (2008) a rewarding stimulus activates many brain systems at the same time. There are three types of reward components: (1) liking: the hedonic impact of reward; (2) wanting: the motivation to obtain a reward and (3) representation: the cognitive processes about the rewards. The hedonic brain mechanisms being

similar in humans and other animals, the way is open for a comparative "affective neuroscience of pleasure".

Based on these considerations one may conclude that the decision of the 'female beholder' is as much related to the pleasure she experiences as to the characteristics of the signals she receives. Search of sensations that are pleasing for themselves is sufficient a motivation to trigger search behaviour in conjunction with pleasant stimuli, even in the absence of physiological needs. Animals are probably encouraged to simply looking for hedonic rewards. Objects and events that are able to provide such rewards have obviously an incentive value. During the evolution of cognition, pleasentness has allowed the construction of mental categories in which particular objects or events are regarded as being "good". We are here quite close to the Darwinian idea, that the animal brain like the human brain has built a sense of beauty (Kreutzer 2012). Moreover studies on addiction have demonstrated that a "runaway process" can transform the search of satisfaction that was initially related to the pleasure provided by useful objects or events into a search of pleasure for pleasure. The receiver's hedonism can drive to dependence.

12.7.2 Life, Social life and Pleasure

Berridge and Kringelbach (2008, p. 459) considerably enlarge the vision that rewards should only mediate sensory pleasure such as food and sex, mainly because:

> … social interactions with conspecifics are important to propagation of genes in all social animals such as humans … (thus particular social activities) … are also likely to be part of the repertoire of fundamental pleasures. Social pleasures in animals other than humans might be conceived as essentially similar to basis sensory pleasures or conceivably even in some nonhuman species as something more abstract. Social pleasure includes sensory visual features such as faces, touch features of grooming and caress, as well as in humans more abstract and cognitive features of social rewards.

Several studies have clearly demonstrated the link between pleasure and social life, particularly in the context of play, singing, pair formation and attachment (Panksepp1998 for a review; Panksepp 2005). A close association between opiates and play in juvenile rats was discovered by Ikemoto and Panksepp (1999). Low doses of morphine increased play, and opioids blockade with naloxone reduced play. From this one may conclude that opioids may enhance the pleasure and rewards associated with playing. Singing in songbirds, should be also a source of pleasure. Male zebra finches may use 'directed songs' for courtship and 'undirected songs' when singing alone. Hara et al. (2007), Huang and Hessler (2008) demonstrated that in VTA (ventral tegmental area) the neurons are more strongly activated during directed songs (courtship) than during undirected songs. Thus social context provides modulation to forebrain rewards' circuitry. Dopaminergic neurons of these birds work in a similar way as those of the mammalian (VTA) in the rewards circuitry. Moreover, such results support the idea that social encounters can trigger the same pathways as addictive drugs.

Insel (2003) studied the prairie and pine voles who form partner preferences and pair bound after mating contrary to montane and meadow voles who generally do not form such preferences. The neurobiology for pair bound is correlated with the mesolimbic dopamine activation of a particular kind of receptors that are necessary and sufficient for the development of partner preference. The processes involved in social attachment are close to those observed in an addictive process. Aragona et al. (2003) also showed in prairie voles that the administration of haloperidol directly into the NAcc (Nucleus accumbens, core shell) blocked partner preferences induced by mating. But, on the contrary, administration of apomorphine into the NAcc induced partner preference even in the absence of mating. These use of pharmacological techniques thus manipulated both the dopaminergic circuitry and the pair bound formation with its correlated attachment.

These results suggest that widely distinct groups of animals may experience similar positive emotional states while undergoing different types of social interactions. From this we can easily conceive that learning, displays, vocalisations, and partners' perception are impossible to imagine without hedonic processes. Therefore, animals should definitively be regarded as close to humans and not simply as complex mechanistic automatons. As Balcombe said (2006, p. 22):

> Feeling good is a powerful motivator that steers animals towards behaviour that keep them alive and help them reproduce … survival and pleasure are mutually compatible.

12.7.3 Are Love and Beauty Abstractions or Rooted in Basic Brain Circuitry?

Animal studies and human imaging have contributed to the understanding of the psychobiology of attachment and social bounding. When comparing the neuronal circuitry of maternal love, romantic love, and long-term attachment, neurobiology (Stein 2009) shows that they both overlap and differ. In these circuits, molecules, which have been demonstrated to play a role in the psychobiology of attachment and social bounding, include dopamine, serotonin, opioids, and vasopressin. Relevant circuitry has included the anterior cingulate, medial insula, striatum, and ventral tegmental area (VTA). Both maternal and romantic loves involve: anterior cingulate, medial insula, caudate nucleus, and the VTA. Thus sophisticated human behaviour is rooted in mammalian biology. Complicated concepts and processes such as love, reward, beauty, addiction, emotion or even rejection in love are, therefore, embodied in more basic and overlapping structures. During the course of evolution these functions were rooted in existing neuro circuitry and neurochemistry (Fisher 2004; Fisher et al. 2005, 2010).

From Bartels and Zeki (2004) studies comparing maternal and romantic loves emerge three points: (1) both involve a unique and overlapping set of areas, as well as areas that are specific to each; (2) the activated regions belong to the reward system and are also known to contain a high density of receptors for oxytocin and vasopressin, suggesting that the neuro hormonal control of these strong forms of

attachment observed in animals also applied to humans; (3) both forms of attachment suppress activities in regions associated with negative emotions, as well as regions associated with 'minding' and social judgments. This suggests that emotional ties to other persons inhibit not only negative emotions but also affect the network involved in making social judgements about a person. Attachment processes activate a specific pathway of the reward system and at the same time deactivate circuits that are responsible for critical social assessment and for negative emotions.

12.8 Conclusion: What does it mean to Have an "Aesthetic Sense"?

Vallet and Kreutzer 1995; Draganoiu et al. 2002; Suthers et al. 2012 have amply tested the acoustic preferences of the female songbirds and confirmed such sensory bias, sensory trap and honest signalling theories. However, more is needed to understand the female's attraction to a male's songs. When evaluating the signals exhibited by the male, the choosing and choosy female experiences the hedonic impact of reward: that is, emotions, feelings and liking. These are greater when morphology and displays of the male are close to the prototype she has in her mind, and they are necessarily based on an 'aesthetic judgement' depending on her 'sense of beauty' or 'taste for the beautiful'.

The position of Welsch (2004), a convinced advocate that animals, like humans, have an "aesthetic sense" could be summarised in the following way. While Darwin had advocated the existence of an aesthetic sense in some animals, most contemporary evolutionists have reduced aesthetics to mere survival value. They try to unmask aesthetic appreciation as a mere manifestation of fitness. From this (neo-Darwinian and especially sociobiological) perspective, there is simply no space for an aesthetic attitude. Even if one assumes that beauty means fitness in a hidden way, and that this is ultimately the reason why the beautiful is esteemed, one cannot get round the fact that what the female appreciates in the first place is the beautiful as such. The proximate goal and the ultimate goal would not be reached if aesthetic appreciation had not taken place. The aesthetic momentum remains indispensable. But it can only be reached through the perception and estimation of the beauty of the beautiful.

As noted by Welsch (2004), Darwin, contrary to most of his evolutionist successors never used the term "aesthetics judgement" when referring to female choice. Most of the time he mentioned that they had a "taste for the beautiful" or a "sense of beauty", and only rarely that they had an "aesthetic faculty". The concept of "taste", going back to eighteenth century philosophy, held the judgement of beauty to be immediate and disinterested. This means that the pleasure of beauty is not useful. Later, during the nineteenth century, the concept of "aesthetic" replaced the notion of "taste". Darwin not being a philosopher referred to "aesthetic faculty", "taste for the beautiful" and "sense of beauty" as synonyms, without giving a definition or a clear and constant meaning of these concepts.

Today, when authors refer to these Darwinian concepts, they often use the expression "aesthetic judgement". The meaning of "aesthetic judgment" is certainly different from the meaning of "taste", because it implies some underlying general principles that have yet to be discovered. The immediacy and disinterestedness, which encompass the general sense of taste, fit better with "aesthetic attitude", which refers to contemplation and to the work of nature for its own sake. It is also more in line with Darwin's writings that underline the un-usefulness of the males' traits selected by females.

However, "aesthetic attitude" is far from "aesthetics of the object", the objects being the salient cues of the animal's morphology and displays, which fit the psychology of the receiver. In fact most of these authors never use the term aesthetic. It is certainly the concept of "aesthetic experience" that will best correspond to the "conspicuous indicators" that sociobiology and behavioural ecology present as adaptive and revealing the vigour or good genes of the males. Petts (2000) establishes a link between the objects and the feeling they raise, for humans he says:

> Aesthetics experience is a natural felt response … adaptive … revealing value in the world. (Petts 2000, p. 70)

> The aesthetic experience is not a response to having checked that things have worked according to plan; rather there is a feeling that things are just so. This feeling of harmony or rightness that come about in our experience of things is a feature basic to our aesthetically experiencing them. (Petts 2000, p. 65)

As we see, the authors depending on whether they take into account the honest emitter, the hedonic receiver or the adaptive process, may use one or another definition. But, whatever the definition of aesthetic sense, of aesthetic faculty, of aesthetic judgment, of aesthetic attitude or aesthetic experience, they remain useful concepts to explore the continuity within the mind of the beholders, either human or animal.

References

Aharon I, Etcoff N, Ariely D, Chabris CF, O'Connor E, Breiter HC (2001) Beautiful faces have variable reward value: fMRI and behavioral evidence. Neuron 32(3):537–551

Alley TR, Cunningham MR (1991) Average faces are attractive, but very attractive faces are not average. Psychol Sci 2(2):123–125

Anderson M (1994) Sexual selection. Princeton University Press, Princeton

Aragona BJ, Liu Y, Curtis T, Stephan FK, Wang Z (2003) A critical role for Nucleus accumbens dopamine in partner preference formation in male prairie voles. J Neurosci 28(8):3483–3480

Balcombe J (2006) Pleasurable kingdom, animals and the nature of feeling good. Macmillan, New York

Bartels A, Zeki S (2004) The neural correlates of maternal and romantic love. Neuroimage 21:1155–1166

Bateman AJ (1948) Intra-sexual selection in *Drosophila*. Heredity 2:349–368

Bekoff M (2007) The emotional lives of animals. New World Library, California

Berridge KC, Kringelbach ML (2008) Affective neuroscience of pleasure: reward in humans and animals. Psychopharmacology (Berl) 199(3):457–480

Bishop MP, Elder ST, Health RG (1963) Intracranial self-stimulation in man. Science 140:394–396

Bösiger E 1974. The role of sexual selection in the maintenance of the genital heterogeneity of *Drosophila* populations and its genetic basis. In: van Abeelen JFH (ed) Genetic of behaviour. Elsevier, New York
Burley NT, Symanski R (1998) A taste for the beautiful: latent aesthetic mate preferences for white crests in two species of Australian Grassfinches. Am Nat 152(6):792–802
Buss DM (1989) Sex differences in human mate preferences: evolutionary hypotheses tested in 37 cultures. Behav Brain Sci 12(1):1–49
Buss DM (1994) The evolution of desire. Basic Books, New York
Buss DM (1998) The psychology of human mate selection: exploring the complexity of the strategic repertoire. In: Crawford C, Mahwah DKD (eds) Handbook of evolutionary psychology: ideas, issues, and applications. Lawrence Erlbaum Associates, New Jersey, pp 405–429
Buss DM, Barnes M (1986) Preferences in human mate selection. J Pers Soc Psychol 50(3):559–570
Cary MS (1978) The role of gaze in the initiation of conversation. Social Psychol 41(3):269–271
Cosmides L, Tooby J (1997) Evolutionary psychology : a primer. http://www.psych.ucsb.edu/research/cep/primer.html. Accessed 18 May 2012
Crook JH (1972a) Sexual selection, dimorphism, and social organization in primates. In: Campbell B (ed) Sexual selection and the descent of man 1871–1971. Aldine, Chicago, pp 180–230
Crook JH (1972b) The socio-ecology of primates. In: Crook JH (ed) Social behavior in birds and mammals: essays on the social ethology of animals and man. Academic, London
Cunningham MR (1986) Measuring the physical in physical attractiveness: quasi-experiments in the sociobiology of female facial beauty. J Pers Soc Psychol 50(5):925–935
Darwin C (1859) On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life. John Murray, London
Darwin C (1871) The descent of man and selection in relation to sex, vol 1–2. John Murray, London
Darwin C (1872) The expression of the emotions in man and animals. John Murray, London
Dickinson A, Balleine B (2009) Hedonics: the cognitive-motivational interface. In: Kringelbach ML, Berridge KC (eds) Pleasures of the brain. Oxford University Press, Oxford, pp 74–84
Draganoiu T, Nagle L, Kreutzer M (2002) Directional female preference for an exaggerated male trait in canary (*Serinus canaria*) song. Proc Royal Soc Lond 269:2525–2531
Eagly AH, Wood W (1999) The origins of sex differences in human behavior: evolves dispositions versus social roles. Am Psychol 54(6):408–423
Eagly AH, Ashmore RD, Makhijani MG, Longo LC (1991) What is beautiful is good, but…: a meta-analytic review of research on the physical attractiveness stereotype. Psychol Bull 110(1):109–128
Fink B, Penton-Voak I (2002) Evolutionary psychology of facial attractiveness. Curr Directions Psychol Sci 11(5):154–158
Fisher RA (1930) The genetical theory of natural selection. Clarendon, Oxford
Fisher H (2004) Why we love: the nature and chemistry of romantic love. Henry Holt, New York
Fisher H, Aron A, Brown LL (2005) Romantic love : an fMRI study of a neural mechanism for mate choice. J Comp Neurol 493:58–62
Fisher K, Brown LL, Aron A, Strong G, Mashek D (2010) Reward, addiction, and emotion regulation systems associated with rejection in love. J Neurophysiol 104:51–60
Guilford T, Dawkins MS (1991) Receiver psychology and the evolution of animal signals. Anim Behav 42(1):1–14
Guilford T, Dawkins MS (1993) Receiver psychology and the design animal signals. Trends Neurosci 16(11):430–436
Haldane JBS (1932) The causes of evolution. Longmans, Green and Co, London
Hamilton WD, Zuk M (1982) Heritable true fitness and bright birds: a role for parasites? Science 218(4570):384–387
Hara E, Kubikova L, Hessler N, Jarvis E (2007) Role of the midbrain dopaminergic system in modulation of vocal brain activation by social context. J Neurosci 25(11):3406–3416

Haufe C (2007) Sexual selection and mate choice in evolutionary psychology. Biol Philos 23(1):115–128
Herrnstein RJ (1984) Objects, categories and discriminative stimuli. In: Roitblat HL, Bever TG, Terrace (eds) Animal cognition. Erlbaum, Hillsdale, pp 233–261
Hill G, Nolan PM, Stoehr AM (1999) Pairing success relative to male plumage redness and pigment symmetry in the house finch: temporal and geographical constancy. Behav Ecol 10(1):48–53
Hoquet T (2009) Darwin contre Darwin: Comment lire l'origine des espèces? Seuil, Paris
Huang Y, Hessler NA (2008) Social modulation during songbird courtship potentiates midbrain dopaminergic neurons. Plos ONE 3(10):e3281. doi:10. 1371/journal.pone.0003281
Huxley JS (1914) The courtship-habits of the great Crested Grebe (*Podiceps cristatus*). With an addition to the theory of sexual selection. Proc Zool Soc 35:491–562
Ikemoto S, Panksepp J (1999) The role of nucleus accumbens dopamine in motivated behavior: a unifying interpretation with special reference to reward-seeking. Brain Res 31(1):6–41
Insel TR (2003) Is social attachment an addictive disorder? Physiol Behav 79:351–357
Jones D (1995) Sexual selection, physical attractiveness and facial neoteny: cross-cultural evidence and implications. Curr Anthropol 36(5):723–748
Jones D, Hill K (1993) Criteria of facial attractiveness in five populations. Hum Nat 4(3):271–296
Kawabata H, Zeki S (2004) Neural correlates of beauty. J Neurophysiol 91:1699–1705
Kelley AE, Berridge KC (2002) The neuroscience of natural rewards: relevance to addictive drugs. J Neurosci 22(9):3306–3311
Kenrick DT, Montello DR, Gutierres SE, Trost MR (1993) Effects of physical attractiveness on affect and perceptual judgements: when social comparison overrides social reinforcement. Personal Soc Psychol Bull 19(2):195–199
Kreutzer M (2012) La beauté est-elle honnête? Pour la Science 412:63
Langlois JH, Roggman LA (1990) Attractive faces are only average. Psychol Sci 1(2):115–121
Langlois JH, Ritter JM, Roggman LA, Vaughn LS (1991) Facial diversity and infant preferences for attractive faces. Dev Psychol 27(1):79–84
Li NP, Kenrick DT (2006) Sex similarities and differences in preferences for short-term mates: what, whether, and why. J Pers Soc Psychol 90(3):468–489
Marcus DK, Miller RS (2003) Sex differences in judgments of physical attractiveness: a social relations analysis. Personal Soc Psychol Bull 29(3):325–335
Maynard Smith J (1989) Evolutionary genetics, 2nd edn. Oxford University Press, Oxford
Mayr E (1942) Systematics and the origin of species. Columbia University Press, New York
Milam EL (2010) Looking for a few good males. Female choice in evolutionary biology. Johns Hopkins University Press, Baltimore
Miller G (2000) Evolution of human music through sexual selection. In: Wallin NLB, Merker B, Brown S (eds) The origin of music. The MIT Press, Cambridge, pp 329–360
Mithen S (2006) The singing neanderthals, the origins of music, language, mind and body. Harvard University Press, Massachusetts
Møller AP (1992) Female swallow preference for symmetrical male sexual ornements. Nature 357:238–240
Møller AP (1996) Parasitism and developmental instability of hosts: a review. Oikos 75:189–196
Moore MM (1985) Nonverbal courtship patterns in women. Context and consequences. Ethol Sociobiol 6(4):237–247
Olds J, Milner P (1954) Positive reinforcement produced by electrical stimulation of septal area and others regions of rat brain. J Comp Psychol 47:419–427
Olson IR, Marshuetz C (2005) Facial attractiveness is appraised in a glance. Emotion 5(4):498–502
Panksepp J (1998) Affective neuroscience, the foundations of human and animal emotions. Oxford University Press, New York
Panksepp J (2005) Beyong a joke : from animal laugher to human joy. Science 308(5118):62–63
Perrett DI, Lee KJ, Penton-Voak I, Rowland D, Yoshikawa S, Burt DM, Henzik SP, Castles DL, Akamatsu S (1998) Effects of sexual dimorphism on facial attractiveness. Nature 394(6696):884–887

Petit C (1958) Le déterminisme génétique et psycho-physiologique de la compétition sexuelle chez *Drosophila melanogaster*. Bulletin biologique de la France et de la Belgique 92(3):248–329
Petts J (2000) Aesthetic experiences and the revelation of value. J Aesthet Art Critic 58(1):61–71
Portman A (1952) Animal forms and patterns. A study of the appearance of animals. Faber and Faber, London
Potter T, Corneille O (2008) Locating attractiveness in the face space: faces are more attractive when closer to their group prototype. Psychon Bull Rev 15(3):615–622
Rhodes G, Tremewan T (1996) Averageness, exaggeration and facial attractiveness. Psychol Sci 7:105–110
Roitblat HL (1985) Introduction to comparative cognition. W. H. Freeman and Company, New York
Romanes GJ (1881) Animal intelligence. Kegan Paul, Trench, London
Rosch E, Mervis CB (1975) Family resemblances: studies in the internal structure of categories. Cogn Psychol 7:573–605
Rowe C (1999) Receiver psychology and the evolution of multicomponent signals. Animal Behav 58:921–931
Ryan MJ (1990) Sexual selection, sensory systems and sensory exploitation. Oxford Surv Evol Biol 7:157–195
Sanderson CA (2010) Social psychology. Wiley, Hoboken
Schultz W (2006) Behavioral theories and neurophysiology of reward. Annu Rev Psychol 57:87–115
Slotten R (2004) The life of Alfred Wallace, the heretic in Darwin's court. Lewis, Colombia
Spinoza B de (1901) The chiefs works of Benedict de Spinoza, [translated from the Latin, with an introduction by Elwes RHM, vol 2 De Intellectus Emendatione. Ethica. (Selected Letters) Revised edition]. George Bell and Sons, London
Stein DJ (2009) Love and attachment: the psychobiology of social bounding. CNS Spectr 14(5):239–242
Suthers R, Vallet E, Kreutzer M (2012) Bilateral coordination and the motor basis of female preference for sexual signals in canary song. J Exp Biol 215:2950–2959
Swaddle JP (1996) Reproductive success and symmetry in zebra finches. Anim Behav 51:203–210
Swami V, Furnham A (2006) The science of attraction. Psychol 19(6):362–365
Symons D (1979) The evolution of human sexuality. Oxford University Press, New York
Symons D (1989) A critique of Darwinian anthropology. Ethol Sociobiol 10(1–3):131–144
Thompson RKR (1995). Natural and relational concepts in animals. In: Roitblat HL, Meyer J-A (eds) Comparative approaches to cognitive Science. MIT, Cambridge, pp 176–224
Thornhill R, Gangestad SW (1993) Human facial beauty: averageness, symmetry and parasite resistance. Hum Nat 4:237–269
Thornhill R, Gangestad SW (1999) Facial attractiveness. Trends Cogn Sci 3(12):452–460
Tooby J, Cosmides L (1990) The past explains the present: emotional adaptations and the structure of ancestral environments. Ethol Sociobiol 11(4–5):375–424
Tovée MJ, Tasker K, Benson PJ (2000) Is symmetry a visual cue to attractiveness in human female body? Evol Hum Behav 21:191–200
Trivers R (1972) Parental investment and sexual selection. In: Campbell BC (ed) Sexual selection and the descent of man, 1871–1971. Aldine, Chicago
Vallet E, Kreutzer M (1995) Female canaries are sexually responsive to special song phrases. Anim Behav 49:1603–1610
Wallace AR (1858) On the tendency of varieties to depart indefinitely from the original type; instability of varieties supposed to prove the permanent distinctiveness of species. J Proc Linnaean Soc Lond (Zool) 3:53–62
Wallace AR (1864) The origin of human races and the antiquity of man deduced from the theory of 'Natural selection'. J Anthropol Soc Lond 2:clxvi
Walster E, Aronson V, Abrahams D, Rottman L (1966) Importance of physical attractiveness in dating behavior. J Pers Soc Psychol 4(5):508–516
Watanabe S (2012) Animal aesthetics from the perspective of comparative cognition. In: Watanabe S, Kuczaj S (eds) Emotions of animals and humans: comparative perspective. Springer, Tokyo

Welsch W (2004) Animal aesthetics. Contemporary Aesthetics, online journal. http://www.contempaesthetics.org/newvolume/pages/article.php?articleID=243. Accessed 30 April 2012
Winkielman P, Halberstadt J, Fazendeiro T, Catty S (2006) Prototypes are attractive because they are easy on the mind. Psychol Sci 17(9):799–806
Wise RA (2004) Dopamine, learning and motivation. Nat Rev Neurosci 5:483–494
Wood W, Eagly AH (2000) Once again, the origins of sex differences. Am Psychol 55(9):1062–1063
Zahavi A (1975) Mate selection—a selection for a handicap. J Theor Biol 53:205–214
Zahavi A (1977) The cost of honesty (further remarks on the handicap principle). J Theor Biol 67:603–605
Zajonc RB (1980) Feeling and thinking: preferences need no inferences. Am Psychol 35(2):151–175
Zanna M, Pack S (1975) On the self-fulfilling nature of apparent sex differences in behavior. J Exp Soc Psychol 11(6):583–591