Chapter 8
Human Artistic Behaviour: Adaptation, Byproduct, or Cultural Group Selection?

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8.1 Art as a Human Universal

One morning, when writer Elizabeth Gibson was on her way for coffee as usual, she spotted a conspicuous and colourful canvas in a pile of rubbish. Although she knew nothing of modern art, she felt compelled to take the painting to her crammed Manhattan apartment because, as she put it, "it had a strange power". The canvas hung for several years in her flat until she discovered that it was actually the famed work *Tres Personajes* by the Mexican painter Rufino Tamayo, stolen some twenty years before. After realizing its value, Gibson returned the picture to its rightful owners. This anecdote illustrates that we have an intuitive concept of art—even without any formal training in aesthetics or art history, we recognize art when we see it. Indeed, experimental studies (e.g., Seifert, 1992) reveal that Western college students without any formal training in art display and freely express aesthetic sensitivities to works of visual art, even if they are unfamiliar with them, like African sculpture.

What is it that we see and intuit in works that we denote as 'art'? This is one of the most outstanding problems in contemporary philosophy of art, and attempting a solution to this problem falls outside the scope of this paper. Objects and performances that we routinely classify as art share features like skill, strikingness and

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K.S. Plaisance and T.A.C. Reydon (eds.), *Philosophy of Behavioral Biology*,
Boston Studies in the Philosophy of Science 282, DOI 10.1007/978-94-007-1951-4_8,

beauty, but it is easy to come up with counterexamples for each of these features; for example, ready-mades do not clearly exhibit artistic skill. Some philosophers of art (e.g., Dutton, 2006) have therefore proposed to take only unproblematic cases to guide any definition of art. Others (e.g., Gaut, 2005) propose a cluster concept of art, where an art object can have several characterizing features, but where none of these is necessary, while some suggest a plurality of art concepts (Mag Uidhir and Magnus, 2011). All these approaches have in common that they focus on the objects, rather than on the causes of these objects.

Instead of taking the art objects as a starting point, we examine the human cognitive faculties and behaviours that are responsible for the creation and enjoyment of these objects. This shift in focus allows us to include objects and performances from distant places and cultures. It is an oft-stated truism that other cultures do not have a term equivalent to our western notion of art for art's sake. Yet although Hellenistic sculptors, Gothic architects and Melanesian wood carvers did not possess the modern western concept of art, we readily appreciate and appropriate their work. And just as sculptures from sub-Saharan Africa and Oceania adorn western homes, artists from these cultures have eagerly adopted western styles and media. In his inventory of human universal characteristics, Brown (1991) cites art, including music, dance, oral or written literature, visual art and performance. It occurs in complex societies as well as in societies with very little material culture, where it often appears in the shape of beads or other forms of body decoration. As will be expounded later, forms of body decoration are also found in great quantities in prehistoric hunter-gatherer living sites. Interestingly, once we move away from the western concept of art for art's sake, and focus on human behaviour, the similarities between western art production and the production of objects and performances in other cultures become apparent.

The universality of artistic behaviour across cultures seems to warrant an explanation in biological terms (Carroll, 2004). This view is strengthened by the fact that both the ability to create and to appreciate art arise remarkably early in development. From the age of about two years onwards, young children spontaneously engage in singing, dancing and drawing, and they move and vocalize to music even before their first birthday. Although they are not skilled artists, toddlers nevertheless name their drawings using the same names as the real-world objects that capture their interest, such as ‘cat’ or ‘daddy’. As Bloom (2000) has remarked, these early works are similar to those of adult artists in that both the artist and the child take an intentional perspective towards categorizing and naming the artwork. Also, like adults, children as young as two years take the intention of the maker when they name a drawing. For example, when they witness an adult drawing a circle that could be either of two unfamiliar disc-shaped objects, they take the gaze direction of the artist as a cue for which of the items was depicted. The toddlers reliably point at the object that the adult was looking at when asked which object was being depicted (Preissler and Bloom, 2008). Slightly older children also assume this stance for their own work: when one asks four-year-olds to draw a picture of a lollipop and a balloon, the drawings look virtually identical. Yet the children will consistently refer to the pictures according to what they intended to depict when they produced the drawings (Bloom and Markson, 1998).

Although representational visual art is not produced in all cultures, several systematic studies have shown that people unfamiliar with fairly abstract, pictorial representations can recognize these images spontaneously. An early study (Hochberg and Brooks, 1962) focused on a western child, brought up without exposure to any pictorial representations, such as picture books, television or figurative wallpaper. At 19 months, the boy was able to recognize and reliably name drawings made by others of his toys and common objects. Deregowski et al. (1972) showed line drawings of fairly complex scenes, such as a hunter stalking a goat, to people from an Ethiopian culture without pictures or drawings. Again, these people recognized and named the drawings correctly. Martlew and Connolly (1996) asked children from a Papua New Guinean culture without figurative art or access to photography to draw a man. Although the children had never produced drawings before, they drew recognizable anthropomorphic figures, often resembling the stick figures made by western three-year-olds.

8.2 Is Art an Adaptation?

8.2.1 Adaptationist Explanations of Art

The universality of art across cultures, our ability to recognize and appreciate it and its early emergence in development seem to suggest that producing and enjoying art may be a stable part of human cognition. There are two possible evolutionary explanations for this: either it is an adaptation, which has evolved in direct response to one or more selective pressures in our ancestral past, or it is a byproduct of other adaptations without being adaptive in itself. Its complexity makes it implausible that artistic behaviour would have evolved through random genetic drift, which is the only other explanation in evolutionary terms at the level of the individual organism.

Those who favour the view that art is an adaptation invoke its universality across cultures, its costliness, and its early and spontaneous development in children. Miller (2000) argues that art and other forms of human creative behaviour evolved as the result of sexual selection: their costliness in terms of time and energy provided ancestral hominid females with an honest signal of the fitness of the art-producing male. Just like a lush but burdensome tail in peacocks or birds of paradise are good signals of their owners' qualities to live with such a handicap, the artist's works are honest signals of his qualities as a mate. Tooby and Cosmides (2001) point out that pretend play emerges universally in toddlers. They argue that this ability provides us with the imagined worlds of (oral) literature and visual art, risk-free environments where learning can take place through vicarious experience. Dissanayake (2000) proposes that art is the intentional act of making everyday behaviour special through exaggeration, formalization, or manipulation of expectations: dance exaggerates and formalizes normal bodily movements; songs distort normal speech and prosody. Performing these actions in groups relieves tension and anxiety, thus improving social bonds within the community. She traces the evolutionary precursor to these behaviours to mother-infant dyadic interactions, where mothers and infants spontaneously modify their vocalizations, facial expressions and gestures.

8.2.2 Problems With Adaptationist Explanations of Art

Clearly, it is not difficult to imagine adaptive functions for art, but that is exactly the problem of such adaptationist accounts—theorizing about them remains fairly unconstrained. Also, the category of objects that is being explained is wider than what we conceive of as art. Miller explains not only art, but also humour and even conspicuous consumption. Tooby and Cosmides themselves point out that their adaptive account is about fiction, the broad human ability to imagine counterfactual worlds and situations, rather than about art specifically. Dissanayake provides an explanation not only for art but also for ritual and even ritualized behaviour, which is not restricted to humans, but can be observed in many animals living in captivity.

Another potential problem with the adaptationist view of art is that the neural structures responsible for artistic behaviour would have to be modularly organized. If artistic behaviour is directly targeted by natural selection, we expect its organization in the brain to be modular. The evolvability argument, developed by biologists like Lewontin (1978) and philosophers like Wimsatt (2001) and Sterelny (2004), holds that unless cognition is to some important degree modular, it is incapable of evolving away from its current organization. In a nonmodular brain, a change in one component will be connected to many other changes, thus the slightest modification might have disastrous effects for the organism. Only modularly organized cognitive capacities can evolve without affecting the rest of the brain. Although the extent to which the human brain is modularly organized is subject to debate, most evolutionary psychologists endorse a modular conception of the human mind (see e.g., Cosmides and Tooby (1994) for a theoretical discussion of the central position of modularity in the evolutionary psychological research programme). Moreover, if a given capacity is modular, evolutionary psychologists often take this to be a strong indication of its adaptive value. From the perspective of evolutionary psychology, one would therefore expect that cognitive faculties that evolved through natural or sexual selection are modularly organized.

The most straightforward way to find out if a given cognitive faculty is modularly organized is to examine whether it consistently activates the same network of neural circuits. Tasks that probe our theory of mind, for example, consistently activate the same network of neural circuits, including the medial prefrontal cortex, superior temporal sulcus, and temporal poles across a wide diversity of mentalizing tasks, such as hearing stories, seeing objects move intentionally across a screen and interpreting cartoons (Gallagher and Frith, 2003). However, a series of independent neuroimaging studies indicates that perceiving art or engaging in artistic behaviour does not yield a consistent activation of the same neural network. Instead, different forms of art recruit different neural pathways. A PET study of subjects who tango (Brown et al., 2006) revealed that dance involves a network of neural circuits normally involved in ordinary bipedal locomotion and the organization of complex sequences of movements. In contrast, music exploits modules normally involved in auditory processing. Remarkably, New World monkeys that do not produce music themselves can distinguish between atonal and tonal melodies, and can recognize a melody played in different keys (Hauser and McDermott, 2003). Thus, music likely exploits auditory sensitivities that are phylogenetically ancient and that did not evolve for music appreciation. Within visual art, different kinds of works elicit different sensory responses. While the pure forms and shapes of Piet Mondriaan and Kazimir Malevich activate orientation-selective cells in the primary visual system that respond selectively to straight lines (Zeki, 1999), kinetic art, such as Jean Tinguely's mobiles, targets the motion-sensitive cells of area V5 (Zeki and Lamb, 1994).

A comparison of the regions of interest (i.e., regions where most neural activity takes place) reveals that there is no area common to all forms of art perception, hence current cognitive neuroscience has not detected a specialized art centre in the brain. Rather, art hijacks the properties of the normal perceptual neural circuits. Lesion studies of visual artists provide an equally compelling case: art production seems to continue irrespective of the location or extent of the lesions in the artists' brain (see Zaidel (2005) for a comprehensive overview). Remarkably, some cases of brain damage even lead to the emergence of artistic skills in individuals who previously did not engage in artistic behaviour: patients with fronto-temporal dementia, who as a result of this have impaired linguistic and social skills but spared manual and visual capacities, sometimes start painting obsessively and produce impressive works of art (Miller et al., 1998). Some cases of brain damage can lead to changes in style in artistic production: an Asian-American artist, for instance, who suffered from fronto-temporal dementia, evolved from conventional Chinese-style paintings to expressionist and fauvist-like works as her illness progressed (Mell et al., 2003). If artistic behaviour just exploits brain circuits that fulfil normal functions, and if it persists despite various forms of brain damage, it seems rather doubtful that it would be a biological adaptation.

8.3 Is Art a Byproduct?

8.3.1 Byproduct Explanations of Art

Some evolutionary psychologists propose that art is not an adaptation, but a byproduct. One of the most influential proponents of this view is Pinker (1997, 524–525), who argues that art's primary purpose is "to press our pleasure buttons". Art exploits aesthetic preferences that were adaptive in other contexts, just like cheesecake gratifies our ancestral craving for sugar and fat. Indeed, Blood and Zatorre (2001) have shown that aesthetically pleasing stimuli activate reward-based emotional circuits in the brain: participants who listened to their favourite music showed stronger activation in reward and motivation-related brain areas compared to control compositions. Subjects who look at paintings they deem beautiful, activate reward-based emotional circuits compared to duller paintings (Vartanian and Goel, 2004). A plausible reason why art should press our pleasure buttons is that artworks exploit evolved tendencies of the human brain, such as sensitivity to clear lines and marked colour contrasts that is characteristic of the primate visual system. Because of their importance to the survival and reproduction of the organism, some cues are given priority by the early perceptual systems. Ramachandran and Hirstein (1999) propose that visual artists maximally exploit these tendencies, thereby eliciting strong emotional responses. This would explain why works of art typically tap into several normal perceptual input systems and why they activate reward-based neural circuits. The cross-cultural prevalence of some art forms can be explained by their efficient exploitation of our cognitive predispositions. Newborns, for example, can already discriminate faces from other objects by detecting the shadowy patches created by the eye sockets and the mouth. Masks across the world exaggerate these facial features. Thus, they act as a superstimulus for our face recognition module, a compelling explanation for the use of masks in many cultures past and present across the globe (Sperber and Hirschfeld, 2004).

8.3.2 Problems With Byproduct Explanations of Art

At first blush, the byproduct explanation for art seems more cogent than the adaptationist approach. However, it faces two important problems. First, it predicts that we would invariably prefer works of art that maximally conform to evolved aesthetic preferences. Yet academic art by painters like William Adolphe Bougereau and Jean-Antoine Watteau which generally responds to our evolved tastes in depicting attractive people in lush landscapes, is nowadays derisively referred to as overpolished and clichéd. Experimental studies (Martindale, 1998) indicate that the lay public prefer academic art, and this is in line with byproduct explanations. But this does not explain the enduring appeal of works of visual art that are hardly eye candy, such as Francisco Goya's gloomy political canvases or Francis Bacon's haunting papal portraits.

Second, the costs in terms of time, material and energy that art requires seem difficult to reconcile with byproduct accounts. Pinker's view might seem plausible in the light of modern society, where we are constantly immersed in music and visual and narrative art, but art emerged within Palaeolithic hunter-gatherer societies where artists could not afford to live exclusively from their work but were hunting, gathering, building camps and crafting tools like everyone else. Among the oldest examples of representational art are mammoth ivory figurines from Swabia, Germany dated at about 35,000 years ago (Conard, 2003). Due to the growth structure of mammoth tusks, this material is notably difficult to work with and each of these tiny figures probably took several days to make. Likewise, in contemporary small-scale societies, such as hunter-gatherer and horticulturalist groups, people put a disproportionate amount of time and energy in the production of art. Why do these costly behaviours persist over such long stretches of time, when we would expect strong selective forces operating against such wastes of time and energy? To date, byproduct explanations of art have not addressed this question.

8.4 A Cultural Group-Selectionist Alternative

8.4.1 What is Cultural Group Selection?

At present, neither the adaptationist nor the byproduct account can adequately explain the data. While this by itself is not a reason to reject such explanations out of hand, it does provide room for an alternative explanation that will be explored here. This explanation, we will argue, accords well with empirical observations of art use in contemporary small-scale societies and with the archaeological record of Palaeolithic art. According to this explanation, some forms of art evolved through cultural group selection, in particular as a means to emphasize within-group identity. In the remainder of the paper, we will examine the proliferation of some forms of art in the Late Pleistocene (in particular, the mobiliary art from the Magdalenian) by appeal to cultural group selection. Group selection was originally proposed as a mechanism to explain altruism (e.g., Wynne-Edwards 1962). In this view, groups composed of altruists do better as a whole than groups composed of selfish individuals, favouring the retention of altruistic behaviour. In the second half of the 20th century, prominent evolutionary theorists like John Maynard Smith (1964) and George Williams (1966) argued that the assumptions on which group selection relies are very implausible. For one thing, altruistic groups are vulnerable to subversion from within—given that a single cheater within a group of altruists has higher fitness, this individual's genetic success will far outstrip the success of the altruists, as the latter have costs as well as benefits. Moreover, the replicators in biological evolution are genes, and it turns out that most instances of altruism can be explained in terms of the propagation of these genes (kin selection). As a result, group selectionist ideas fell on hard times in mainstream evolutionary theory. While no one claimed that group selection was inherently impossible, it was argued that special conditions need to be fulfilled before it could work. Group selectionist ideas are making a comeback, both in theories of altruism in the natural world (e.g., Wilson and Hölldobler, 2005) and in models of the cultural evolution of human altruistic behaviour (e.g., Henrich, 2004). Cumulative culture, which gives humans the capacity to transmit complex behavioural traits at a fast rate, indeed creates a set of special circumstances that might allow for group selection to occur.

A sensible way to interpret group selection is to see it as claiming that groups can fulfil the same role as organisms. In mainstream evolutionary theory, a distinction is made between *replicators* (genes) and *vehicles* (entities that interact with the environment). Genes can interact as cohesive wholes with their environment through their vehicles, typically organisms. Thus the behaviour of a given vehicle has direct consequences for its replicators: the vehicles' differential reproductive success ultimately causes the reproductive success of their replicators, thereby making them important units of selection (Sterelny, 1996). From this, it already becomes intuitively clear that groups must be distinct from each other and form cohesive wholes for group selection to occur.

Group selection requires that the fitness benefits of altruistic groups over selfish groups must outweigh the fitness benefits of selfish individuals over altruistic individuals within mixed groups. This condition can be mathematically described using the Price equation (Price, 1972), which provides a formal way to study changes in the frequency of heritable traits at two levels. In this case, we are interested to find out whether the benefits of art for the group (i.e., all members of the group together, including nonproducers) is greater than the fitness costs of the production of art by individual members of the group. The Price equation is a statistical statement that relates the expected change in the frequency of a gene or cultural trait ($\Delta\bar{x}$) per generation, the absolute fitness W_j, and the current frequency of the trait x_j. We start with a population of N individuals subdivided into groups indexed by j, each with n_j members. There are no restrictions on how the groups are composed, except that all groups must contain at least one individual.

$$\bar{w}\Delta\bar{x} = \overbrace{Cov(w_j, x_j)}^{\textit{between groups}} + \overbrace{E(W_j \Delta x_j)}^{\textit{within groups}} \tag{1}$$

The first term on the right side of equation 1 represents the relationship between the fitness of the groups and the initial frequency of the culturally transmitted trait within them, i.e., what is the effect of having this trait in the group as a whole as compared to other groups. The second part represents the expected changes in this trait, based on its impact on the fitness of individual members of the group. Given that covariance expresses the product of a variance and a regression coefficient (β), we can rewrite the Price equation as follows (simplifying by ignoring factors like mutation and recombination):

$$\bar{w}\Delta\bar{x} = \beta_{w_j, x_j} Var(x_j) + E\left(\beta_{w_{ij}, x_{ij}} Var(x_{ij})\right) \tag{2}$$

The two terms on the right side of the equations 1 and 2 oppose each other, since altruism increases group fitness but decreases individual fitness to a certain extent. If most of the variance in the population is within the group, but all groups have nearly the same frequency of the culturally transmitted traits, then the variation between groups *Var* (x_j) will be very small, whereas the expectation of the variation within groups *Var* (x_{ij}) will be nearly the entire variance of the population. In this case, cultural traits that favour altruism will not be maintained. If groups can be isolated from each other, the variance between groups can become larger than the variance within groups due to cultural drift, which provides an ideal basis for the development of altruistic behaviour. Cultural drift is the emergence and spread of cultural elements that arise by chance within a given group and that are copied randomly by members of that group. This is a mechanism that results in between-group differences when groups are sufficiently isolated. However, frequent contact between groups and migration can quickly undermine this: behavioural traits from one group can percolate into another, which increases variation within groups *Var* (x_{ij}) at the expense of variation between groups *Var* (x_j). Cultural mechanisms that enable humans to mark group identity and to maintain between-group differences can counter these effects, giving rise to within-group altruistic behaviour. Subversion from within is routinely countered by social rules, such as altruistic punishment (Fehr and Gächter, 2002), that discourage selfish behaviour and non-conformism. Furthermore, the presence of conformists dramatically increases the group size for which cooperation can be sustained (Guzmán et al., 2007).

Henrich's (2004) derivation of the Price equation (see equation 3) also shows that group selection only works if the benefits of being in an altruistic group outweigh the costs of bestowing benefits to other members of the group:

$$\beta_{w_i x_i} + \beta_{w_i x_j} \beta_{x_j x_i} > 0 \tag{3}$$

The first term of equation 3 is always positive, as it models the benefits of being in an altruistic group. The second term is always negative, because it represents the costs of bestowing benefits to others. Obviously, the sum of both terms needs to be larger than 0 for cultural group selection to occur.

Cultural group selection is one type of group selection in which the group is defined through cultural markers, such as distinct language or dialect, religious beliefs, dress code, food taboos, or other cultural norms. Cultural groups are fairly stable because people have a conformist bias: they tend to follow the norms of the culture in which they were raised. This conformist tendency is well attested ethnographically (Richerson and Boyd, 2005; Tehrani and Collard, 2002) and archaeologically (Collard et al., 2006), in the way material culture tends to evolve together with a particular ethnic group. As groups are culturally, rather than genetically, defined, and given that such culturally defined groups are fairly stable, cultural group selection can be invoked to explain human prosociality, i.e., the exceptional degree of cooperation and altruism found within most human societies. Rather than explaining this through genetic changes, one could argue that human culture, with its ability to differentiate groups from each other, allowed for the formation of distinct groups that each have their own norms and cultural practices (Henrich, 2004). As we have seen above, once stable groups have been formed, altruistic behaviour can be favoured within such groups, and the individuals within such groups will have higher reproductive success compared to members of other groups.

During the Late Pleistocene (126,000-10,000 years ago) members of *Homo sapiens* began to create various forms of material culture that, because of their aesthetic properties and putative symbolic value, are often referred to as visual art. Unfortunately, the archaeological record does not provide reliable evidence for music until much later, namely the recovery of flutes made of bird bone and mammoth ivory of Aurignacian sites in southwest Germany, dated at about 36,000 years ago (Conard et al., 2009). The evidence for dance can be indirectly inferred, from Magdalenian representations of dancers, for instance in the Grotte des trois frères. Because of the poor archaeological preservation of music and dance, we will here concentrate on visual material culture. The earliest convincing examples of visual art are in the form of body decoration, in particular shell beads from Israel and Algeria, dated to 135,000-100,000 years ago (Vanhaeren et al., 2006), shell beads from Blombos cave, South Africa, dated to 75,000 years ago (Henshilwood et al., 2004) and ostrich eggshell beads from Kenya, dated to 50,000 years ago (Ambrose, 1998). As we will explain in more detail later, there are good reasons why the earliest art is in the form of body decoration. For reasons of space and clarity, we leave aside the engraved ochre artefacts from Blombos and other South African sites, as their status as art objects is still contested within the archaeological community. Figurative art, such as figurines, paintings and engravings, appear somewhat later still.

Although it remains unclear whether cognitive or cultural changes lie at the basis of this transition, theoretical models (e.g., Powell et al., 2009) indicate that cultural changes brought about by different patterns of interaction and population density can explain the emergence of art without the need to invoke new cognitive capacities due to genetic mutations. A cultural account of art is also supported by the fact that different art forms (e.g., musical instruments, beads, rock paintings, engravings) emerged independently at different time periods across the world, a pattern that cannot be explained by gaps in the archaeological record alone. To give but one example, figurative paintings on rock surfaces appear significantly earlier in Europe (about 33,000 years ago, in Chauvet cave, France) than in Africa (about 27–25,000 years ago, Apollo 11 cave in Namibia (Conard, 2003)), or in Australia (about 17,500 years ago, Kimberley region, northern Australia (Roberts et al., 1997)). We here propose that some forms of Palaeolithic art, in particular mobiliary art and body decoration, could have been invented as a way to signal group identity which allows for a differentiation between groups, an essential condition for cultural group selection to occur. We will now consider two theoretical models to explain in detail this signalling function of art: green beards and ethnic markers. We will pit these models against the archaeological record to determine how useful they are for explaining the emergence of some forms of art.

8.4.2 Green Beards

Art may have been used as a conspicuous tag to signal altruism directly. In theoretical models such tags are often referred to as *green beards*: if green-bearded creatures bestow their altruism exclusively on fellow green beards, natural selection will promote the presence of the tag as well as the altruism. This theoretical framework can be easily extended to cultural evolution. Simulations (e.g., Riolo et al., 2001) indicate that cooperation can evolve easily in a population of agents who follow the simple rule "cooperate with others who bear the same tag as you". But as Dawkins (1989) already recognized, green beard altruism can be undermined by cheaters, who show the tag

Table 8.1 Different fitness outcomes of signallers and non-signallers, adapted from McElreath and Boyd 2007, p. 202

Genotype	Phenotype	Fitness
NN	Non-altruist, no green beard	w_0
NG	Non-altruist, green beard	$pb + w_0$
AN	Altruist, no green beard	$q(-c) + w_0$
AG	Altruist, green beard	$pb - cq + w_0$

but are not altruistic. The inherent instability of green beards has been demonstrated extensively in models of biological forms of green beard, where the linkage between the allele that signals the altruism (*A*) and the allele that codes for the display of the altruistic trait (*G*) gets disrupted (McElreath and Boyd, 2007). The possible combinations of such genes in a haploid organism are summarized in table 1.

Here, fitness outcomes are calculated as follows: genotype *NN* represents baseline fitness w_0, p is the frequency of altruists in the population, b is the benefit one receives from an altruistic donor. Given that signalling nonaltruists *NG* can always expect to get b, but that they do not incur costs (c), their benefit is $pb + W_0$. Altruists without signal (*AN*) are worst off, because they only suffer costs c whenever they encounter a potential recipient who signals, the frequency of which is given by q. Finally, altruistic signallers (*AG*) get benefit pb but have to pay cost qc. It is easy to see that genotype *NG* always has higher fitness than any other type as long as $c > 0$ and $b > 0$. Therefore, any process that breaks up the association between the tag *G* and the altruism *A* can result in an invasion of *NG*s thus eroding the value of the signal. Selective forces work against linkage between *A* and *G*. This association can be expressed as *D* (linkage disequilibrium). If *A* is associated with *G*, *D* is positive, if *A* and *G* are assorted at random, $D = 0$, and if *A* is paired with *N*, *D* will be negative. Because *NG* has the higher fitness, *D* will decline, until selection no longer favours the *A* allele. (Note that the selective force that breaks the linkage between the alleles coding for green beards and altruism does not play when green beards are rare alleles that are good proxies of relatedness. Due to the dynamics of kin selection, if two organisms that are reasonably closely related have the same rare marker, they can use this as a reliable indicator of relatedness.)

In cultural evolution, to counter this effect, one can change the tag regularly. Once a tag becomes too common, the chance increases that one encounters an organism with the tag but not the altruistic intentions. This can be mathematically expressed in equation 4:

$$\beta(p_j, q_j) = \frac{\frac{pq + D}{q} - p}{1 - q} = \frac{D}{q(1-q)} \tag{4}$$

Here p_j is the frequency of the altruism trait in the donor given the frequency of the green beard characteristic in the recipient q_j, p is the frequency of altruists in the population, and q is the frequency of green beards. As mentioned earlier, *D* expresses the association between green beard and altruism. One can see that the strength of cultural group selection through tags is proportional to the amount of *D*, but inversely proportional to the variance of the green beard trait, in other words, rare markers work best. Additionally, green beards can repel cheaters if the tag is costlier to produce for cheaters than for cooperators. As simulations (e.g., van Baalen and Jansen, 2003) show, a population of agents that signal their altruism through green beards can withstand cheaters when the temptation to cheat is very low, i.e., when the costs of adopting the tag are very high.

When we pit these criteria against the archaeological record, it seems unlikely that green beards can be a good model for the evolution of Palaeolithic art. As art is not a genetic characteristic, D will not be high—there is no intrinsic reason why those who make and/or display art would be more altruistic than those who do not. Therefore, populations using art as a signal for altruism can be easily invaded by cheaters. Furthermore, as rare markers work best, green beard models predict that the signal for mutual altruism should be rare and subject to frequent stylistic turnovers. However, taking taphonomic and other destructive processes in consideration, Palaeolithic art is found in abundance. Next to this, art styles in the Upper Palaeolithic are remarkably stable in space and time: they are typically in use for several thousands of years with few stylistic changes over large areas (we refer to section 8.4.4. for an example). Although mobiliary art requires much effort to produce, it can be displayed by anyone. Several Upper Palaeolithic child burials have been found, where the individuals were covered with hundreds, or sometimes thousands of beads, each of which took considerable skill, time and energy to make—it seems unlikely that the children would have produced these beads themselves. The positioning of the beads suggests that they were attached to clothing, such as shoes, trousers or parkas, suggesting that the children did not receive them as exceptional grave gifts, but that they were part of their attire (Vanhaeren and d'Errico, 2005). Clearly, the person who made the beads and bore the costs of its production was not always the one who displayed the tag, and this association is a necessary condition for green beards to work. It is also not clear how mobiliary art could be less costly to produce for people who behave altruistically than for those who do not. In sum, green beard dynamics are an unlikely explanation for the emergence of Palaeolithic art.

8.4.3 Ethnic Markers

Like green beards, ethnic markers are easily recognizable tags that mutual altruists can use to exhibit or infer altruistic intentions. The crucial difference is that ethnic markers do not signal altruism per se, but provide information on an agent's behaviour during social interactions—they are a proxy for social norms and conventions, such as marriage rules, religion, or moral practices. As social norms and conventions are not readily observable, arbitrary characteristics, like hairstyle or dress code, can provide good indications for them. Meeting an individual with similar ethnic markers facilitates social interactions which can be conducive to cooperation. An influential illustration of how ethnic markers can work is Nettle and Dunbar's (1997) model of languages and dialects. Their simulation indicates that individuals with similar languages or dialects can cooperate better and as a result of this achieve higher fitness. Given a limited memory-span, these individuals can withstand invasion from cheaters who speak the same language, especially given that cheaters need to relearn another language each time they are found out and have to move to another group where they are not known as cheaters. We will now examine how art could have been used as an ethnic marker. Cross-culturally, artistic ethnic markers are widely observed. Examples include decorated functional artefacts, where the style gives information about the ethnic group the owner belongs to, such as arrow point style as social information in Kalahari San (Wiessner, 1983). Artistic style enables individuals to distinguish people who belong to the ingroup from those who do not. Like dialects, artistic styles are difficult to imitate—it typically takes years for an artist to master a particular style.

Anthropological studies show that hunter-gatherers typically live in small bands of about 25 individuals; they are highly mobile within a large territory, moving on when resources are depleted. During parts of the year when resources are concentrated and abundant, these small groups aggregate with other bands that share their language, customs and beliefs. Group size is then between 200 and 800 individuals, depending on the capacity of the environment. During such seasonal aggregations, information, gifts and sexual partners are exchanged (Stein Mandryk, 1993). In the Upper Palaeolithic, we see the alternation between these group sizes in two types of sites: smaller residential sites with relatively little material culture, and larger sites with high concentrations of material culture. Altruism within small bands is widely attested in the ethnographic record in the form of food sharing (Hill, 2002) or alloparenting (Ivey, 2000). It can be easily explained by two well-established evolutionary mechanisms: kin selection (since most members of these small bands are related) and reciprocal altruism (since all members have social contact on a daily basis). There is also anthropological evidence that members of maximum bands help each other in times of hardship (Whallon, 2006). This type of altruism is much more difficult to explain through biological evolutionary mechanisms, since most people within the maximum band are not that closely related, and social contact between them typically takes place sporadically. Thus, kin selection and reciprocal altruism alone cannot explain why people from different small groups would help those of other groups.

From a behavioural ecological point of view, it is easy to understand why hunter-gatherers who live under marginal or unpredictable climatological circumstances, such as the present-day Inuit or the Kalahari !Kung, help each other to lessen the risk of local scarcity. When resources are unevenly spread in the landscape, small bands will sometimes starve before they find food. Under very difficult circumstances that are both cold and dry (the environment typical for Late Pleistocene Europe) it is not uncommon that 10% of the population dies of starvation each year (Stein Mandryk, 1993). This is a situation that is characteristic for Late Pleistocene Europe (126,000-10,000 years ago), where people mainly subsisted on herds of large animals, like reindeer, horse, mammoth and bison. Under these circumstances, where the main sources of food are unpredictable and patchy in distribution, inter-group contact and movement will become increasingly advantageous and necessary. Fruitless (wrong) moves can be lethal, leading to starvation and population decline. Not only do groups need information on where to find resources, they must also get access to them. These conditions set the stage for alliance networks between minimum bands, who can through visits, gift-giving and other regular contacts exchange valuable information on resources, and help each other in times of need. This help can take the form of passive tolerance, for instance, allowing another group to trespass on their territory, or can consist of active food sharing (Whallon, 1989). Social security networks come with a set of defined rights and obligations that people can exercise when they are in need or that they must fulfil when others are in distress (Gamble, 1982; Whallon, 1989). Such mutualistic ties are widely attested in ethnographically documented hunter-gatherers from tundra and arctic environments, such as the Tareumiut and the Nunamiut Inuit in northwest Alaska (Minc, 1986), and desert and arid environments, such as the well-known *hxaro* network of the Kalahari hunter-gatherers.

How could such networks be maintained? Although face-to-face contacts can play an important role, they are limited to adjacent local groups, and cannot be used to establish relationships between individuals from groups that have little or no previous face-to-face contacts. The use of a tag turns out to be a stable strategy to signal social security network membership. The *hxaro* network of the Kalahari !Kung uses ostrich eggshell beads as gifts to keep their social security network up to date. Ostrich eggshell is difficult to obtain, because the eggs are jealously guarded by both parents who ferociously defend their brood. The shell is also notably difficult to work: it has to be fresh but nevertheless fractures easily. Interestingly, ostrich eggshell beads from the Kenyan Middle Stone Age site of Enkapune Ya Muto are among the oldest examples of uncontested body decoration, dated to about 50,000 years ago (Ambrose, 1998). Many of the beads broke prematurely and were discarded as waste, which shows how difficult it is to produce them. Other anthropological parallels of long-distance exchange networks include the Trobriand exchange of shell necklaces and bracelets in the Kula ring, or the exchange of woven mats by women from Tonga and surrounding archipelagos. Upper Palaeolithic Europe saw a prolific production of beads from mammoth ivory, tooth and shell. Interestingly, although some beads were found in burial contexts, most of them were found in living sites (White, 1982). These findings suggest that beads were part of the everyday attire of European Ice Age hunter-gatherers. The production of the beads and the acquisition of the raw materials required effort and time. Experimental archaeological studies (e.g., White, 1997) indicate that fashioning one mammoth ivory bead, as is found in Aurignacian western European sites, takes one to two hours. Some beads were made of shells that are found in sites up to 600 kilometres removed from the Atlantic or Mediterranean coasts (Whallon, 2006). Such high investments of time and energy can be explained when one interprets these objects as ethnic markers.

8.4.4 The Case of the Magdalenian

We will focus now on the Magdalenian, a European cultural complex, which presents a pertinent illustration of how art may have played an important role in maintaining social security networks. Although the Magdalenian spanned Europe from the Pyrenees to Poland and Ukraine, its material culture was remarkably invariant.

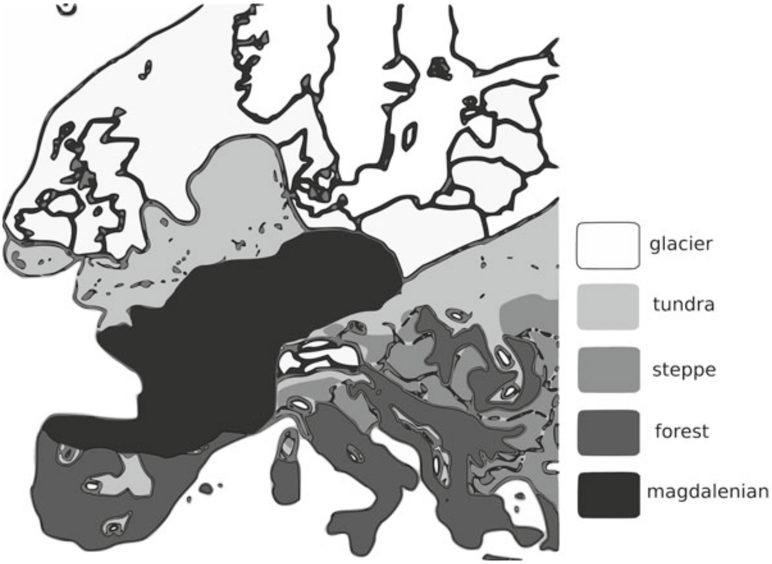

Fig. 8.1 Extent of vegetation types at the end of the Last Glacial Maximum and range of distribution of the Magdalenian, adapted from Jochim et al. (1999)

During the Last Glacial Maximum, which lasted from about 25,000 to 18,000 years ago, temperatures had plunged and ice sheets had expanded from Scandinavia and the Alps. Most of Europe was depopulated, because conditions were too harsh for human subsistence. Only southern France and northern Iberia were hospitable enough to maintain high population densities. From these regions, humans gradually recolonized Europe between 18,000 and 11,000 years ago. The recolonization is supported by archaeological data, which show the spread of the Magdalenian, a markedly uniform material culture from south of the Loire to the rest of Europe (Jochim et al., 1999). It is also confirmed by analysis of mtDNA sequence variations in extant European populations which indicate that a population originating from southern France and northern Iberia spread to central and eastern Europe about 15,000 years ago (e.g., Torroni et al., 1998). Due to the severe population bottleneck that took place during the Last Glacial Maximum, about 60% of the European mitochondrial DNA lineages (Richards et al., 2002) and even a higher proportion of Y chromosome lineages (Semino et al., 2000) can be traced back to the Magdalenian recolonization. Figure 8.1 shows the area of distribution of the Magdalenian, as well as the vegetation types at the end of the Last Glacial Maximum.

Since the Magdalenian spans an enormous geographic area with a low population density, we would expect human groups to become isolated and their artistic production and other forms of material culture to diverge. Also, the climate, the geography of the areas and types of prey show considerable variability across Europe, which again leads to the prediction that these groups would diverge. For example, settlements closer to water relied to an important extent on aquatic food

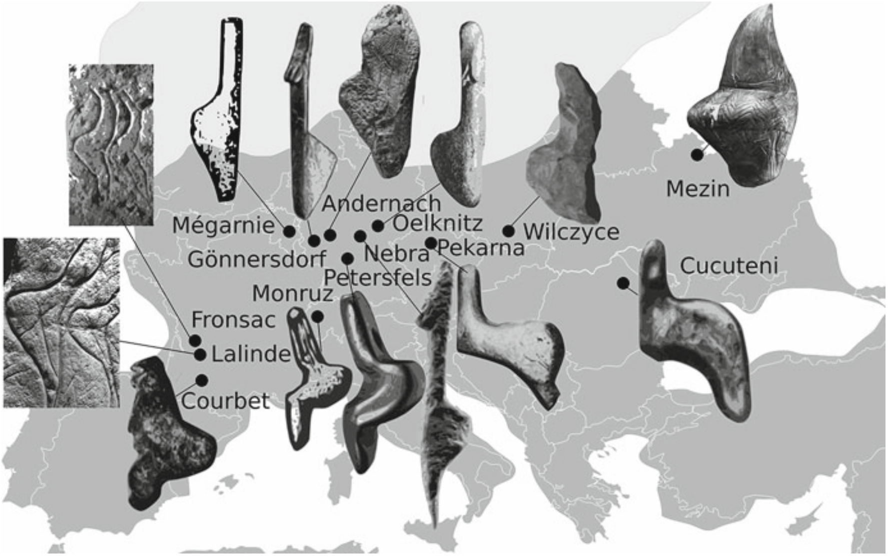

Fig. 8.2 A selection of Magdalenian so-called Gönnersdorf-Lalinde type Venus figurines and their locations

resources, whereas groups living inland subsisted mainly on reindeer and other large terrestrial mammals, reflected in a larger size of the settlements as preying upon large herds requires many hunters and can sustain higher population densities. However, the striking uniformity of the Magdalenian material culture suggests that groups maintained extensive contacts. Cultural innovations such as harpoons and spear-throwers (the latter already invented during the preceding Solutrean) were ubiquitous. Also, the frequent occurrence of exotic shells, amber and nonlocal stones found hundreds of kilometres away from their place of origin suggests the maintenance of long-distance exchange networks (Dolukhanov, 1997). The Magdalenian expansion was also characterized by a significant increase in population density. During the Last Glacial Maximum, the density of sites across the southwest European landscape remained low, suggesting a population size of about 4400 to 5900 individuals. The Magdalenian recolonization led to a marked increase in site density across western and central Europe, suggesting a population of up to 28,800 individuals (Bocquet-Appel et al., 2005).

Colonizing marginal territory requires extensive social security networks, since environmental conditions are unpredictable. Similar mobiliary art and body decoration in the form of beads and pendants enabled these small bands to maintain contact and to signal membership of large aggregation bands. Over thousands of kilometres, Magdalenian art shows striking stylistic similarities, including perforated bone discs with zoomorphic figures, antler spear-throwers with zoomorphic sculpture, and hundreds of stylized female figures in profile. These figurines have been found in a wide geographical area from the Dordogne to Ukraine, as can be seen in Fig. 8.2.

These objects were sculpted from a wide variety of materials, including flint, bone, ivory and steatite, which all have specific properties in terms of workability, fracturing and density. Despite this diversity in raw materials, they are stylistically markedly homogeneous, representing stylized women in profile with large buttocks, elongated headless torsos, small or absent breasts, without arms or feet. None of the figurines, including those made of flint, show traces of wear so they were not used as tools, but often they exhibit traces of extensive polishing, which firmly establishes that the artisans were concerned with their aesthetic properties. The statuettes fall within the Late Magdalenian, between 16,000 and 14,000 years ago (Fiedorczuk et al., 2007), a period characterized by population expansion and settlement of humans in large open-air and rock shelter sites. Long-distance contacts are documented in the transfers of exotic materials such as Mediterranean shells and Baltic amber found more than 600 kilometres from their places of origin (Gamble et al., 2005). We propose that the abundance of these figurines within living sites, e.g., more than 20 in Wilczyce, Poland (Fiedorczuk et al., 2007), the continent-wide adherence to a canon, and the care with which the objects were made suggest their use as ethnic markers. The fact that some of the objects (e.g., in Monruz, Switzerland, and Petersfels, southern Germany) have holes for suspension (Braun, 2005) strengthens this interpretation, as they were probably worn by individuals, as necklaces or other types of body decoration signaling group identity. Importantly, none were found in burial sites, which indicates they were not associated with particular individuals but rather with groups. As the climate became milder due to the start of an interglacial period, Magdalenian visual art in all its forms disappeared. Large animals became extinct or rare, and were replaced by smaller game such as deer, birds and hares, which are more evenly spread across the landscape. Although we still find evidence of long-distance contact in the form of exchange of seashells, which were probably valued for their exotic character, the risk of starvation became smaller and social security networks were less essential for survival in this richer environment. The lack of material manifestations of social safety nets in the archaeological record during this period supports our hypothesis.

8.5 Conclusion

Based on converging lines of evidence, we have sketched a cultural group selectionist model in which Palaeolithic mobiliary art and body decoration were used as a signal of membership of mutual altruistic groups. Archaeological and genetic evidence show that anatomically modern humans migrated out of Africa during the Last Ice Age. Around 50,000 years ago, they colonized Australia, including the arid inland with its inhospitable and unpredictable climate. At around 45,000 years ago they expanded into arctic Siberia. As ethnographic parallels and our case study of the Magdalenian show, risky and marginal environments can only be colonized by hunter-gatherer groups if they form social security networks. These networks require recognizable ethnic markers in the form of portable art and body decoration. It is no coincidence that mobiliary art and pierced shell beads were first made during the last two Ice Ages, as soon as population density allowed it (first in Africa and later in Eurasia), as at least some forms of art can be explained as an adaptive cultural response to harsh and unpredictable environmental conditions. Mutual altruism was necessary for Upper Palaeolithic hunter-gatherers, since they lived in uncertain and marginal environments, where the risk of starvation was always considerable.

It is important to note that our model was not designed to provide an all encompassing explanation for artistic behaviour, in the sense that traditional adaptationist approaches have attempted. Indeed, the fact that art spontaneously arises as a byproduct of normal perceptual and motivational processes leads us to suspect that no silver bullet theory will be able to successfully explain all forms of art production. Art objects have a diversity of roles and meanings in present and past human societies, and each of these roles and meanings might require different explanatory frameworks. The purpose of this paper was to examine how some forms of art in a particular context (such as the mobiliary art from the Magdalenian) could proliferate and be maintained through cultural group selection.

Acknowledgements We would like to thank Katie Plaisance, Thomas Reydon, an anonymous reviewer and members of the Human Evolution and Behavior Network (HEBEN) for their comments on an earlier version of this paper. This research was funded by grant 3H070815 from the Research Foundation Flanders and grant COM07/PWM/001 from Ghent University.

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