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Neurobiological foundations of aesthetics and art

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ABSTRACT

A theory of the neurobiological foundations of aesthetics and art is described. This has its roots in emotion, in which what is pleasant or unpleasant, a reward or punisher, is the result of an evolutionary process in which genes define the (pleasant or unpleasant) goals for action. To this is added the operation of the reasoning, syntactic, brain system which evolved to help solve difficult, multistep, problems, and the use of which is encouraged by pleasant feelings when elegant, simple, and hence aesthetic solutions are found that are advantageous because they are parsimonious, and follow Occam's Razor. The combination of these two systems, and the interactions between them, provide an approach to understanding aesthetics that is rooted in evolution and its effects on brain design and function.

1. Introduction

A theory of the neurobiological foundations of aesthetics and art is described. This has its roots in emotion, in which what is pleasant or unpleasant, a reward or punisher, is the result of an evolutionary process in which genes define the (pleasant or unpleasant) goals for action (Rolls, 2005, 2014a). It is argued that combinations of multiple such factors provide part of the basis for aesthetics. To this is added the operation of the reasoning, syntactic, brain system which evolved to help solve difficult, multistep, problems, and the use of which is encouraged by pleasant feelings when elegant, simple, and hence aesthetic solutions are found that are advantageous because they are parsimonious, and follow Occam's Razor. The combination of these two systems, and the interactions between them, provide an approach to understanding aesthetics that is rooted in evolution and its effects on brain design and function (Rolls, 2011c, 2012b, 2014a, 2016a).

I start by considering how affective value is generated in the brain as a solution to the problem of how genes can specify useful goals for actions. This is more efficient and produces more flexible behaviour than by specifying the actions themselves. Then, in Sections 5 and 6, I develop this theory further into a theory of the foundations of aesthetics and art.

2. Emotions as states elicited by rewards and punishers

Emotions can usefully be defined (operationally) as states elicited by rewards and punishers that have particular functions (Rolls, 1999, 2005, 2014a). The functions are defined below, and include working to obtain or avoid the rewards and punishers. A reward is anything for which an animal (which includes humans) will work. A punisher is anything that an animal will escape from or avoid. A diagram summarizing some of the emotions associated with the delivery of a particular reward or punisher or a stimulus associated with them, or with the omission of a reward or punishment, is shown in Fig. 1. It is emphasized that this shows states elicited by any one reward of punisher, and that there are many different rewards and punishers. This helps to account for many different emotions (Rolls, 1999, 2005, 2014a).

The proposal that emotions can be usefully seen as states produced by instrumental reinforcing stimuli follows earlier work by Millenson (1967), Weiskrantz (1968), Gray (1975, 1987), and Rolls (1986a, 1986b), 1986b, 1990; 1999, 2000; 2005). (Instrumental reinforcers are stimuli which, if their occurrence, termination, or omission is made contingent upon the making of a response (action), alter the probability of the future emission of that response.)

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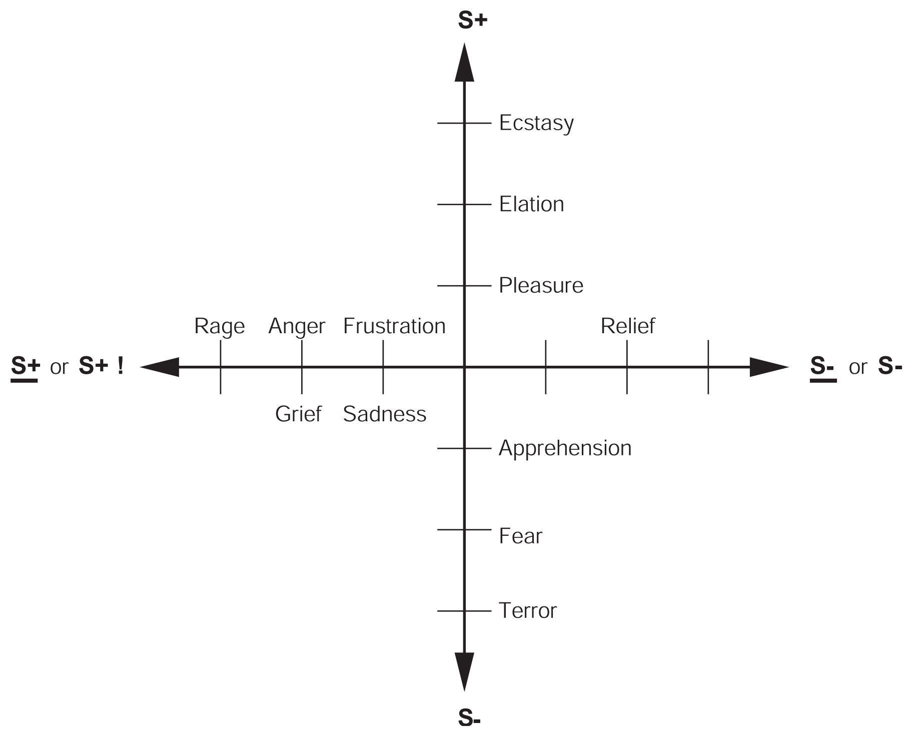

Fig. 1. Some of the emotions associated with different reinforcement contingencies are indicated. Intensity increases away from the centre of the diagram, on a continuous scale. The classification scheme created by the different reinforcement contingencies consists of (1) the presentation of a positive reinforcer (S+), (2) the presentation of a negative reinforcer (S-), (3) the omission of a positive reinforcer (S+) or the termination of a positive reinforcer (S+!), and (4) the omission of a negative reinforcer (S-) or the termination of a negative reinforcer (S-!).

Some stimuli are unlearned reinforcers (e.g., the taste of food if the animal is hungry, or pain); while others may become reinforcing by learning, because of their association with such primary reinforcers, thereby becoming 'secondary reinforcers'.

This foundation has been developed (see Rolls, 1986a, 1986b, 1986b, 1990, 1999, 2000, 2005, 2014a) to show how a very wide range of emotions can be accounted for, as a result of the operation of a number of factors, including the following:

1 The *reinforcement contingency* (e.g., whether reward or punishment is given, or withheld) (see Fig. 1).
2 The *intensity* of the reinforcer (see Fig. 1).
3 Any environmental stimulus might have a *number of different reinforcement associations*. (For example, a stimulus might be associated both with the presentation of a reward and of a punisher, allowing states such as conflict and guilt to arise.)
4 Emotions elicited by stimuli associated with *different primary reinforcers* will be different. A list of some primary reinforcers to illustrate some of the different affective states is provided in *Emotion and Decision-Making Explained* (Rolls, 2014a, 2014b, 2014c) and in *Neuroculture* (Rolls, 2012a, 2012b).
5 Emotions elicited by *different secondary reinforcing stimuli* will be different from each other (even if the primary reinforcer is similar).
6 The emotion elicited can depend on whether an *active or passive behavioural response* is possible. (For example, if an active behavioural response can occur to the omission of a positive reinforcer, then anger might be produced, but if only passive behaviour is possible, then sadness, depression or grief might occur.)

By combining these six factors, it is possible to account for a very wide range of emotions (for elaboration see Rolls, 2014a, 2014b, 2014c).

3. The functions of emotion

The most important functions can be summarized as follows (Rolls, 1990, 1999, 2005, 2014a):

1 The *elicitation of autonomic responses* (e.g., a change in heart rate) and *endocrine responses* (e.g., the release of adrenaline). These prepare the body for action.
2 *Flexibility of behavioural responses to reinforcing stimuli*. Emotional (and motivational) states allow a simple interface between sensory inputs and action systems. The essence of this idea is that goals for behaviour are specified by reward and punishment evaluation. When an environmental stimulus has been decoded as a primary reward or punishment, or (after previous stimulus-reinforcer association learning) a secondary rewarding or punishing stimulus, then it becomes a goal for action. The person can then perform any action (instrumental response) to obtain the reward, or to avoid the punisher. Thus there is flexibility of action.

The emotional state intervenes between delivery of the stimulus and its decoding as rewarding or punishing, which produces the emotional state, and the learning and performance of the action, which may only be possible with some delay. In this sense, for goal-directed action, an intervening state is required. For overlearned stimulus-response habit-based responses, no intervening state is necessary, and emotional states need not be present. This is one of the reasons why I propose that emotions are part of a brain/behaviour system in which arbitrary actions must be learned to reinforcing stimuli to obtain goals. This is an important reason why I relate emotions to the evolution of instrumental actions to rewarding and punishing stimuli, as intervening states are needed in this process (Rolls, 2014a, 2014b, 2014c). The motivation that is part of the intervening state is to obtain the reward or avoid the punisher, and animals must be built to obtain certain rewards and avoid certain punishers. Further, and very importantly for this shows why emotions have evolved, primary or unlearned rewards and punishers are specified by genes which effectively specify the goals for action. This is the solution which natural selection has found for how genes can influence behaviour to promote their fitness (as measured by reproductive success), and for how the brain could interface sensory systems to action systems, and is an important part of Rolls' theory of emotion (1990; 1999; 2005, 2014a).

Selecting between available rewards with their associated costs, and avoiding punishers with their associated costs, is a process that can take place both implicitly (unconsciously), and explicitly using a language system to enable long-term plans to be made (Rolls, 2005, 2008). These many different brain systems, some involving implicit evaluation of rewards, and others explicit, verbal, conscious, evaluation of rewards and planned long-term goals, must all enter into the selector of behaviour (see Fig. 2). This selector is poorly understood, but it might include a process of competition between all the competing calls on output, and might involve the anterior cingulate cortex and basal ganglia in the brain (Rolls, 2005, 2008, 2014a) (see Fig. 2).

4. Dual routes to action: gene-defined goals, and syntactic reasoning

The first route is via the brain systems that have been present in non-human primates such as monkeys, and to some extent in other mammals, for millions of years, and have built in the brain a system for defining these goals. Achieving these goals feels pleasant or unpleasant. The goals may be primary reinforcers, or stimuli associated with them by learning.

The second route in humans and perhaps closely related animals involves a computation with many 'if...then' statements, to implement a plan to obtain a reward. In this case, the reward may actually be *deferred* as part of the plan, which might involve working first to obtain one reward, and only then to work for a second more highly valued reward, if this was thought to be overall an optimal strategy in terms of resource usage (e.g., time). In this case, syntax is required, because the many symbols (e.g., names of people) that are part of the plan must be correctly linked or bound. Such linking might be of the form: "if A does this, then B is likely to do this, and this will cause C to do this …". The requirement of syntax for this type of planning implies that an output to language systems in the brain is required for this type of planning (see Fig. 2). Thus the explicit language system in humans may allow working for deferred rewards by enabling use of a one-off, individual, plan appropriate for each situation.

The question then arises of how decisions are made in animals such as humans that have both the implicit, direct reward-based instrumental action, and the explicit, rational, planning systems (see Fig. 2) (Rolls, 2008, 2014a, 2016a). One particular situation in which the first, implicit, system may be especially important is when the interests of the genes are being maintained. In contrast, when the implicit system continually makes errors, it would then be beneficial for the organism to switch from automatic, direct, action based on obtaining what the orbitofrontal cortex system decodes as being the most positively reinforcing choice currently available, to the explicit conscious control system that can evaluate with its long-term planning algorithms what action should be performed next.

The second route to action allows, by reasoning, decisions to be taken that might not be in the interests of the genes, might be longer term decisions, and might be in the interests of the individual. Thus we may speak of the choice as sometimes being between the "Selfish Genes" (Dawkins, 1989) and the "Selfish Phenes" (Rolls, 2011a, 2011b, 2011c, 2012b, 2013b, 2014a, 2016a).

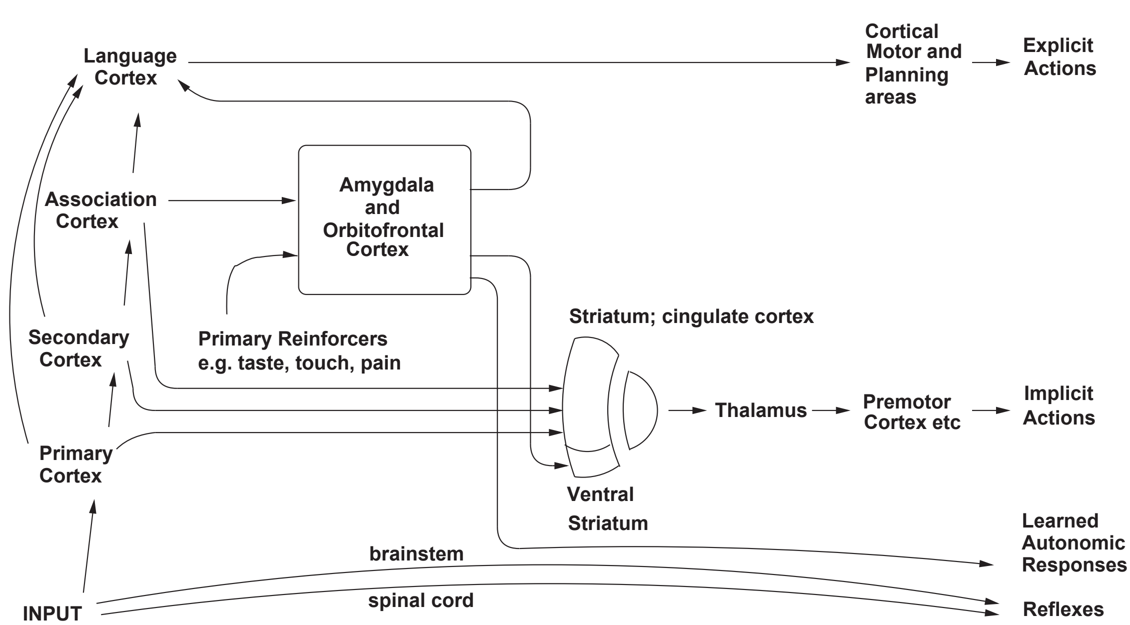

Fig. 2. Dual routes to the initiation of action in response to rewarding and punishing stimuli. The inputs from different sensory systems to brain structures such as the orbitofrontal cortex and amygdala allow these brain structures to evaluate the reward- or punishment-related value of incoming stimuli, or of remembered stimuli. The different sensory inputs enable evaluations within the orbitofrontal cortex and amygdala based mainly on the primary (unlearned) reinforcement value for taste, touch and olfactory stimuli, and on the secondary (learned) reinforcement value for visual and auditory stimuli. In the case of vision, the 'association cortex' which outputs representations of objects to the amygdala and orbitofrontal cortex is the inferior temporal visual cortex. One route for the outputs from these evaluative brain structures is via projections directly to structures such as the basal ganglia (including the striatum and ventral striatum) to enable implicit, direct behavioural responses based on the reward or punishment-related evaluation of the stimuli to be made. The second route is via the language systems of the brain, which allow explicit decisions involving multi-step syntactic planning to be implemented.

5. A theory of the neurobiological foundations of aesthetics and art

5.1. Introduction to and outline of the theory

Now that we have a fundamental, Darwinian, approach to the value of people, objects, relationships etc, I propose that this provides a fundamental neurobiological approach to understanding aesthetics and art. I propose that while the gene-specified rewards and punishers define many things that have aesthetic value, the value that we place on items is enhanced by the reasoning, rational, system, which enables what produces aesthetic value to become highly intellectualized, as in music.

I emphasize at the outset that this does not at all reduce aesthetics to a common denominator. Genetic variation is essential to evolution by natural selection, and this is one reason why we should expect different people to assign aesthetic value differently. But rational thought, which will lead in different directions in different people, partly because of noise caused by random neuronal firing times in the brain (Rolls & Deco, 2010; Rolls, 2014a, 2014b, 2014c, 2016a), and because of what they have learned from the environment, and because different brain areas will be emphasized in different people, will also be different between individuals, so that the rational system will also contribute to differences between individuals in what is considered aesthetic.

Indeed, although the theory presented here on the origin of aesthetics is a reductive explanation, in that it treats the underlying bases and causes, it should not be seen at all to 'reduce' aesthetics. Far from it. When we understand the underlying origins and bases of aesthetics, we see that the processes involved are elegant and beautiful, as part of a Darwinian theory. (The processes involved in Darwinian evolution are elegant and beautiful, in that an efficient way to search a high dimensional space with multiple peaks of optimality is to use recombination of gene complexes produced by sexual reproduction to implement local hill-climbing in the space, and occasional mutations to produce a jump to a random position in the space to search for local optima there (Ackley, 1987; Goldberg, 1989; Rolls, 2016a, 2016b)). But the approach also provides important pointers about how to enhance aesthetics. For example, by understanding that verbal level cognitive factors that can be produced by reasoning have a top-down modulatory influence on the first cortical area where value (reward) is made explicit in the representation, the orbitofrontal cortex (Rolls, 2013a, 2013b, 2014a, 2016a; Grabenhorst, Rolls, & Bilderbeck, 2008; McCabe, Rolls, Bilderbeck, & McGlone, 2008; de Araujo, Rolls, Velazco, Margot, & Cayeux, 2005), we can see ways in which we can enhance our aesthetic feelings. (For example, if love be the thing, then it can be heightened by explicitly choosing the musical treatment of it in Tristan and Isolde.)

I should also emphasize that aesthetic value judgements will usually be influenced by a number of different value factors, so that while accounting for an aesthetic judgement by just one of the value factors I describe is and will often seem too simple, it does seem that aesthetic value judgements can be understood by combinations of some of the factors I describe (Rolls, 2011c, 2012b, 2014b, 2014c).

I emphasize that rewards contribute to what makes stimuli or brain processing positively aesthetic, beautiful; and that the punishers contribute to what makes stimuli or processing in the brain aesthetically negative, lacking beauty, ugly, or distasteful. Both rewards and punishers are needed for the theory of aesthetics.

The overall theory of the origin of aesthetics I propose is that natural selection, whether operating by 'survival or adaptation selection', or by sexual selection, operates by specifying goals for action, and these goals are aesthetically and subjectively attractive or beautiful (Rolls, 2005, 2014a, 2016a), or the opposite, and provide what I argue here is the origin of many judgements of what is aesthetic. (Many other behaviours can be elicited by other routes, for example by stimulus-response habits, as illustrated in Fig. 2 (Rolls, 2016a, 2016b), and these are not relevant to aesthetics, according to Rolls' theory of neuroaesthetics (Rolls, 2012a, 2012b)).

5.2. Refinements of the theory of aesthetics

In this section I refine my approach to aesthetics, and distinguish between the roles of value in aesthetics, beauty, art, emotion, liking, pleasure, reward, and wanting; and the roles of our gene-based reward vs rational systems in these.

Reward value is at the heart of my approach to and theory of emotion (Rolls, 2014a, 2014b, 2014c). The role of reward value in emotion is to specify *the goals for action* instrumental in obtaining reward, and avoiding punishment. Emotions can be defined as states elicited by rewards and punishers (Rolls, 2016a, 2016b). These ideas on reward value provide a basis not only for understanding emotion, as states when stimuli with reward/punishment value are or are not obtained (Rolls, 2014a, 2014b, 2014c), but also for understanding motivation, as states when stimuli with reward/punishment value, the goals for action, are being worked for or avoided (Rolls, 2016a, 2016b). Liking can be thought of as the state when a reward is received, and although this implies a subjective state, is sometimes used for behavioural measures such as whether the mouth is opened to receive a food (Berridge, Robinson, & Aldridge, 2009). Pleasure is strictly the subjective pleasure reported by humans to a reward stimulus, and can be measured by subjective pleasantness/unpleasantness ratings on for example a visual analogue rating scale (Rolls, 2016a, 2016b). The pleasantness of a very wide range of stimuli is linearly related to the BOLD (blood-oxygenation-level dependent) response in the medial orbitofrontal cortex and pregenual cingulate cortex; and the subjective unpleasantness rating is linearly related to the BOLD response in the lateral orbitofrontal cortex and supracallosal anterior cingulate cortex (Grabenhorst & Rolls, 2011, 2011b, 2011c; Rolls & Grabenhorst, 2008; Rolls, 2016a, 2016b). Quite abstract rewards and punishers, including winning money or losing money, also linearly activate these regions (O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001). Given that reward vale and subjective pleasantness are represented in the orbitofrontal cortex, any study that claimed to show that aesthetics was represented in this and related brain regions would need to make a clear distinction between reward value in relation to emotion etc, and aesthetic value.

Aesthetics refers to the ways in which humans describe nature or works of art as beautiful, ugly, or having qualities that should be appreciated. Value is clearly involved, but the nature of the value involved needs to be specified and considered carefully. The value is different from that involved in emotion, in that the value is not specifically biological adaptive value or utility primarily involved in guiding actions towards rewards that will enhance the success of the genes by promoting reproductive success (see Sections 4 and 5.3), nor the type of longer term value that the rational system may determine has value for the phenotype, as well as perhaps for the genes (Rolls, 2014a, 2014b, 2014c) (see Section 4). Instead, aesthetics is the investigation of judgements about nature and objects including art and architecture that are about their beauty, ugliness, etc. In this paper, I argue that underlying biological adaptive value may be one factor that influences very many judgements of aesthetic value. For example, a low waist-to-hip ratio may have reward value to men, as a sign of reproductive fertility, and this is frequently correlated with ratings of beauty (Buss, 2015). And this may contribute to what makes a work of art aesthetically pleasing. Similarly, facial symmetry, closeness to an average, smoothness, and youthfulness (large eyes, large upper part of the face relative to the lower part, and fair hair) may contribute to ratings of beauty, but are biologically relevant indicators of not being damaged at birth, not having diseases, and of fertility (Buss, 2015; Rolls, 2014a, 2014b, 2014c). Similarly, the display in a painting of a man's wealth, financial resources, and power, in a painting, which may have been thought to contribute to the aesthetic value of a painting, are in fact indicators of resources with biological adaptive value in that they are valued by women because of their potential biological utility for her offspring with such a man; and hence also come to be valued by men (Buss, 2015; Rolls, 2014a, 2014b, 2014c).

Novelty, creative advance, is also a factor that may make a work of art have great aesthetic value. For example, we value the music of J. S. Bach in part because it made such great advances in harmony. If a composer were today to compose a piece of music that was very closely in the style of Bach, yet was clearly attributable to a modern composer, we would value it aesthetically much less than a work by Bach. Thus, novelty, which is likely to reflect creativity and which has potential biological adaptive value, is another important factor in aesthetics. Indeed, in my view, finding new combinations of inputs (for example, colours, shapes) or jumping to a new part of a thought space (Rolls & Deco, 2010; Rolls, 2012a, 2012b, 2016a) may be an important aspect of aesthetics. But here, not just random combinations may lead to art with high aesthetic value; after the creativity phase, there may be an evaluation and selection phase during the development of a work of art, to help the work to proceed in what may be judged to be interesting new directions by the artist. Of course, if a work of art is completely abstract, and does not appeal to biological foundations, there may be less likelihood that a work of art will meet widespread acclaim, or will have lasting aesthetic value, because it does not have a universal, biologically-related, appeal.

Simple lines in a drawing, such as a line drawing by Matisse or Picasso, may be attractive because they capture some of what biological vision is trying to extract from complex visual scenes (Amir, Biederman, & Hayworth, 2011; Biederman, 1987; Rolls, 2012a, 2012b).

Beauty in nature may also, in at least some instances, reflect an indicator that is biologically useful, such as a clear sunset (which may indicate that there are unlikely to be dangerous storms in the night); and large open landscapes like those of the savannah, which may be attractive in part because they offer a clear view of potential predators (Huston, Nadal, Mora, Agnati, & Cela-Conde, 2015; Schellekens & Goldie, 2011).

Other factors may contribute to aesthetic judgements that may have little clear biological adaptive value. For example, one factor that in a painting by Mark Rothko may increase the aesthetic appreciation of what appears to be a brown rectangle on a rectangular canvas is the quality of the brushwork, which when viewed closely by an experienced artist may lead to aesthetic appreciation. But even here, the appreciation may reflect admiration of a capacity for innovation that may relate to creativity, and indeed be an indicator of useful creativity, which does have clear biological utility. Another factor is sexual selection, which can lead to runaway selection even when it may not have obvious adaptive value (Miller, 2000, 2001). For example, the peacock's ‘tail’ is regarded by peahens as attractive, yet the tail is of no apparent adaptive value to the male. However, the explanation for this may lie in sexual selection, which in this case might have adaptive value, in that it indicates to a female just how fit the peacock is, if he can afford to put such effort in his tail, for it may indeed handicap him, and so is a real sign of fitness (Rolls, 2014a, 2014b, 2014c; Zahavi, 1975, 1978). Men's judgements that large, fast, (expensive) cars are aesthetically pleasing may have a similar basis, at least in part, as well as being an indicator of resources. (Creating art, writing novels, etc, may also be in part a similar process, for it indicates time and resources to spend on such activities.)

Another factor that some may relate to aesthetic value is fashion. Works of art, and what is valued as aesthetic, may go into and out of fashion. This may relate to long-term sensory-specific satiety (which we so named when refugees in an Ethiopian refugee camp chose to switch to a new diet that had not been available in the last six months, even though short-term sensory-specific satiety was equated (Rolls & de Waal, 1985)). Now, such long-term sensory-specific satiety may have adaptive biological value, because, after a long time, switching to a new type of reward might bring in new nutrients, new types of gene combination afforded by a new partnership during reproduction after several babies with a long-term partner, etc. Indeed, long-term sensory-specific satiety may be as important a property as (short-term) sensory-specific satiety is in influencing reward selection, and may be an important factor in fashion, which may relate to the underlying adaptive value of having long-term sensory-specific satiety a property of all reward systems (Rolls, 2014a, 2014b, 2014c). Of course, given these underlying mechanisms, fashion may repeat itself. A related process is market factors, which are not clearly related to underlying biological adaptive value, but which with ‘fashion’ may artificially increase the ‘value’ of a commodity. Another factor is that fashion may constantly change because of the competition between females. The value of something (such an outfit) decreases as soon as it is possessed by others. Then, because the fashion helps to identify one as a member of an elite group, fashion has to change as the item is acquired by more and more people. Fashion can then become a marker of social hierarchy amongst females.

Part of the value of limited editions in art may be to prevent this degradation of value, because a limited edition keeps the item scarce. In a sense, it may be that aesthetic judgements may be influenced by this aspect of fashion, which relates to how common the item is.

The preceding paragraphs have thus shown ways in which aesthetics and emotion differ; but have also emphasized that very many of the factors that underlie judgements of aesthetic value have at least some relation to biological adaptive value. My argument is essentially that aesthetic judgements and art are related to what we have evolved biologically to like, sometimes as gene-related rewards, and often as products of a mind that can think creatively and adaptively, which leads eventually to better reproduction by the creative individual and the creative genes being passed on to the next generation. The implication of the latter argument is that aesthetics might well be suitably biased towards creativity of the type that might be related to adaptive value. This would be very different from an aesthetics in which just random combinations would constitute something aesthetically pleasing and artistically good. There is an interesting implication here for what is judged to be aesthetically pleasing and good art. This argument would favour creations that reflect the biologically adaptive aspects of creativity, rather than just random moves or even destructive moves in art.

I now turn to some differences between art and aesthetics. Art refers to (mainly) objects (including painting, sculpture, music, drama, and literature) made by humans typically for aesthetic reasons. Aesthetics is concerned not only with art, but also with what may make many other things appear beautiful to us, including nature, and ideas (Rolls, 2014a, 2014b, 2014c).

I also emphasize that aesthetics is not just about beauty. We may think that Francis Bacon's paintings are mostly not beautiful. But they do open up a new avenue of aesthetic experience, and open our minds to new contrasts, even if the experiences are not pleasant. Further, tragedy in drama and opera may produce highly aesthetic experiences, even if what is portrayed does not have a beautiful and happy end. We may learn about life from these experiences, including for example great journeys such as Homer's Odyssey or Wagner's Ring Cycle, which often portray events that we may not find beautiful, but in which we may be interested, for example because they enable us to learn about possible life events, and what the outcomes may be, but from a position of current safety, without experiencing the real life events (Rolls, 2011a, 2011b, 2011c, 2014a).

Attempts have been made to perform neuroimaging studies to identify which parts of the brain may be involved in aesthetic judgements (Chatterjee, 2011; Di Dio, Canessa, Cappa, & Rizzolatti, 2011; Huston et al., 2015; Ishizu & Zeki, 2013; Kawabata & Zeki, 2004; Tsukiura & Cabeza, 2011a, 2011b; Umilta, Berchio, Sestito, Freedberg, & Gallese, 2012). However, it is important in such studies to separate out 'aesthetic judgements' from 'liking', 'reward value', 'emotional value', and 'pleasantness' in line with the points made above.

In the remainder of this paper, I draw out some of these issues in more detail, but Sections 5.1 and 5.2 do set out the framework that I have developed for approaching aesthetics, and art (Rolls, 2011b, 2011c, 2012b, 2014b, Rolls, 2012a, 2012b, 2014b, 2011b; Rolls, 2011a, 2011b, 2011c).

5.3. 'Survival' or 'adaptation' selection (natural selection in a narrow sense)

'Natural selection' encompasses in its broad sense both 'survival or adaptation selection', and sexual selection. Both are processes now understood to be driven by the selection of genes, and it is gene competition and replication into the next generation that is the driving force of biological evolution (Dawkins, 1986, 1989). The distinction can be made that with 'survival or adaptation selection', the genes being selected for make the individual stronger, healthier, and more likely to survive and reproduce; whereas sexual selection operates by sexual choice selecting for genes that may or may not have survival value to the individual, but enable the individual to be selected as a mate or to compete for a mate in intra-sexual selection, and thus pass on the genes selected by intra-sexual or inter-sexual selection to the offspring. More generally, we might have other types of selection as further types of natural selection, including selection for good parental care, and kin selection.

Many of the reward and punishment systems described by Rolls (2014a, 2014b, 2014c) deal with reward and punishment decoding that has evolved to enable genes to influence behaviour in directions in a high-dimensional space of rewards and punishments that are adaptive for survival and health of the individual, and thus promote reproductive success or fitness of the genes that build such adaptive functionality. We can include kin-related altruistic behaviours because the behaviour is adaptive in promoting the survival of kin, and thus promoting the likelihood that the kin (who contain one's genes, and are likely to share the genes for kin altruism) survive and reproduce. We can also include reciprocal altruism as an example of 'survival or adaptation' selection. Tribalism can be treated similarly, for it probably has its origins in altruism. Resources and wealth are also understood at least in part as being selected by 'survival' natural selection, in that resources and wealth may enable the individual to survive better. As we will see next, resources and wealth can also be attractive as a result of sexual selection.

5.4. Sexual selection

Darwin (1871) also recognized that evolution can occur by sexual selection, when what is being selected for is attractive to potential mates (*inter-sexual selection*, for example the peacock's 'tail', and a slim young-looking physique in females as a signal of fertility), or helps in competing with others of the same sex (*intra-sexual selection*, e.g. the deer's large antlers, and a strong male physique).

Overall, Darwinian natural or survival selection increases health, strength, and potentially resources, and survival of the individual, and thus ability to mate and reproduce, and to look handsome or beautiful. Inter-sexual sexual selection does not make the individual healthier, but does make the individual more attractive as a mate, as in female choice, an example of intersexual selection. Intrasexual sexual selection does not necessarily help survival of the individual, but does help in competition for a mate, for example in intimidation of one male by another (Darwin, 1871; Kappeler & van Schaik, 2004). The differences between 'survival' and sexual selection are elaborated elsewhere (Rolls, 2011a, 2011b, 2011c, 2012b, 2014a). In all cases, it is the ability to pass on genes to the next generation that is crucial (Dawkins, 1976; Hamilton, 1996).

5.5. Beauty in men and women

Given this background in the processes that drive evolution to make certain stimuli and types of brain processing rewarding or punishing, in this Section I examine how they contribute to what factors make men and women aesthetically beautiful, and that influence their depiction in Art.

5.5.1. Female preferences: factors that make men attractive

Factors that across a range of species influence female selection of male mates include the following (Buss, 2015).

5.5.1.1. Athleticism. The ability to compete well in mate selection (including being healthy and strong), as this will be useful for her genes when present in her male offspring. Consistently, women show a strong preference for tall, strong, athletic men (Buss & Schmitt, 1993).

5.5.1.2. Resources, power and wealth. In species with shared parental investment (which include many birds and humans), having power and wealth may be attractive to the female, because they are indicators of resources that may be provided for her young. Consistently, women place a greater premium on income or financial prospects than men (Buss, 1989, 2015).

5.5.1.3. Status. Status correlates with the control of resources (e.g. alpha male chimpanzees take precedence in feeding), and therefore acts as a good cue for women. Women should therefore find men of high status attractive (e.g. rock stars, politicians, and tribal rulers), and these men should be able to attract the most attractive partners. Consistent with this, cross-culturally women regard high social status as more valuable than do men; and attractive women marry men of high status (Buss, 1989, 2015). Status may be attractive because of direct effects (e.g. as an indicator of resources for children), or because of indirect effects (because high status implies good genes for offspring).

5.5.1.4. Age. Status and higher income are generally only achieved with age, and therefore women should generally find older men attractive. Cross-culturally women prefer older men (3.42 years older on average; and marriage records from 27 countries show that the average age difference was 2.99 years) (Buss, 1989).

5.5.1.5. Ambition and industriousness. Which may be good predictors of future occupational status and income, are attractive to women (Buss, 1989).

5.5.1.6. Testosterone-dependent features may also be attractive. These features include a strong (longer and broader) jaw, a broad chin, strong cheekbones, defined eyebrow ridges, a forward central face, and a lengthened lower face (secondary sexual characteristics that are a result of pubertal hormone levels).

5.5.1.7. Symmetry (in both males and females) may be attractive. In that it may reflect good development in utero, a non-harmful birth, adequate nutrition, and lack of disease and parasitic infections (Thornhill & Gangestad, 1999).

5.5.1.8. Dependability and faithfulness may be attractive. Particularly where there is paternal investment in bringing up the young, as these characteristics may indicate stability of resources (Buss, Abbott, & Angleitner, 1990).

5.5.1.9. Risk-taking by men may be attractive to women. Perhaps because it is a form of competitive advertising: surviving the risk may be an honest indicator of high quality genes (Barrett, Dunbar, & Lycett, 2002).

5.5.1.10. Characteristics that may not be adaptive in terms of the survival of the male. But that may be attractive because of intersexual sexual selection, are common in birds, perhaps less common in most mammals, though present in some primates (Kappeler & van Schaik, 2004), and may be present in humans (see Section 5.3).

5.5.1.11. Odour. The preference by women for the odour of symmetrical men is correlated with the probability of fertility of women as influenced by their cycle (Gangestad & Simpson, 2000). Another way in which odour can influence preference is by pheromones that are related to major histocompatibility complex (MHC) genes, which may provide a molecular mechanism for producing genetic diversity by influencing those who are considered attractive as mates (Rolls, 2011a, 2011b, 2011c, 2012b, 2014a).

5.5.2. Male preferences: what makes women attractive and beautiful to men

Males are not always indiscriminate. When a male chooses to invest (for example to produce offspring), there are preferences for the partner with whom he will make the investment. Accurate evaluation of female quality (reproductive value) is therefore important, and males look out for cues to this, and find these cues attractive, beautiful, and rewarding. The factors that influence attractiveness include the following (Barrett et al., 2002; Buss, 2015; Rolls, 2011a, 2011b, 2011c, 2012b, 2014a).

5.5.2.1. Youth. As fertility and reproductive value in females is linked to age (reproductive value is higher when younger, and actual fertility in humans peaks in the twenties), males (unlike females) place a special premium on youth. It is not youth per se that men find attractive, but indicators of youth, for example neotenous traits such as blonde hair and wide eyes. An example of this preference is that male college students preferred an age difference on average of 2.5 years younger (Buss, 1989). Another indicator of youth might be a small body frame, and it is interesting that this might contribute to the small body frame of some women in this example of sexual dimorphism.

5.5.2.2. Beautiful features. Features that are most commonly described as the most attractive tend to be those that are oestrogen-dependent, e.g. full lips and cheeks, and short lower facial features. (Oestrogen caps the growth of certain facial bones.)

Why do women apparently compete for men by paying attention to their own beauty and fashion? Perhaps the answer is that males who are willing to make major investments of time and resources in raising the children of a partner are a somewhat limiting resource (as other factors may make it advantageous genetically for men not to invest all their resources in one partner), and because women are competing to obtain and maintain this scarce resource, being beautiful and fashionable is important to women. Faithful men may be a limited resource because there are alternative strategies that may have a low cost, whereas women are essentially committed to a considerable investment in their offspring.

Given that men are a scare resource, and that women have such a major investment in their offspring that they must be sure of a man's commitment to invest before they commit in any way, we have a scientific basis for understanding why women are reserved and more cautious and shy in their interactions with men, which has been noticed to be prevalent in visual art, in which men look at women, but less vice versa (Berger, 1972).

5.5.2.3. Body fat. The face is not the only cue to a woman's reproductive capacity, and her attractiveness, and beauty. Although the ideal body weight varies significantly with culture (in cultures with scarcity, obesity is attractive, and relates to status, a trend evident in beautiful painting throughout its history), the ideal distribution of body fat seems to be a universal standard, as measured by the waist-to-hip ratio (which cancels out effects of actual body weight). Consistently, across cultures, men preferred an average ratio of 0.7 (small waist/bigger hips) when rating female figures (line drawings and photographic images) for attractiveness (Singh & Luis, 1995). At a simpler level, a low waist to hip ratio is an indication that a woman is not already pregnant, and is thus a contributor to attractiveness and beauty.

5.5.2.4. Fidelity. The desire for fidelity in females is most obviously related to concealed ovulation (see next paragraph and *Emotion and Decision-Making Explained* (Rolls, 2014a, 2014b, 2014c), and therefore the degree of paternity uncertainty that males may suffer.

5.5.2.5. Attractiveness and the time of ovulation. Although ovulation in some primates and in humans is concealed, it would be at a premium for men to pick up other cues to ovulation, and find women highly desirable (and beautiful) at these times. Possible cues include an increased body temperature reflected in the warm glow of vascularized skin (Vandenberghe & Frost, 1986), and pheromonal cues. Another possibly unconscious influence might be on the use of cosmetics and the types of clothes worn, which may be different close to the time of ovulation.

In humans, male investment in caring for the offspring means that male choice has a strong effect on intrasexual selection in women. Female cosmetic use and designer clothing could be seen as weapons in this competition, and perhaps are reflected in extreme female self-grooming behaviour such as cosmetic surgery, or pathological disorders such as anorexia, bulimia and body dysmorphic disorder. The modern media, by bombarding people with images of beautiful women, may heighten intrasexual selection even further, pushing women's competitive mating mechanisms to a major scale.

5.6. Pair-bonding, love, and a beautiful partner

Attachment to a particular partner by pair bonding in a monogamous relationship, which in humans becomes manifest in love between pair-bonded parents, and which occurs in humans in relation to the advantage to the man of investing in his offspring, may have special mechanisms to facilitate it. One is oxytocin, a hormone released from the posterior pituitary, whose other actions include the milk let-down response, which is released during mating and which promotes attachment, making a partner attractive (Carter, 2014; Lee, Macbeth, Pagani, & Young, 2009).

Are similar mechanisms at work in humans to promote pair-bonding and love (and what is found to be aesthetically attractive, and to influence depictions in art)? In humans, oxytocin is released by intercourse, and especially at the time of orgasm, in both women and men, and can even be released by prolonged eye contact during courtship (Carter, 2014; Churchland & Winkielman, 2012; Kruger et al., 2003; Meston & Frohlich, 2000). In humans, oxytocin acts to allow the high levels of social sensitivity and attunement necessary for human sociality and for rearing a human child (Carter, 2014). Under optimal conditions oxytocin may create an emotional sense of safety and trust (Carter, 2014).

5.7. Parental attachment: beautiful children

Many mammal females make strong attachments to their own offspring, and this is also facilitated in many species by oxytocin. In humans, oxytocin is released during natural childbirth, and rapid placing of the baby to breast feed and release of more oxytocin, might further facilitate maternal attachment to her baby (Carter, 2014). Prolactin, the female hormone that promotes milk production, may also influence maternal attachment, and how beautiful a mother thinks her child is. It is certainly a major factor in humans that bonding can change quite suddenly at the time that a child is born, with women having a strong tendency to shift their interests markedly towards the baby as soon as it is born (probably in part under hormonal influences), and this can result in relatively less attachment behaviour to the husband.

The tendency to find babies beautiful is not of course restricted to parents of their own children. Part of the reason for this is that in the societies in which our genes evolved with relatively small groups, babies encountered might often be genetically related, and the tendency to find babies beautiful is probably a way to increase the success of selfish genes. One may still make these aesthetic judgements of babies in distant countries with no close genetic relationship, but this does not of course mean that such judgements do not have their evolutionary origin in kin-related advantageous behaviour.

5.8. Synthesis on beauty in humans

We see that many factors are involved in making humans attractive, and beautiful. All may contribute, to different extents, and differently in different individuals, and moreover we may not be conscious of some of the origins of our aesthetic judgements, but may confabulate reasons for what we judge to be aesthetic.

When there is a biological foundation for art, for example when it is figurative, and especially when it is about human figures, there may be a basis for consensus about what is good art — art that stimulates our rational system, and at the same time speaks to what we find beautiful due to our evolutionary history. However, if art becomes totally abstract, we lack the biological foundation for judging whether it is aesthetically beautiful, and judgements may be much more arbitrary, and driven by short-term fashion. Some abstraction away from very realistic and figurative in art can of course have advantages for it allows the viewer to create in their own experience of a work of art by adding their own interpretation. Some abstraction can also help the artist to emphasize the properties of form that are attractive, with an example being some of Matisse's line drawings of the body.

There is an important point here about the separation between art and the world. Objects of art can idealize beauty, and enhance it. An example is the emphasis on thin bodies, long limbs, and athletic poses found in some Art Deco sculpture, for example in the works of Lorenzl. Here what is beautiful can be made super-normal, one might say in the literal sense super-natural. Another example is in the emotion in the music of Tristan and Isolde. We see that art can emphasize and thus idealize some of the properties of the real world, and lose other details that do not enhance, or distract. This abstraction of what we find beautiful due to evolution can be seen in some semi-figurative/semi-abstract art, as in some of the line drawings of humans by Matisse and Picasso. It is also found in the sculptures of human forms of Brancusi. What I argue is that if art goes too abstract, then it loses the aesthetic value that can be contributed by tapping into these evolutionary origins. Interesting cases are found in the sculptures of Barbara Hepworth and Henry Moore. In the case of Barbara Hepworth, I find it interesting that she often retains sufficient figurative contribution to her sculpture to tap into evolutionary origins, in that some of her sculptures do seem to have some relation to male and female forms and relations. Much of the sculpture of Henry Moore is clearly figurative, and where it becomes apparently very abstract it may lose what is gained by tapping into evolutionary origins, but may gain by association and interpretation in relation to his more figurative work.

Where art becomes very abstract, as in some of the work of Mark Rothko, perhaps those especially interested are those who have expertise themselves in what is being achieved technically, such as the painting of colours by Rothko. Very abstract art, in which biological underpinnings may not be present, runs the risk of being ruled by fashion in the art market, and may not be as likely to have enduring appeal and value as art that taps into the biological underpinnings described here.

5.9. Sexual selection of mental ability, survival or adaptation selection of mental ability, and the origin of aesthetics

Miller (2000, 2001) has developed the hypothesis that courtship provides an opportunity for sexual selection to select non-sexual mental characteristics such as kindness, humour, the ability to tell stories, creativity, art, and even language. He postulates that these are “courtship tools, evolved to attract and entertain sexual partners”.

Miller (2000, 2001) also suggests that art, language and creativity can be explained by sexual selection, and that they are difficult to account for by survival selection. He suggests that art develops from courtship ornamentation, and uses bowerbirds as an evolutionary example. Male bowerbirds ornament their often enormous and structurally elaborate nests or bowers with mosses, ferns, shells, berries and bark to attract female bowerbirds. The nests are used just to attract females, and after insemination the females go off and build their own cup-shaped nests, lay their eggs, and raise their offspring by themselves with no male support. In this sense, the bowers are useless ornamentation, that do not have survival value. Darwin (1871) himself viewed human ornamentation and clothing as outcomes of sexual selection. Sexual selection for artistic ability does not mean of course that the art itself needs to be about sex. This example helps to show that sexual selection can lead to changes in what is valued and found attractive, in areas that might be precursors to art in humans. In Miller's (2001) view, the fine arts are just the most recent and pretentious manifestations of a universal human instinct for visual self-ornamentation, which in turn is a manifestation of sexual selection's universal tendency to ornament individuals with visual advertisements of their fitness. Thus, the human capacity for visual artistry is viewed as a ‘fitness indicator’, evolved like the peacock's tail and the bowerbird's bower for a courtship function. So although inherently useless, the bower or work of art is seen as attractive because it is difficult to produce, and might only be made by a brain that is very competent in general, and thus the bower or work of art may act as a fitness indicator.

A useful point (Miller, 2001) is that although art-works are now commodified and spread wide so that we may not know the artist producing the ornament, when we seek the evolutionary origins of art, we should remember that any art-work our prehistoric ancestors would have been able to see, would have probably been made by a living individual with whom they could have interacted socially or sexually. The artist was never far from his or her work, or else the work could not have functioned as the artist's extended phenotype.

Miller (2000) further suggests that language and creativity may be related to systems that can explore random new ideas, and also is a courtship device in males to attract females. My view, elaborated here and elsewhere (Rolls, 2008, 2012b, 2014a; Rolls & Deco, 2010), is that language and creativity have functions that have survival value, and thus are not just sexually selected.

Indeed, a criticism of the approach of Miller (2000) is that many of these characteristics (e.g. language, creative solutions, originality, problem solving) may have survival value, and are not purely or primarily sexually selected. For example, syntax and language have many uses in problem solving, planning ahead, and correcting multiple step plans that are likely to be very important to enable immediate rewards to be deferred, and longer term goals to be achieved (Rolls, 2008, 2012b, 2014a; Pinker & Bloom, 1992). In relation to aesthetics, I argue that when syntax is used successfully to solve a difficult problem, we feel aesthetic pleasure, and I argue that the generation of pleasure generated by the survival value of good ideas contributes to the appeal of those ideas, and that sexual selection of the ideas as mental ornaments is not the only process at work in aesthetics.

Moreover, the notion (Miller, 2000, 2001) that art has to do with useless ornaments (useless in the sense that sexual selection is for characteristics that may not have ‘survival’ value, but may be attractive because they are ‘indicators of fitness’) does not have much to say about the utilitarian arts such as simplicity of design in architecture. Perhaps the structure of a piece of music can appeal, and be pleasing, because it taps into our syntactic system that finds that elegant and simple solutions to problem-solving produce pleasure. Further, interest in social relations and knowledge about them is adaptive as it may help to understand who is doing what to whom, and more generally to understand what can happen to people, and much fictional literature addresses these issues, and is not primarily ornamental and without inherent value. Thus although Miller (2000, 2001) may well be right that there are aspects of art that may be primarily ornamental and useless, and are just indicators of general mental fitness, though attractive to members of the opposite sex in courtship, I suggest that much art has its roots in goals that have been specified as pleasurable or unpleasurable because of their adaptive or survival value, whether as primary reinforcers, other stimuli associated by learning with these, or rewards of a more cognitive origin that accrue when difficult cognitive, syntactic, problems are solved (Rolls, 2011a, 2011b, 2011c, 2012b, 2014a). Parsimonious accounts of complex intellectual problems may be more likely to be correct than over-complicated, baroque, accounts, and this may contribute because of its evolutionary adaptive value to the pleasure we feel in simple solutions in for example mathematics (Kragh, 2002), and the feeling that they are elegant solutions.

Miller (2000) considers the hypothesis that men might have evolved to have artistic creativity, to provide an ornament that women might find attractive because it is a fitness indicator. Evidence on this is difficult to evaluate, because there have been fewer opportunities available for women in the past, as argued for so beautifully by Virginia Woolf in *A Room of One's Own* (1929), and I come to no conclusions, but have the following thoughts. Whereas Virginia Woolf argues about circumstances, one can consider in addition the possibility that women's and men's brains have been subject to different selective pressure in evolution, and that this might contribute to differences in the ways in which they are creative. In terms of artists, composers of music, poets, writers of drama and non-fiction, there appears to be on average a preponderance of men relative to women. This is on average, and there are individual women who given the distribution around the average are undoubtedly highly creative in these areas, and have made enormous contributions. If this is the case (and it might take a long time into the future to know, given the imbalance of opportunity in the past), does this mean that sexual selection is the underlying process? I suggest that this would not necessarily be the case. Such a “sexual dimorphism” could occur by natural (adaptation) selection, not by sexual selection, in that women might have specialized for an environmental niche to emphasize child rearing, cultivation including food gathering and preparation, fashioning of clothing, and creating peaceful order among siblings and parents. On the other hand, men might have specialized for an environmental niche to emphasize spatial problem solving, useful for producing and using tools, building shelters, creating structures etc, and navigational problem solving useful for hunting, all of which would be good for survival. Interestingly, the same (narrow) natural selection pressure might have provided a survival advantage for men to have a stronger physique which is likely be advantageous when manufacturing items useful for survival such as shelters. Thus interestingly, one of the predictions of sexual selection, sexual dimorphism, including human mental problem solving as well as physique, could in this case have its origin at least partly in adaptation and survival.

There is however a possible exception to the generalization that at least in the past men have been more likely to be creative in “art” than women, and this is the area of literary fiction, where there are many women with high reputations as novelists (e.g. Jane Austen, George Eliot, Virginia Woolf). If women take more to this area of creative art, might this be because of the adaptive value of gossip to women, so knowing about who is doing what to whom, and having an interest and expertise in this, could be adaptive, perhaps helping a woman, and her children, to survive better (Dunbar, 1996)? If this were the case, there might even be a prediction that women might be relatively more excellent, on average, in areas of fiction, such as novels, where this interest and expertise in mind-reading and gossip, might be especially engaged. More generally, the evolutionary survival value approach might argue that women have adapted to relational, social, caring, problem solving, and the novel, particularly the novel of manners, is ideally suited to displaying this specialization. Indeed, the specialization for a caring role is consonant with Carol Gilligan's argument in *a Different Voice* (1982) that women's sense of morality concerns itself with the activity of “care, … Responsibility, and relationships”.

The overall point I make is that natural selection, sometimes operating by ‘survival or adaptation selection’, and sometimes by sexual selection (and sometimes both, see above), operates by specifying goals for action, and these goals are aesthetically and subjectively attractive or beautiful (Rolls, 2012a, 2012b, 2014a), or the opposite, and provide what I argue here is the origin of many judgements of what is aesthetic. Many examples of these rewards and punishers, many of which operate for ‘survival or adaptation selection’, and many of which contribute to aesthetic experience and judgements, are described elsewhere (Rolls, 2011a, 2011b, 2011c, 2012b, 2014a).

5.10. Fashion, and memes

We have seen that sexual selection can provide runaway selective pressure for what is not something that is produced by 'survival or adaptation' selection. In a sense, a proclivity for fashion or useless ornaments (which may indicate fitness) can be selected for genetically.

However, fashions are strong characteristics of many human aesthetic judgements, and we may ask if there are further reasons for this that are not to do with genetic variation (which necessarily takes place over generations), but that operate over timescales of months to years. Such fashions (in for example clothing) may occur because they fit adaptations of the human mind, themselves the result of adaptive pressure in evolutionary history. For example, the human mind will be attracted towards new ideas (of clear adaptive value, for it is only by exploring new ideas that advantage may be gained partly as a result of finding a match with one's own genetically influenced capacities) (Rolls, 2014a, 2014b, 2014c). In this way, there may be runaway changes that do not necessarily make the individual better adapted to the environment. Of course, many factors, again frequently of evolutionary origin, influence fashion, including its cost (of which the label is an indicator) which helps to make it attractive as it indicates wealth, resources and status; and the elegance and simplicity of the idea, which, as argued below, the human mind finds attractive because simplicity often is a good indicator of a correct and useful solution to a problem. It is argued that memes (Blackmore, 1999), ideas that follow some of the rules of fashion, fit these properties of the human mind. A concept here is that novelty may be rewarding, with a genetic foundation, because it helps us to explore new ideas and stimuli in the environment that may have reward value, and would be undiscovered unless novelty was rewarding (Rolls, 2014a, 2014b, 2014c). It may be a consequence of this biological underpinning that the reward value of novelty may contribute to the aesthetic experiences we have with art, music, literature, and artefacts.

5.11. The elegance and beauty of ideas, and solving problems in the reasoning system

Solving difficult problems feels good, and we often speak about elegant (and beautiful) solutions. What is the origin of the pleasure we obtain from elegant ideas, what makes them aesthetically pleasing? It is suggested that solving problems should feel good to us, to make us keep trying, as being able to solve difficult problems that require syntactic operations may have survival value (Rolls, 2014a, 2014b, 2014c). But what is it that makes simple ideas and solutions (those with fewest premises, fewest steps to the solution, and fewest exceptions for a given level of complexity of a problem) particularly aesthetically pleasing, so much so that physicists may use this as a guide to their thinking? It is suggested that the human brain has become adapted to find simple solutions aesthetically pleasing because they are more likely to be correct (Rolls, 2012a, 2012b, 2014a), and this is exactly the thrust of parsimony and Occam's Razor. (Occam's Razor is the principle or heuristic that entities and hypotheses should not be multiplied needlessly; the simplest of two competing and otherwise equally effective theories is to be preferred. The principle states that the explanation of any phenomenon should make as few assumptions as possible, eliminating those that make no difference in the observable predictions of the explanation or theory.)

This finds expression in art: in for example the structure of a piece of music; in the solution of how to incorporate perspective into painting (which took hundreds of years and was helped by the camera obscura); and in the interest by Vitruvius and Leonardo in the proportions of the human body (tapping into our gene-based appreciation of that) to provide rules for proportions in architecture. Of course, focus on intellectual aspects of art can lead to art that we may find fascinating and revealing, if not conventionally physically beautiful, as in some of the work of Francis Bacon. Factors such as cultural heritage and familiarity with the rules of a system can also make a style of architecture more appealing than something very unfamiliar. Some of the history of ecclesiastical architecture in England from the eleventh to the fifteenth century (from Norman through Early English and Decorated to Perpendicular) can also be seen as solutions to difficult architectural problems, of how to increase the light and feeling of space in a building, and its impression of grand and daring height.

5.12. Cognition and aesthetics

Not only can operation of our reasoning, syntactic, explicit, system lead to pleasure and aesthetic value, as just described, but also this cognitive system can modulate activity in the emotional, implicit, gene-identified goal system. This cognitive modulation, from the level of word descriptions, can have modulatory effects right down into the first cortical area, the orbitofrontal cortex, where affective value, including aesthetic value, such as the beauty in a face, is first made explicit in the representation (de Araujo et al., 2005; Grabenhorst & Rolls, 2011, 2011b, 2011c; Grabenhorst et al., 2008; McCabe et al., 2008; O'Doherty et al., 2003; Rolls, 2012a, 2012b, 2014a; Rolls & Grabenhorst, 2008). Indeed, cognition and attention can be used to enhance the emotional aspect of aesthetic experience, as described in Section 5.1. The importance of interactions between the cognitive and emotional systems in the brain has also been emphasized by Pessoa (2015).

The human mind may create objects such as sculpture and painting in ways that depend to different extents on the explicit reasoning system and the more implicit emotional system. I know at least one sculptor who intentionally reduces cognitive processing by turning off attention to cognitive processing when creating works of art, and then follows this with an explicit, conscious, reasoning stage in which selections and further changes may be made, with the whole creation involving many such cycles.

Because cognition can by top-down cortico-cortical backprojections influence representations at lower levels, it is possible that training, including cognitive guidance, can help to make more separate the representations of stimuli and their reward value at early levels of cortical processing (Rolls & Deco, 2002; Rolls & Treves, 1998; Rolls, 2008, 2016a). This top-down effect may add to the bottom-up effects of self-organization in competitive networks that also through repeated training help representations of stimuli to be separated from and made more different to each other (Rolls & Deco, 2002; Rolls & Treves, 1998; Rolls, 2008, 2016a). These effects may be important in many aesthetic judgements that are affected by training, including the appreciation of fine art, architecture, and wine.

In addition, because emotion and value are in a lower dimensional space than cognitive processes such as memory and perception, these cognitive processes may be squashed together somewhat into a lower dimensional space with for example lower memory capacity, because value increases the correlations between variable in the memory or perceptual space (Rolls & Stringer, 2001).

5.13. Wealth, power, resources, and reputation

As described above, wealth, power, resources and status are attractive qualities, aesthetically attractive, because resources are likely to be beneficial to the survival of genes. Reputation is similar, in that guarding one's reputation can be important in reproductive success: trust is important in a mate, or in reciprocal altruism, and hormones such as oxytocin may contribute to trust (Carter, 2014; Lee et al., 2009). This provides some insight into the history of Western art, in which individual and family portraits frequently have as one of their aims the portrayal of wealth, power, and resources. The clothes and background are consistent with a contribution of these underlying origins. Commissioned portraits thus frequently emphasize beauty, status, wealth, and resources. Interestingly, because self-portraits are rarely commissioned, they are less likely to emphasize these characteristics (Cumming, 2009), and of course can also reflect subjective knowledge of the person portrayed. An additional property that can add value judged as aesthetic to a portrait is that an image of someone dear is associated with that person, and what that person means to the viewer, and the attraction of photographic images illustrates this. Religion and its accompanying states aiming often at everlasting happiness (Rolls, 2012a, 2012b) must also be recognized as drivers of art.

5.14. The beauty of scenery and places

Many topological features of landscapes may be aesthetically attractive because they tap into brain systems that evolved to provide signals of safety, food, etc. Open space may be attractive because potential predators can be seen; cover may be attractive as a place to hide (Appleton, 1975); a verdant landscape may be attractive because it indicates abundant food; flowers may be attractive as predictors of fruit later in the season. The colour blue is preferred by monkeys, and this may be because blue sky, seen from the canopy, is an indicator of a safe place away from predators on the ground (Humphrey, 1971). A clear red/orange sunset may be attractive as a predictor of good weather, and of safety overnight without bad weather. These factors do not operate alone to produce beauty, but may as origins contribute to aesthetic beauty which I argue is multifactorial, influenced by many of the factors described in this theory of the origin of aesthetics.

5.15. The beauty of music

Vocalization is used for emotional communication between humans, with an origin evident in other primates (Rolls, Critchley, Browning, & Inoue, 2006). Examples include warning calls, warlike encouragement to action, and a soothing lullaby or song to an infant. It is suggested that this emotional communication channel is tapped into by music, and indeed consonant vs dissonant sounds differentially activate the orbitofrontal cortex (Blood & Zatorre, 2001; Blood, Zatorre, Bermudez, & Evans, 1999), involved in emotion (Rolls, 2014a, 2014b, 2014c). Of course, the reasoning system then provides its own input to the development, pleasure, and aesthetic value of music, in ways described in Sections 5.11 and 5.12.

What may underlie the greater pleasure and aesthetic value that many people accord to consonant vs dissonant music? I suggest that consonance is generally pleasant because it is associated with natural including vocal sounds with a single source that naturally has harmonics. A good example is a calm female voice. Dissonance may often occur when there are multiple un-related sources, such as those that might be produced by a catastrophe such as an earthquake, or boulders grinding against each other (or strings on a violin that are not tuned to be harmonics of each other). Further, a human voice when angry, shouting, etc (and therefore by evolutionary adaptation affectively unpleasant) might have nonlinearities, in for example the vocal cords due to over-exertion, and these may be harmonically much less pure than when the voice is calm and softer.

5.16. Beauty, pleasure, and pain

If a mildly unpleasant stimulus is added to a pleasant stimulus, sometimes the overall pleasantness of the stimulus, its attractive value and perhaps its beauty, can be enhanced. A striking example is the sweet, floral scent of jasmine, which as it occurs naturally in *Jasminum grandiflorum* contains typically 2–3% of indole, a pure chemical which on its own at the same concentration is usually rated as unpleasant. The mixture can, at least in some people (and this may depend on their olfactory sensitivity to the different components), increase the pleasantness of the jasmine compared to the same odour without the indole. Why might this occur? One investigation has shown that parts of the brain such as the medial orbitofrontal cortex that represent the pleasantness of odors (Anderson et al., 2003; Grabenhorst & Rolls, 2009; Rolls, Kringelbach, & de Araujo, 2003) can respond even more strongly to jasmine when it contains the unpleasant component indole, compared to when it only contains individually pleasant components (Grabenhorst, Rolls, Margot, da Silva, & Velazco, 2007). Thus one brain mechanism that may underlie the enhancement effect is a principle that brain areas that represent the pleasantness of stimuli can do this in a way that is at least partly independent of unpleasant components, thereby emphasizing the pleasant component of a hedonically complex mixture.

A second factor that may contribute to the enhanced pleasantness of the mixture of jasmine and indole is that the indole may produce a contrast effect in the brain areas that represent the pleasant components of the mixture. An indication of this was found in increased activations in the medial orbitofrontal cortex (which represents the pleasantness of many stimuli) when the jasmine-indole mixture was being applied, compared to just the jasmine alone (Grabenhorst et al., 2007). To the extent that the pleasantness representation may drive hedonic experience separately from unpleasantness representations (Grabenhorst et al., 2007), and this might be facilitated by paying attention selectively to the pleasantness of a stimulus vs its unpleasantness (Rolls, Grabenhorst, Margot, da Silva, & Velazco, 2008), then a factor might be the increased activation of pleasantness representations if there is a component to the stimulus that is unpleasant, and can enhance the pleasantness representation by a contrast effect. Another example of pleasantness enhancement of pleasant by unpleasant stimuli occurs when an odour become more pleasant if it is preceded by an unpleasant (compared to a pleasant) odour, an effect represented in the human orbitofrontal cortex (Grabenhorst & Rolls, 2009).

A third factor is that the interaction between the pleasant (jasmine) and unpleasant (indole) components makes the complex hedonic mixture (jasmine + indole) capture attention (which in turn may enhance and prolong the activation of the brain by the complex hedonic mixture), and evidence for the capture of attentional mechanisms in the brain by the pleasant-unpleasant mixture has been found (Grabenhorst, Rolls, & Margot, 2011).

These principles may of course operate in most areas where pleasant and unpleasant stimuli combine. Examples might include the pleasure we get from demanding terrain (high cliffs, high mountains, high seas); from spicy food that activates capsaicin (hot somatosensory) as well as gustatory and olfactory receptors (Rolls, 2007); from tragedy in literature, though empathy makes a large contribution here; from difficult feats, such as those performed by Odysseus (Rolls & Deco, 2010), etc.

Let us consider the paradox of Tragedy. For Aristotle, tragedy purged one of anxieties (Herwitz, 2008). Somehow the depiction of tragedy in drama, which raises unpleasant emotions such as sadness at the tragedy, can also as drama afford pleasure. Hume's explanation was that the beauty of the language and the eloquence of the artist's depictive talents are the source of pleasure (Hume, 1757; Yanal, 1991). Is there more to say about this? Schadenfreude, gloating, pleasure at the distress of an envied person, is associated with activation of brain areas that respond to pleasant stimuli (Shamay-Tsoory, Tibi-Elhanany, & Aharon-Peretz, 2007; Takahashi et al., 2009), and I suggest is related to the evolutionary origin of competition between individuals, and winning the competition. It is probably not an important factor in the appreciation of tragedy in drama. What may be more important is first that we (and this is especially strong in women) always want to know what is happening to whom, and gossip has evolutionary value (Dunbar, 1996) in that this can provide information about how others are likely to treat you, and more generally, about the things that can happen to people in life, and from which we can potentially learn. Second, the ability to empathize with another's emotions, and indeed to be good at this and find it rewarding, may also be important in communities, in order to facilitate kin or reciprocal altruism (Ridley, 1996). Third, the ability to have a theory of other people's minds is adaptive in facilitating prediction of their behaviour (Frith & Singer, 2008), and fascination with this should again in an evolutionary context be rewarding, and be associated with pleasure. It is suggested that these three factors are at least important contributors to the pleasure that people find in tragedy in drama. The same factors also I suggest are important contributors to the popularity of novels. In the cases of both drama and novels, we know that they are fiction, or at least are not happening to the spectator or reader, and this helps to make them particularly rewarding ways to learn about social relations and life events, because there is no risk to the spectator or reader.

In the history of art, and in what shaped concepts of aesthetics in the past, beauty was often at a premium, for some of the reasons described above, including displaying wealth and status in society, and being attractive to members of the opposite sex. However, now that many of the technical problems in art have found solutions, including perspective, and now that photography is available to capture images, more modern art is not so confined to those boundaries, and exploration of shapes, colour, and texture, and the great drive for novelty, appear to be strong driving forces. Further, given that beauty is not always now the over-riding goal for the reasons just provided, the exploration has often gone far beyond what is beautiful, into areas where art that is novel and striking may be produced that is not necessarily beautiful or that has strong biological underpinnings, as for example in the creations of Francis Bacon.

Knowing that the work of art (music, literature, painting, sculpture) is a fiction may also account for why the emotions related to these art forms are not as long-lasting, and are not as motivating, as the goals in real life.

5.17. Absolute value in aesthetics and art

The approach described here proposes that what we find aesthetic has its roots and origins in two main processes, gene-specified goals, rewards and punishers; and the value that is felt when our reasoning system produces, and understands, elegant and simple solutions to problems (Rolls, 2012a, 2012b). What implications does this have for absolute aesthetic value? The implication is that while there is no absolute aesthetic value that is independent of these processes, we will nevertheless find considerable agreement between individuals, especially when the aesthetic value being judged has its roots in the two main processes described. However, as described here, there will be variation for good evolutionary reasons between what different individuals find of value because of the genetic variation that drives evolution, and there will be variation in individuals' thought processes caused by their cultural heritage, and by noise in the brain which is an important component to creativity (Rolls & Deco, 2010; Rolls, 2012a, 2012b). For these reasons, and because aesthetic value is multifactorial (i.e. is influenced by multiple conscious and unconscious processes), we must expect variation in aesthetic value across people, time, and place, with no absolute aesthetic value.

When it is asked whether emotions, or aesthetic values, are natural kinds (Quine, 1969), a scientific answer is that emotions have common properties such as being states elicited by reinforcers with particular functions including being related to goals for action, and insofar as aesthetics has biological underpinnings, there are some properties that are shared by aesthetic stimuli, as set out in Section 5.

6. Is what is attractive, also beautiful and aesthetic?

I wish to counter a possible objection to the theory of the origin of aesthetics described here. The possible objection is that some of the goals specified by our genes, such as the reward value and pleasantness of a high energy high fat diet, might seem rather unsavoury, and not quite aesthetic. The point I make is that it is not just the gene-specified rewards and punishers that make stimuli have aesthetic value. My proposal is that the reasoning (rational) system also contributes to aesthetic value, in a number of ways. It makes rather longer term goals attractive. It introduces the further goal that innovation is attractive, as this is likely to help solve difficult problems and move the person into a new part of state space where the person may have an advantage. It introduces the use of syntactic relational structure to provide another way of computation, and problem solving with this reasoning system is encouraged by simple elegant solutions being rewarding and having aesthetic value, as described above. These factors would help the sophisticated structure in a Bach partita and fugue to contribute to what we judge as aesthetically pleasing, because such music taps not only into our emotional systems, but also into the systems that provide intellectual pleasure because difficult and complex structural problems are posed, and solutions to these difficult structural problems are provided, which as described provides aesthetic pleasure.

In this sense, aesthetic value may have its roots partly in gene-specified rewards (and punishers), but also in the pleasure that the rational system can provide when it is posed, and finds, elegant and simple solutions (which by parsimony are likely to be correct) to complex problems. For this reason, emotions may not be perfectly aligned with aesthetic value. Although both have their origin in gene-specified rewards, emotions may be produced by any one of a large number of reinforcers, whereas aesthetic value usually includes contributions of the reasoning (rational) system, as just described.

Art as a whole is a larger issue than aesthetics, and beauty. The content of Art might I suggest be seen as the result of multiple separate trajectories through a state space in which each trajectory is guided by the origins of aesthetics (products of adaptations for survival and of sexual selection for useless sometimes handicapping ornament, and rational thought to develop structure in which an elegant and simple solution is pleasing, and including novelty), and depends on each previous trajectory, the history of art in each culture. Each trajectory is not itself deterministic, because it is influenced by noise, random variation (Rolls & Deco, 2010; Rolls, 2012a, 2012b) (as is Darwinian evolution). Thus the particular future trajectories cannot be predicted. In each trajectory though a number of factors guide, including new-ness (novelty, which is biologically attractive as argued above), wildness (as in Beethoven's late string quartets), as well as what we rationally find aesthetic (as described above), and what survival and sexual selection have also provided in us as some of the origins of aesthetics. A further analysis is presented in Section 5.

7. Comparison with other theories of aesthetics

Much research I have performed shows that there is a perceptual representation of objects formed in cortical areas that is kept separate from the representation of the affective value of objects, which happens further on in processing, in brain regions such as the orbitofrontal cortex (and in an area to which it projects, the anterior cingulate cortex) and the amygdala (see Fig. 2) (Rolls, 2008, 2012b, 2014a).

There are good functional and adaptive reasons for separate representations of objects and of their affective value. We can still see and recognize objects (including tastes, smell, the sight of objects etc) even when they are not rewarding to us, for example if they are foods and we are not hungry. (We do not go blind to objects when they are not rewarding or punishing.) Moreover, it is adaptive to be able to learn about where we have seen objects, people, etc, even if they are not currently rewarding, so that we can find them later when they are needed. Thus there is strong neuroscientific evidence, and sound biological arguments, for separate representations of perceptual objects and of their affective value. Baumgarten (1750) expressed this thought in his book *Aesthetica* when he suggested that sensation, the use of the five senses, is separate from sensibility, which is something more, a "kind of intuition/cognition/formulation of the thing which judges it beautiful", and in doing so gave rise to the term aesthetics (Herwitz, 2008). Before this, abstract questions such as "What is beauty?" "What is art?" had not been treated in philosophy, although before this Aristotle had discussed the social role of drama as purging us of ever present anxiety, and Plato had dismissed poetry as obfuscating by sending the mind reeling into hypnotic trances instead of focusing on rational deductions and argument (Herwitz, 2008).

David Hume (1777) takes a broad view of taste (which engages beauty), and argues for five standards of ('delicacy of') taste that might be shown by experts: "Strong sense, united to delicate sentiment, improved by practice, perfected by comparison, and cleared of all prejudice, can alone entitle critics to this valuable character; and the joint verdict of such, wherever they are to be found, is the true standard of taste and beauty". Hume's difficulty is that he believes taste is objective, because delicacy is the probing instrument for truth; but instead, taste is a circular and constructivist enterprise (Herwitz, 2008). My approach has in contrast a clear foundation for aesthetics in brain function and its evolutionary design, with clear views about how it includes rational thought which provides its own pleasures, and about how art can idealize beyond the normal world by building on these foundations and origins.

Immanuel Kant (1724–1804) distinguishes between liking something and finding it beautiful. According to Kant when I find a painting beautiful this is not conditioned by any causal relation between its properties and my pleasures. For Kant, a judgement of beauty carries the weight of 'ought', that others should judge it beautiful too, so his theory has moral implications. His judgement of beauty is a 'disinterested' judgement, one that is not peculiar to him. He wants the beauty to be in the person, but not causally dependent on the properties of the object in the world such as the pleasure it produces (Kant, 1790). He thus appears to be committed to an objective and universal view of beauty (Schellekens, 2011, pp. 221–235), with exactly how this view is arrived at not at all clear. The biological and neuroscientific view that I propose indicates that, in contrast, beauty, aesthetics, and good art are not universal or objective, but instead can be judged good if they tap into many of the human rational and gene-based reward systems (see further Sections 6, 5.1 and 5.2), with therefore individual differences expected, as described in Section 5.17.

Darwin (1871) recognized that evolution can occur by sexual selection, when what is being selected for has no inherent adaptive or survival value, but is attractive to potential mates (inter-sexual selection), or helps in competing with others of the same sex (intra-sexual selection). His view was that natural beauty arose through competition to attract a sexual partner. His process of sexual selection through mate choice – the struggle to reproduce, not to survive – drove the evolution of visual ornamentation and artistry, from flowers through bird plumage to human self-adornment. Many have developed or ascribed to this idea (including Thorstein Veblen (1899), Ernst Gombrich (1977), Amotz Zahavi (1978) and Denis Dutton (2009)), and Miller (2000, 2001) has proposed a sexual selection theory of art. The implication of Miller's theory is that art has to do with what are frequently useless ornaments (useless in the sense that sexual selection is for characteristics that do not have 'survival' value, but are usually just attractive because they are handicaps and are indicators of fitness). I agree that useless handicapping ornament produced by sexual selection does play a role in aesthetics. However, the sexual selection theory does not therefore have much to say about the utilitarian arts such as simple design in architecture. Perhaps the structure of a piece of music can appeal, and be pleasing, because it taps into our syntactic system that finds that adaptive, survival value-related, elegant and simple solutions to problem-solving produce pleasure. As I argued above, interest in social relations and knowledge about them is adaptive and has survival value as it may help to understand who is doing what to whom, and more generally to understand what can happen to people, and much fictional literature addresses these issues, and is not purely ornamental and without inherent value. Thus although Miller may well be right that there are aspects of art that may be primarily ornamental and useless, though attractive to members of the opposite sex in courtship, I suggest that much art has its roots in goals that have been specified as pleasurable or unpleasurable because of their 'survival or adaptive' value, whether as primary reinforcers, other stimuli associated by learning with these, or rewards of a more cognitive origin that accrue when difficult cognitive, syntactic, problems are solved. I also emphasize that some of the characteristics emphasized by sexual selection may have some inherent survival value (mechanisms i–ii in Section 5.4).

In relation to broad questions about aesthetic perception, we can consider several issues. Is aesthetic perception related to action planning? My answer is that insofar as aesthetic perception has a biological underpinning in reward value, whether gene-defined or in the interests of the individual (or phenotype), then there is a biological underpinning related to action, in that the goals, the objects with reward value, have that value in part because they are the goals for action. One of the goals here it must be remembered is novelty, which has adaptive value and is a reward. Are emotions, or aesthetic values, natural kinds (Quine, 1969)? A scientific answer is that emotions have common properties such as being states elicited by reinforcers with particular functions including being related to goals for action, and insofar as aesthetics has biological underpinnings, there are some properties that are shared by aesthetic stimuli. Are aesthetics objective and universal, as Kant (1790) suggested? The biological and neuroscientific view that I propose indicates, in contrast, that art is not universal or objective, but instead can be judged good art if it taps into some of the many human rational and gene-based reward systems (see further Section 6), with therefore individual differences expected and no universal attributes, as described in Section 5.17.

Another interesting aspect of aesthetics is whether there might be gender differences in the appreciation of art. If there are biological underpinnings to aesthetics and art, as argued here, then the somewhat different reward systems of males and females might make different types of art more appealing, on average, to people with different genders. In particular, the evolutionary biology of what females value in a pair-bonding relationship include resources, of value to her and her offspring to maximize her reproductive potential (Buss, 2015; Rolls, 2014a, 2014b, 2014c). These resources might include for example wealth, jewellery, a protecting house and indeed protection, food, children, especially her own children, and social situations. It is suggested that this might make art that includes indicators of wealth such as jewellery, fine clothes, a good warm house, fine food, children, and social situations, especially appealing, on average, to women. The evolutionary biology of what males value in a relationship include reproductive potential, as indicated by youthfulness, body symmetry, a smooth and healthy-looking complexion, a small waist-to-hip ratio, and faithfulness, in order to maximize his reproductive potential (Buss, 2015; Rolls, 2014a, 2014b, 2014c). It is suggested that this might make art that includes these indicators of fertility particularly attractive to men, as well as images of power, wealth, and success (attractive to women), which might include successful battle scenes, heroic exploits, large country houses, etc. This of course does not mean that many other factors are not important in aesthetics and art in both genders. It is just a suggestion that there could be a bias in the direction indicated in what types of art are rated and valued highly by people of different genders. An investigation of this type would be easy to perform.

To end, my theory (the Rolls' theory) of the foundations of aesthetics and Art thus specifies the roles of Darwinian ‘survival or adaptive’ selection and sexual selection in aesthetics (Rolls, 2011a, 2011b, 2011c, 2012b). It is thus thoroughly Darwinian. A key idea is that many of the things that provide pleasure, or its opposite, do so because they are, or are related to, the gene-specified goals for action. Motivational states arise when trying to obtain these goals, and emotional or affective states when these goals are obtained, or are not obtained. These states are associated with affect and value, and with subjective pleasantness or unpleasantness, because it is an efficient way in which genes can influence their own (reproductive) success (“fitness”), and much more efficient and effective as a Darwinian process than prescribing that the animal should make particular responses to particular stimuli (Rolls, 2014a, 2014b, 2014c). The theory is that aesthetic value has its roots partly in these gene-specified rewards that have survival or adaptive value; but also in the pleasure that the rational system can provide when it is posed, and finds, elegant and simple solutions (which by parsimony are likely to be correct and hence adaptive) to complex problems; and to some extent in sexual selection. What makes good art can be influenced by many factors, as described here, so is complex and multi-faceted, and these factors must include whether the effect of the art is for good or for harm. It also follows that attempts in aesthetics to produce a systematic account based on consistent explicit beliefs will not succeed, for many factors that are not necessarily consistent with each other are involved in aesthetic values, and because some of these factors operate at least partly unconsciously and non-propositionally/non-syntactically, that is, using computational systems in the brain that do not involve reasoning (Rolls, 2012a, 2012b, 2014a).

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