LONG ARTICLE

The Evolutionary Significance of the Arts: Exploring the By-product Hypothesis in the Context of Ritual, Precursors, and Cultural Evolution

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Abstract The role of the arts has become crucial to understanding the origins of "modern human behavior," but continues to be highly controversial as it is not always clear why the arts evolved and persisted. This issue is often addressed by appealing to adaptive biological explanations. However, we will argue that the arts have evolved culturally rather than biologically, exploiting biological adaptations rather than extending them. In order to support this line of inquiry, evidence from a number of disciplines will be presented showing how the relationship between the arts, evolution, and adaptation can be better understood by regarding cultural transmission as an important second inheritance system. This will allow an alternative proposal to be formulated as to the proper place of the arts in human evolution. However, in order for the role of the arts to be fully addressed, the relationship of culture to genes and adaptation will be explored. Based on an assessment of the cognitive, biological, and cultural aspects of the arts, and their close relationship with ritual and associated activities, we will conclude with the null hypothesis that the arts evolved as a necessary but nonfunctional concomitant of other traits that cannot currently be refuted.

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The arts have recently become fundamental to debates on human cognitive evolution on a number of counts, with many arguing that they set humans apart from other species and are one of the main traits that define modern humans (e.g., Henshilwood and Marean 2003). As a result, evidence of early artistic behavior has given rise to intense debate. Interestingly, various artifacts have been found that increasingly consign the origins of modern human behavior to a period ever closer to when Homo sapiens sapiens first appeared as an anatomically modern species ($\sim 180,000$ BP). Partially in response to these recent finds, the debate as to whether the arts are biologically adaptive or are more culturally derived has intensified. As the arts are central to this debate, it is essential to determine their proper place in evolution. The aim of this article is to assess the role of the arts in relation to the trajectory of human evolution in order to avoid the confusion and pitfalls that have hindered this debate.

The first part of this article will examine the relevance of aesthetics to the debate, after which we will identify the appropriate context for assessing the role of the arts and, by implication, their natural point of reference. Some recent theories that attempt to explain the arts from the perspective of evolution will then be considered in light of the foregoing. By way of illustration, specific examples from the archaeological record of how the arts were utilized by ancient peoples will be presented. Having identified the practical and theoretical standpoints for assessing the role of the arts, the ramifications arising will then be explored in the second part ("Originating Mechanisms") with a special focus on the relationship between biological adaptation, exaptation, and by-product approaches that will be assessed



within a gene-culture coevolutionary (aka dual inheritance) framework. The final section will address the consequences arising from the possibility that the arts may not be biologically adaptive. More specifically, we will claim that the evolution of the arts (not their origins) has been tightly linked to ritual and associated activities throughout the major part of evolutionary history, to the extent that they should be regarded as a complex whole. This behavioral complex, we will argue, has fitness costs for its participants that, on average, may overrule any of the evolutionary benefits deriving from each of the arts.

Setting the Context

Aesthetics and Art

Before considering these issues, the relevance of aesthetics needs to be clarified, especially as the concept is often conflated with "art" with regard to evolutionary explanations. Brown and Dissanayake (2009) point out that, although aesthetics may sometimes play a role in the arts, they are neither critical nor essential—a conclusion that may be correct yet is somewhat excessive, as we shall see. This reflects earlier debates on the subject in which the suggestion that aesthetics should be considered crucial to the arts was rejected by anthropologists (Weiner 1994). The main reason for this dismissal is that an overt concern for aesthetics as such only became prominent quite recently (principally in post-Renaissance European art, and especially during the 18th century with the idea of refined taste), which is in contrast to pre-literate tribal/traditionbased communities (including both ancient and modern hunter-gatherer groups, hereafter referred to as AMHGs), where such a preoccupation is accorded low priority—but which is not the same as saying they had no interest in aesthetics. To emphasize, AMHGs will have had an interest in "beauty," and therefore aesthetics, but this was an aesthetic intimately linked to artifacts, which involved a concern for balance, order, symmetry, and so on, and not one of detached contemplation. Aesthetics were therefore of secondary importance to AMHGs (Dissanayake 2011), not least because the arts were employed to meet the requirements of a range of activities relating to supernatural/magical thinking (Eibl and Mellmann 2008; Carneiro 2010) and other more immediate concerns. Thus, the arts were utilized in a different way by such groups compared to how they are often referred to in the modern sense. So,

¹ This is exemplified in the fact that, since the beginning of the 20th century, aesthetic appeal also began to lose its central position in Western art as illustrated by the (in)famous example of Duchamp's urinal of 1917, and by the 1960s the idea of beauty had virtually disappeared from contemporary art (Danto 2003).



although a modern individual might see and emphasize the aesthetic value of artifacts from prehistory or those created by AMHGs, "aesthetics" (even in Davies's (2012) broad sense of seeking and valuing beauty) was probably not the main concern for the authors of the original artifact(s).

For AMHGs, aesthetic concerns were therefore mainly subsidiary to the utilitarian purpose of the arts, which is borne out by Paleolithic art, where many of the depictions are "substandard" and frequently displayed in a haphazard, uncoordinated way. In fact, many of the depicted animals are often lost in multiple superimpositions resulting in a confused mass of lines, or were defaced, hidden, incomplete, distorted, poorly executed, or deliberately obliterated, with many sculptures intentionally smashed or buried (Bahn and Vertut 1997). The same widespread tendency to obliterate or destroy previously made "aesthetic" artifacts can be found at the pre-Neolithic site of Göbekli Tepe dating to around 12,000 years ago (Schmidt 2010) and Catalhöyük, around 9,000 years old (Hodder 2010). Western commentators tend to accentuate the best examples of Upper Paleolithic art because this appeals to their aesthetic inclinations and therefore foreground the flagship cave art of Lascaux, Chauvet, or Altamira, whereas the majority of the art from most of the sites (including the flagship caves) looks unfinished or is fragmented (see below for a discussion of examples from the Mesolithic and Neolithic). Thus, even though some of the depictions of AMHGs may be regarded as aesthetically pleasing to a modern sensibility, for traditionally based tribal groups this was not the overriding concern. In what follows, the emphasis will, therefore, be on investigating the art of AMHGs, in which aesthetics remain subservient to the perceived utility of the artifacts. By examining the arts from this perspective, we will be better placed to understand their true provenance.

Placing the Arts in Context

The majority of world art of the past was integral to the daily life of various communities on a number of different levels. This also applies to AMHGs, where the arts are connected to the effectiveness of the objects employed in rituals related to supernatural thinking, which explains why there is often no word for art in such cultures (Morphy 1994; Soffer and Conkey 1997; Dissanayake 1999). Moreover, even in cases where an object may seem to serve a purely practical purpose, it has been established that such objects are, in fact, associated with more animistic concerns (Ingold 2006; Hodder 2010; Vanpool and Newsome 2012). Thus, what might appear to be purely functional pottery without any decoration turns out to have additional significance that was not obvious in the first instance (Vanpool and Newsome 2012). Other similar examples include the way everyday objects, including actual houses, were intimately associated with ritual at the Neolithic site of Çatalhöyük (date ~ 9,000 BP) (Hodder 2010). In fact, Catalhöyük itself is not only replete with ritualistic significance but is also thought to have originated from the need to perform rituals. As Hodder writes (2010, p.18), "Many now argue that the reason people started agglomerating and creating settled life may have been religious ritual." Indeed, it is now becoming increasingly clear that fundamental changes to social and economic ways of life were due to ritual, as suggested by the pre-Neolithic site of Göbekli Tepe (date ~ 11,000 BP) (Schmidt 2010), and not climatic events or changes to the social fabric. Göbekli Tepe is particularly important as the people responsible for its construction were hunter-gatherers (i.e., not settled farmers), yet spent enormous amounts of time and energy constructing multiple "temples" where ritual practices occurred. These huge constructions were also destroyed in successive boutsreflected in the way Upper Paleolithic paintings were regularly defaced or obliterated—suggesting the intervention of ritual tendencies. Similarly, repeated destruction of artifacts, including carefully prepared paintings, also took place at Catalhöyük. Moreover, most anthropological/ethnographic research shows that the large bulk of artistic behavior in contemporary hunter-gatherer societies is embedded in ritual, and therefore it is reasonable to assume this was the case for the ancient hunter-gatherer societies as well when the arts first emerged. In fact, cognitive archaeologists now argue that the ability to engage in ritual is extremely ancient, perhaps stretching back 500,000 years with the onset of mythic culture (Donald 1991). Therefore, from the beginning, it seems that the arts and ritual were intimately related and did not exist as separate domains. These examples are fundamental to the present debate, as they provide concrete evidence that the earliest art may have been used mainly for ritual purposes.

Thus, the lifeways of AMHGS were invariably suffused with magical thinking to a greater or lesser extent, in that even everyday objects, which might not seem so disposed to a modern commentator, are thereby regarded. This point is crucial because it is often assumed that for AMHGs some forms of art were independent of ritual activities and animistic beliefs. On this basis, it is reasonable to propose that the arts, and by implication aesthetics, are more closely related to ritual than is assumed. This does not suppose that all art is related to ritual, as some aspects may have been purely decorative or aesthetic, yet the latter may, nevertheless, have been exploited purely to draw attention to an object's utility in ritual. We therefore need to remain alert to the fact there is a good chance the arts were often closely related to ritual and animistic concerns both specifically and more generally.

The fact ritual was a major concern in this context has led to the proposition that the term "art" should be dropped and replaced by a more inclusive term, such as "artification" or "making special" (Dissanayake 1988; Brown and Dissanayake 2009), so that the non-functional (with no direct practical utility) is emphasized.² The issue of functionality is important to this discussion as it is employed and understood in different ways by anthropologists and evolutionary biologists and has therefore caused some confusion in the literature. Anthropologists regard most behavior, including ritual and religion, and associated material culture, as functional in some general way (irrespective of whether this is actually the case) in that such behavior is part of the integrated social fabric of a community that serves to sustain a group (Dissanayake 2008; Moore 2012). Evolutionary biologists, however, employ the term in a much narrower sense, with specific and rigorous conditions that must be fulfilled before the requirements of functionality can be met. Confusion has arisen when scholars attempt to inadvertently impose the latter definition of functionality onto the former situation, usually by regarding the anthropological definition of functionality as synonymous with the biological one. For example, Dissanayake (2008) in a somewhat roundabout way attempts to show how ritual and the making of various artifacts are functional to a community and have a positive effect in that these activities increase social bonding. However, this does not take account of the fact these activities often have (additional) unintended negative

² Yet this, in turn, begs the question of what AMHGs themselves meant by functional, as this will have differed from the way it is defined in the modern sense, since in the latter case this depends on a reliable utilitarian outcome predicated on sound empirical evidence. In fact, for AMHGs, the world was considered suffused by and dependent on various forces and invisible agents that a person or community regarded as decisive for survival (Ingold 2006; Fausto 2007; Carneiro 2010; VanPool and Newsome 2012). Thus, AMHGs did not subscribe to the modern dichotomy of functional/nonfunctional in that the significance of most, if not all things, centered on animistic agents that could potentially inhabit, in one form or another, all aspects of the world. Thus, an object from a culture might to modern humans appear purely utilitarian, but, to those originally responsible for the artifact, significance would have been accorded based on other-worldly agents (see, e.g., VanPool and Newsome 2012). This shows that Dissanayake's dichotomy between the functional and non-functional is inappropriate. From this perspective, what is regarded as practical on a functional level today is different from how this is understood by traditional hunter-gatherer groups. For example, AMHGs might hold that the weather could be influenced by appealing to invisible agents and, in this sense, is "functional" in that a particular ritual or the use of an item employed in ritual could generate the required outcome. This is different from how functionality is referred to in modern parlance where a particular utilitarian outcome results from a specified practical procedure based on a naturalistic/materialistic outlook (Carneiro 2010).



consequences that can lead to the demise of a community, as in, e.g., the case of Easter Island where huge resources were expended to assuage the gods, necessitating the destruction of the remaining forests on which the community's ultimate survival depended (Flenley and Bahn 2003). It will be demonstrated, however, that in order to determine whether the arts are adaptive and to avoid such confusion, we need to adhere to the *rigorous* definition of functionality from evolutionary biology. In this case, the question is whether the arts—in serving ritual—gave rise to net fitness costs versus net benefits when *all* of the possible effects on the individuals concerned are considered.

By taking account of the fact that the arts are embedded in the lifeways of AMHGs as expressed in rituals through magical thinking/animism, a basis for a more pragmatic approach to understanding the arts of previous times can potentially be established. Perhaps, therefore, the reason AMHGs did not always possess a word for art is because the main preoccupation centered on ritual, whereby the objects employed (today regarded as art) were produced mainly for their apparent efficacy in such practices. In addition, there would have been no separation between, on the one hand, the various objects utilized and, on the other hand, the activities invoked in ritual. From this perspective, a dynamic interaction existed between dance, visual depictions, music, chanting, and the way the world was perceived that was manifested in a range of different ritual practices.

Critics might argue that different forms of art followed different evolutionary trajectories, with some perhaps being by-products whereas others were adaptive. Yet, this separation of art forms, both from each other and from ritual practices, is a relatively recent phenomenon related to increasing specialization that took place alongside the same tendency in other areas of human activity, such as in technology during the historical period. This separation was reinforced by the dualism of Descartes where mind and matter came to be regarded as separate entities. Many archaeologists and anthropologists, however, now reject this dichotomy in that, for AMHGs, mind, body, matter, objects, and artifacts are viewed as entangled in complex ways (Hodder 2012; Malafouris 2013).

Reframing the "Arts"

From the foregoing, the arts as practiced by AMHGs can be defined as an activity arising from the interactions between cultural evolution, which involves the capacity to learn from others, and biological evolution, that together depend on a cognitive stance that accords significance to an object within a ritualistic or animistic context whether this is expressed explicitly in an artificially contrived artifact/

activity, or is implied in a mundane item. This definition takes into account the fact that for AMHGs different activities and objects (music, dance, visual art, etc.) were employed together in a variety of ways according to the specific requirements of ritual or within the wider framework of animism that was embedded in the social milieu of a community and, as such, directed sensibilities. According to this definition, the arts gave expression to the social matrix that existed at any one time and, as they remain embedded or entangled within this milieu, can become manifest in a variety of ways (Keane 2010, who takes a similar view). This definition also takes into account that the arts did not arise simply from genetic determinants but, fundamentally, also depended on cultural transmission (Verpooten and Nelissen 2010).

Recent Theories of Evolution and Art

A number of scholars have attempted to explain the arts from an evolutionary perspective with various degrees of success. For example, the evolutionary psychologists Tooby and Cosmides (2001) defend the arts as a biological adaptation by focusing on human evolved psychology. Though previously agreeing that the arts may be a byproduct of sensory processes, they later suggested the arts may, nevertheless, have evolved as an adaptation for promoting detachment from the real world thanks to a formidable imaginative capacity underwritten by a dedicated neural system, which, through decoupled cognition, helps prepare the individual for real situations. A further advantage of such an imaginative capability is that knowledge can be shared among group members, thereby raising the number of options available for future action. Put another way, human imaginative abilities enabled the individual to escape from the tyranny of the present in a way that led to a release from proximity (Gamble 1998). This then provided a means to plan for the future through mental time travel that allowed one to reflect on past and present experiences. Even though these imaginative abilities may have conferred benefits, they may also have come with costs (i.e., giving rise to additional maladaptive traits that piggyback on such benefits). Tooby and Cosmides' adaptive explanation of the arts has been criticized for being more concerned with the ability to imagine counterfactual worlds rather than specifically being about the arts (De Smedt and De Cruz 2012). However, as Leslie (1987) has stated, although the mechanism allowing imagination to occur will have been directly adaptive, the contents of imagination are culturally derived. Tooby and Cosmides, therefore, conflate the two criteria by ignoring the fact that the arts are a function of the contents of the imagination and not the mechanism itself. Thus, it is the



underlying cognitive mechanism facilitating imaginative capacities, which depends on theory of mind—as well as an enhanced memory necessary for engaging in suspension of disbelief and greater social interaction—that provided the preconditions for the arts to exist (Hodgson 2013). In sum, imaginative capacities (as well as the capacity to imitate that enables cultural transmission of relevant innovations) can become maladaptive precisely because such capacities are prone to error, which can have deleterious consequences both for the individual and the community when acted on. Thus, if the arts derive from cultural determinants and the cognitive mechanisms (i.e., theory of mind, enhanced memory, ability to imitate, capacity to deal with deception, and so forth) have remained relatively stable, the main evolutionary cause that gave rise to the arts must be cultural evolution.³

Boyd and Richerson (1985, 2005; Richerson and Boyd 2001) propose, by way of dual inheritance theory, that aesthetics and the arts are the outcome of a cultural runaway process. Thus, aesthetic qualities (by which they mean the arts) are sustained as non-functional by-products of biased cultural transmission that ultimately came to be expressed as symbols. Note, however, that they postulate in later work (Boyd and Richerson 2005) that subsequently aesthetic traits and the arts are exapted to function as social markers of ethnic groups, which is not dissimilar to Dissanayake's (2008) position. Although culture evolved to promote survival by providing a means of reliably tracking and counteracting environmental change through transmitting accumulated knowledge across generations, the arts in their runaway model qualify as a culturally evolved byproduct of such cultural determinants for reasons unconnected to survival or fitness. Moreover, cultural adaptation to the environment may be constrained and the processes of cultural evolution may not always result in a fit between individuals and their environment (Sterelny 2006).

Similarly with Brian Boyd's (2009) proposition that fiction, and by implication the arts in general, are adaptive in being derived from adaptive animal play behavior. Although Boyd offers a very comprehensive account of the evolution of the arts, this thesis has been criticized not only because by-product explanations are misrepresented, but also because he fails to take into account how the arts can be alternatively explained as co-opted by-products of adaptive traits as realized in culture. Mellmann (2010) sets out these criticisms succinctly as follows:

An alternative explanation would be that art is an eminently cultural behavior... . We also have to take into account the (not specifically adaptive, or even detrimental) side-effects of these adaptations and, more importantly, the complex cultural combinations of a multitude of instinctive tendencies and their sideeffects. Those combinations were not shaped by natural selection (although they do use a number of biological substrates that were) but rather emerge every now and then in this or that culturally more or less stabilized, conventionalized form, However, in order to eliminate those behaviors from the human genetic program, natural selection would have to eliminate the biological substrates and thus also dispense with the adaptive advantages for which these substrates have been selected, and which have obviously been significant enough to outweigh the concomitant (but less stable) negative side-effects from the outset. [italics in original]

Recently, Stephen Davies (2012) has criticized approaches that have attempted to account for the arts as genetically adaptive, deriving from sexual selection or as a spandrel (by-product), as simplistic. It is to Davies' credit that he brings attention to the inherent complexity of the arts, both as an activity and the way they interrelate with human cognitive, social, and cultural criteria, and therefore do not lend themselves to a reductive analysis based on any one of these approaches. Davies, however, proposes that despite this complexity, culture—of which the arts are a part—is intrinsic to human nature, and can therefore give rise to positive adaptive outcomes. Thus, we need to regard the arts as similarly disposed. However, as Killin (2013) points out, even though this idea is couched within a coevolutionary framework, the model is weak because not enough support is offered regarding the suggested coevolutionary agenda. Furthermore, Davies tends to play down the importance of the rudimentary precursors that gave rise to later, more complex arts. As we will endeavor to show, although culture consists of many activities extraneous to the arts that often lead to positive biological outcomes, it comes with many maladaptive/neutral effects of which the arts and ritual are primary examples.

Are the Arts Adaptive?

The preceding considerations suggest that for AMHGs, the arts served as a means of enacting various rituals or were integrated into and facilitated an animistic belief system. Moreover, even though the arts may have had very different origins, we have considered indications that this integration happened close to the original onset. From this perspective, the arts have always been intimately



³ Not all uses of adaptive psychological mechanisms are adaptive. Thus, (1) the use of these mechanisms for art is only adaptive if, and only if, they have been selectively modified for the evolutionary function art may have. (2) They can be exaptive in cases where they increase reproductive success but without selective modification (i.e., exaptation; see below), and (3) if no benefits, they are a by-product.

intertwined with both rituals and associated belief systems. and this shared association with ritual bonded them together through entanglement (Hodder 2012), forming a complex integrated behavioral whole that was only broken gradually in historic times; a process that culminated recently with the inception of modern art movements of the West where past traditions were rejected in favor of experimentation and innovation (Gombrich 1958). If correct, our approach may simplify the adaptive analysis of the arts significantly, as it conveniently allows the question to be addressed as to whether the arts together—instead of singly—qualify as biological adaptations, cultural exaptations, or co-opted, non-beneficial by-products of sensory biases. In addition, our thesis that the arts have been subservient to ritual and associated activities in AMHGs suggests that whether the arts were adaptive or not may depend to a significant extent on whether these activities themselves were adaptive (see below). The null hypothesis should be that the arts are not an adaptation unless robust evidence is available that proves the opposite (Williams 1966; Buss 2004). With respect to the specific case of adaptation, in his seminal account on natural selection Williams (1966) noted that it carries an onerous burden of proof. Moreover, Williams (1966, p. 11) stressed that adaptation "should be used only as a last resort. It should not be used when less onerous principles ... are sufficient for a complete explanation." Before addressing the question of whether the arts are adaptive, it is first necessary to consider the role of cultural inheritance in human evolution, after which alternative evolutionary explanations can be considered—principally exaptation and by-product approaches.

Unlike most other animals, humans are heavily reliant on sociocultural learning (Henrich and McElreath 2003). Culturally transmitted information has therefore a significant impact on the human behavioral phenotype and on the dynamics of human evolution. Hence, whenever an attempt is made to reconstruct the evolutionary genesis of a particular aspect of complex human behavior and ask whether this is an adaptation or not, it is necessary, in addition to genetic evolution, to investigate the possible role of cultural evolution in its establishment as a persistent component of human nature. This requires some additional explanation. Standard evolutionary theory (i.e., the Modern Synthesis) as utilized in sociobiology and classic evolutionary psychology assumes that changes upon which natural selection can act predominantly arise from gene mutations. However, in accounts that take cultural evolution seriously, as in the gene-culture coevolutionary account, changes in the human behavioral phenotype may originate culturally from population dynamics as a result of adaptive social learning biases (Boyd and Richerson 1985; Richerson and Boyd 2005). These culturally inherited changes may subsequently result in selection for specific gene mutations that further enhance the benefits of a culturally evolved behavior, i.e., "culture-led gene-culture coevolution" (Richerson et al. 2010). However, these subsequent genetic modifications do not always occur. For example, it is unlikely that the evolution of the ability to read or drive a vehicle coincided with selective retention of specific gene mutations to support these abilities. Yet, such abilities may be potentially beneficial from an evolutionary perspective.

An adaptation is a trait that has been selectively modified genetically and is currently maintained for an evolutionary beneficial effect for a particular trait (i.e., increasing reproductive success). An exaptation also has an evolutionary beneficial effect but, in contrast, has not been selectively altered genetically for a particular trait (Andrews et al. 2002). This is consistent with Gould's view on exaptation (Gould and Vrba 1982; Andrews et al. 2002 discuss this in detail). Gould clearly points out that although feathers for insulation were exapted at some point in the history of flight, any subsequent genetically inherited phenotypic modifications feathers underwent for flight are "secondary adaptations," not exaptations. Some human traits, however, may originate, evolve, and persist without any correlated genetic changes; again, it seems unlikely that literacy or the ability to drive a vehicle has been genetically selected, nevertheless both may provide significant benefits (even in evolutionary terms). Such traits can be best described as "cultural exaptations" because they are beneficial and culturally evolved without genetic modifications. Thus, literacy is a cultural exaptation of preexisting abilities (such as dexterity, sight, and language). Also note that literacy and the ability to become literate are nearly universal in contemporary humans (world literacy is currently nearing 90 % according to UNESCO). Thus, universality of a trait is not always a dependable indication of adaptation.

Finally, a by-product is a trait that did not evolve because it was selectively advantageous, but because it was a by-product of selection for another trait. To give another example, some culturally acquired traits may be maintained merely because they are pleasurable, or in Pinker's (1997) terms, because they "push our pleasure buttons," such as is the case with drugs, pornography, and the arts (but not literature). Indeed, such nonfunctional but pleasurable traits may persist as long as they are not countered by natural selection.

Although it is often difficult to identify in practice, theoretically adaptation and the above-cited alternatives can be regarded as mutually exclusive. Whether the arts qualify as an adaptation, exaptation, or by-product depends on answers to the two following questions. First, are the arts evolutionarily beneficial (i.e., do they increase



reproductive success of those that engage in the arts)? If not, a by-product explanation is likely to be the case. If the answer is yes, the arts can either be an adaptation or exaptation. To distinguish between these two options, a second question needs to be answered: have the underlying motivation and capacities for art behavior been selectively altered genetically for a beneficial effect? If the answer is affirmative, the arts qualify as an adaptation. If not, the arts qualify as an exaptation. Finally, if it can be demonstrated that the arts are the result of cultural rather than genetic changes, the arts can be viewed as "culturally evolved" rather than genetically evolved. Thus, in conclusion, and depending on the answers to the above questions, the arts may be a genuine adaptation, a (culturally evolved) exaptation, or a (culturally evolved) by-product.

Thus, even though the arts may be intimately related to culture, as will be shown in the section on sensory biases, the activity can lead to negative or neutral effects as a result of which it may incur net fitness costs but nevertheless continue to be evolutionary maintained. The question then arises as to why the arts depend on cultural transmission.

For culture to occur, social transmission of "information" (i.e., ideas, beliefs, skills, knowledge, behavior) is required, but this also entails individuals remain gullible to the beliefs and influence of others (Boyd and Richerson 1985). As the arts are one of the main ways by which transmission of ideas and beliefs takes place via ritual, they are prone to a range of maladaptive tendencies. Indeed, the central claim of our exploration of the by-product hypothesis of art is that ritual can be said to constitute one of the main vehicles by which maladaptive behavior is transmitted.

Originating Mechanisms: The Arts and Sensory Biases

Although various scholars have proposed that the arts are an adaptation (see, e.g., Wilson 1998; Miller 1999, 2001; Boyd 2005; Carroll 2008; Dissanayake 2008, 2010; Dutton 2009), one of the major criticisms of this hypothesis is the fact that no dedicated areas of the brain have been found that engage art (De Smedt and De Cruz 2012). Rather many areas are recruited that invariably involve sensory and emotional/social neural networks that evolved to deal with problems of survival unrelated to the arts (Aiken 1999; Hodgson 2003; Dehaene and Cohen 2007; Zaidel et al. 2013), e.g., the discrimination of color and pattern for locating food and predators, emotion for regulating fight or flight and interactions between individuals, social factors associated with cooperative and altruistic behavior including the detection of deception, and so on. Given this, it seems unlikely that any part of the brain will have evolved specifically for the purpose of engaging in different arts. This is supported by the fact that the arts perform many different functions depending on cultural context, in the sense that, as an expressive vehicle of ritual, they can have radically different connotations and uses.

Although some universal factors are associated with the arts, which have been cited as evidence for functional adaptation/exaptation (Dissanayake 1995; Boyd 2009; Dutton 2009), these can be explained by the intrinsic appeal of the initiating sensory systems that evoke a nonbeneficial response. Thus, a particular art form is "carried along" with traits that have an adaptive functional design due to the fact that it is coupled with such adaptations, similar to how heat is a by-product of a light bulb (Buss 2004). Moreover, as the arts encompass a vast range of activities, behaviors, and abilities that vary greatly between groups, we need to specify exactly which are universal, a project that seems untenable.

From the outset, it should be emphasized that referring to the arts by such terms as "sensory cheesecake" (Pinker 1997) somewhat trivializes their importance, as this implies the behavior simply diverged from, or existed alongside, more pressing evolutionary concerns. As the arts have been central to the lifeways of most communities throughout time, which has been repeatedly documented by various authorities (Dissanayake 1988, 1995), the preoccupation is crucial to understanding human behavior. The thesis that art is a by-product is however not inconsistent with the observation that it is intricately intertwined with evolved traits that are functional. Therefore, perhaps the phrase "an inevitable consequence of the interactions between brain function and cultural transmission" would provide a less pithy but more accurate description that reflects the "necessary by-products" of Gould and Lewontin (1997). The question then arises as to the relationship that exists between brain function, adaptation, culture, and the arts. In order to address this issue, we need first to identify the evolutionary precursors in the predisposing sensory systems.

Preexisting biases of the female perceptual system (whether incidental by-products of how neural networks are structured or functionally maintained because they are/were adaptive in another context) can become co-opted in the mating system of a species (Ryan 1990, 1998; Arak and Enquist 1993, 1995). For example, the bowers constructed by male bowerbirds to attract females are thought to have first derived from exploitation of a sensory bias in females that was originally directed towards foraging for food such as fruit. This became useful to females in mate selection in that the bowers reduced the search parameters previously required for identifying preferred males (Madden and Tanner 2003). Sometimes, however, exploitation of sensory biases of receivers may not subsequently become



adaptive for receivers, in which case the evolutionary process corresponds to the strict version of sensory exploitation (Ryan 1998).

Verpooten and Nelissen (2010) highlight one such mechanism in fiddler crabs where, although females are attracted to the sand burrow entrance hoods made by courting male crabs, males are also attracted to the same hoods as a result of "sensory trap." This process occurs through self-exploitation of the presenting stimulus. Similarly, the female guppy's preference for the orange spots of male guppies stems from a preference for orange food that is maintained by the fact that it is useful for obtaining such nourishment (Arnqvist 2006). These preferences, however, are accidental consequences that derive from, but remain decoupled from, the originating adaptive mechanism.

Thus, sensory exploitation based on sensory biases is widespread in the natural world, and, although it is thought to have led to and is associated with sexual selection, at the same time it is also found in many other kinds of behavior unconnected with mate preference (Arnqvist 2006). Sensory bias therefore predicts that preferences for and sensitivities to particular kinds of stimuli can exist before coevolution between aesthetic preferences and aesthetic traits has had an influence by provoking interest, thus establishing sensory bias as a critical mechanism in itself. Sensory biases may also become exploited through culturally transmitted signals. For example, humans have a strong bias for faces, due to an extremely sensitive face detection system (Johnson 2011). This bias is likely maintained by natural selection since humans rely heavily on social interactions in which face detection and recognition play a crucial role. However, the original function is obviously not maintained in the context of perceiving an artifact depicting a face, such as a mask (Sperber and Hirschfeld 2004)—a "fake" stimulus that became an abundant part of human material culture. Sensory exploitation by such culturally evolved signals has been shown to be relevant to understanding the evolution and persistence of cultural content attuned to our sensory systems (Verpooten and Nelissen 2010).

Evidence from Nonhuman Primates

The notion that the arts are a non-adaptive/non-functional by-product of sensory systems is supported by studies of chimpanzees. The relevance of considering art-like behavior in nonhuman primates derives from the fact that, if it can be demonstrated that such behavior exists, this would provide evidence that the arts in humans are indeed a by-product of sensory mechanisms. This is because art-like activity is not part of the natural behavioral repertoire of nonhuman primates. Therefore, if nonhuman primates are able to spontaneously produce and take an interest in

art-like behavior, this could only arise as a consequence of already adapted neural mechanisms that exist for reasons unconnected with the arts. This methodology is also used in sensory bias research, where the existence of a pre-existing bias is assessed by testing whether it is latently present in closely related species in which it is not naturally exploited (Ryan 1998).

Research in captive chimpanzees indicates they have an intrinsic motivation to draw in that the visible traces produced are self-reinforcing (Morris 1962; Tanaka et al. 2003), which is thought to be related to exploratory (search) behavior. Even at eleven months of age, chimpanzees take a spontaneous interest in drawing basic lines on an electronic finger touch screen (Tanaka et al. 2003). The fact that infant chimpanzees freely indulge in drawing suggests this is not adaptive but that pleasure is taken in stimulating existing psychosensory systems related to exploratory behavior, of which only the latter is adaptive. As chimps have not been observed making similar marks in the wild, this, again, suggests mark making exploits preexisting psychosensory systems. The fact that the intrinsic motivation to draw is not expressed in chimpanzees in their natural habitat is obviously because they do not possess a material culture that lends itself to creative drawing. The crucial difference, therefore, between human and nonhuman primates with respect to art making may not just be psychological but also sociocultural. Interestingly, chimpanzees possess enough manual dexterity to both produce and complete iconic images but are unable to succeed in this due to a lack of visual memory capacity (Saito et al. 2010).

Similarly, music exploits the neural mechanisms of auditory processing (Changizi 2011), which is supported by the fact that monkeys, who are unable to produce music, respond in a consistent way to species-specific natural calls synthesized and played back as "music." Moreover, they are also able to recognize tonal diatonic melodies, as opposed to the chromatic scale or atonal sounds, though this does not generalize to melodies transposed to different keys (Hauser and McDermott 2003; Snowdon and Teie 2010). As Snowdon and Teie (2010, p. 30) state, "Tamarins were generally indifferent to playbacks of human music, but responded with increased arousal to tamarin threat vocalization based music, and with decreased activity and increased calm behavior to tamarin affective vocalization based music."

In addition, research of (admittedly one) chimpanzee indicates a sensitivity to, and tendency for synchronous movement (tapping) in response to an auditory rhythm (Hattori et al. 2012); a finding, if corroborated, that reflects the above studies of mark making in chimpanzees. Music, therefore, seems to engage phylogenetically ancient auditory mechanisms related to the soundscape important to a



species' survival but which did not evolve for the purpose of music appreciation (Changizi 2011; De Smedt and De Cruz 2012). Thus, certain rudimentary sensory mechanisms that were biologically adaptive may have been recruited for added purposes. Evolution always needs to build on what already exists, so nonhuman precursors will be found to a certain extent. However, these homologous precursors may or may not be recruited for novel purposes in the subsequent independent evolution of different species. As outlined, some monkeys, although not responding to music derived from human speech, do so to music based upon their own species-specific vocalizations (Snowdon and Teie 2010). Within our species this principle is indicated by the observation that most, but not all, scales throughout time employ between five and seven tones, which may be related to the fact that the pentatonic and heptatonic natural scales correlate with the way human speech is perceived (Gill and Purves 2009). In this regard, De Smedt and De Cruz (2010) note that the reconstruction of the 36,000year-old bone flute from Geißenklösterle in Germany produces tones that fall within the minor pentatonic scale (Seeberger 2003)—a scale that is most widely exploited cross-culturally. Musical appreciation may therefore have either originally derived, or alternatively developed, in tandem with previously adapted vocalizing capacities that were co-opted by culture for active musical purposes. However, despite the fact that research suggests that some very basic auditory traits for musicality appear to exist in very young human infants, the majority of what are commonly accepted as musical skills are thought to be culturally determined (Hannon and Trainor 2007).

In summary, research on nonhuman primates suggests they spontaneously engage in non-adaptive art-like activities that derive from the pleasure of engaging in sensory systems that evolved for adaptive reasons, such as search behavior or species-specific calls. Although such fundamentals may seem remote from the artistic behavior of humans, they nevertheless provided a "template" from which complex artistic activities could be realized. The most parsimonious hypothesis, then, would be that the arts recruit primate and species-specific building blocks or precursors, without giving rise to net benefits for individuals. Thus, the by-product explanation should be favored as the null hypothesis unless strong indications are found that the arts confer fitness benefits for which they were selected (i.e., adaptation) or not (i.e., exaptation).

The Cognitive Niche of the Arts and Sensory Biases

Thus, the "arts" may derive from the exploitation of preexisting psycho-sensory correlates through resonance that served as the main driving force in the evolution of artistic behavior (Hodgson 2000, Hodgson and Helvenson 2006; Pinker 1997; Verpooten and Nelissen 2010). In other words, the adaptive mechanism that originally gave rise to neural networks tends to resonate with stimuli similar to that which first led to the formation of a particular neural system. In this sense, the arts can be said to be co-opted (beneficial or not) from preexisting adaptive mechanisms that became important in the cultural domain. From this perspective, the arts conveniently mesh with existing human cognitive abilities and were thereby subject to cultural selection through sensory exploitation (Verpooten and Nelissen 2010). Likewise, neural resonance corresponds to what is termed "content biases," which are transmissible features that are intrinsically memorable or easily accessed due to their close relationship to the structure of the mind (Shennan 2008). The important point here is that even though human minds are generally adaptive and have adaptive functions, they are also prone to produce and prefer fitness-neutral behaviors, ideas, beliefs, and values that often become maladaptive in a given context due to latent biases and biases that are functionally maintained in another context (Henrich and McElreath 2003).

Art and Ritual: Non-beneficial Practices?

Rituals are commonly considered useful or beneficial in some way (Gino and Norton 2013), whether or not their use is cashed out in the currency of fitness and thus would count as truly evolutionary beneficial. However, arguably, many specific kinds of ritual (which are invariably replete with art), especially those that are costly, may not be beneficial. As an irrational means of attempting to control the world, much time and effort is expended in the pursuit of ritual for little or no positive outcome—the many ways in which ritual and associated activities were self-destructive to AMHGs has been aptly catalogued by Edgerton (1992) and Carneiro (2010). In this context, ritual, rather than being regarded as adaptive in a general sense (i.e., culturally adaptive) in being functionally useful for sustaining a group (see, e.g., Rappaport 1999; Sosis 2000), is viewed as a by-product of an enduring sensory and cognitive mechanism relating to a precaution/hazard warning system—the proper adaptive domain (Boyer and Liénard 2008). Hence, ritual developed out of the need for social affiliation that gave what apparently appeared to be control of the environment but which was largely misplaced and therefore, in this sense, was maladaptive, which is a



⁴ We mean *relative* parsimony, as traded against model complexity (i.e., goodness of fit), and not parsimony in absolute terms as in the principle of Occam's razor, since parsimony is not defensible in the generalized way implied by Occam's razor (Sober 2006).

tendency that increased as societies became more hierarchical and prescriptive. Therefore, although ritual, and ultimately religion, may have helped strengthen group cohesion, this was offset by the fact that such behavior was also misapplied in the sense that it was utilized for the control of natural disasters or events that were perceived as capable of being influenced by appealing to other worldly agents. In this regard, rather than ritual and the arts, it was probably prosocial behavior together with increased organizational abilities and foresight that were the main adaptive driving forces in human survival. Thus, as the arts for AMHGs were mainly subservient to ritual, it follows that such activity would generally also have led to maladaptive or evolutionary neutral net outcomes—even though ritual may occasionally appear to have been adaptive in certain contexts. Due to the fact that ritual and associated arts were unable to track or deal with evolutionary threats to survival with any great reliance, it is therefore parsimonious to assume they were not adaptive in a critical sense.

Interestingly, the universal proclivity for supernatural thinking in AMHGs (which continues in the contemporary world) may be a necessary consequence of how the brain has gravitated towards greater neural density, proliferation, reorganization, and neural transmission speed. In this scenario, neural signals tend to increasingly overlap, especially within and between modular structures (Kaas 2008) thus giving rise to conscious awareness, social abilities, imaginative faculties, and deceptive capacities (Dehaene and Naccache 2001; Ghazanfar 2008; Konopka et al. 2012). As one is susceptible to being lured by the arts, and most of the arts are about a willingness to participate in reciprocal deception (Hodgson and Helvenson 2006; Hodgson 2013), one was also liable to indulge in communal playacting that enacted various cultural myths as typified in rituals. Although this may sometimes appear to increase group bonding, at the same time, it may have been more than cancelled out by the irrational behavior associated with ritual practices. Maladaptive behavior is a common symptom of human endeavor and is the cost paid for a large, complex brain and flexible cognition that subserves the associated sociocultural milieu, where ritual represents one example of such a cost that is carried along with adaptive behavioral correlates. As Boyd and Richerson (2007, p. 328) state, culture "comes with a built-in tradeoff: culture provides a rich source of adaptive information, but to use it efficiently individuals have to be 'credulous,' mainly adopting the beliefs of those around them and this credulity allows maladaptive beliefs to spread." This explains why maladaptive traits such as rituals were not culled.

As the arts primarily served the purpose of ritual, the question then becomes, why is ritual so pervasive in human behavior? Ritual is associated with anxiety and, when

chronic, becomes compulsive, which is manifest in ritualized actions as a short-term means of assuaging raised levels of anxiety that leads to even greater anxiety in the medium to long term (Fiske and Haslam 1997; Boyer and Liénard 2008). Ritualized actions mainly involve behavior that becomes detached from the originating cause through displacement, which provides short-term reassurance by imposing order in the face of perceived insecurity/danger. Repetitive behavior is closely associated with anxiety, and, as redundancy is also a defining feature of collective ritual, ritual may have arisen as an irrational means of assuaging perceived threat that subsequently came to be expressed culturally as a means of combating such threat (whether real or imaginary). Boyer and Liénard (2008) see this as deriving from human vigilance—a precaution/hazard warning system that monitors potential danger, thus spurring the individual towards taking aversive action. However, although anxiety is a normal adaptive function that prepares the individual for threat, it becomes maladaptive when chronic. Collective cultural rituals share many of the features of such chronic conditions, especially with regard to rigidity and inflexibility when the emphasis is placed on the procedure rather than the goal (Fiske and Haslam 1997; Boyer and Liénard 2008). Rituals are therefore compelling because the human cognitive system makes such a behavioral repertoire attention grabbing (Liénard and Boyer 2006), which thereby becomes liable to cognitive capture that has much in common with the aforementioned sensory trap. Interestingly, small groups appear to practice what are termed imagistic rituals (as opposed to the doctrinal rituals of settled communities), which are characterized by potent emotions and traumatic practices full of intense imagery (i.e., art) that often give rise to extreme behavior (Atkinson and Whitehouse 2011), and which are likely to have been the type of ritual favored by huntergatherers during the Upper Paleolithic and pre-Neolithic (as evidenced by the aforementioned examples). Thanks to the high attention load, rituals and associated belief systems therefore become an excellent means for transmitting cultural information (not always beneficial), which persisted as a parasitic by-product of the original adaptive mechanism, as is now being increasingly emphasized (Liénard and Boyer 2006; Boyer and Liénard 2008; Atran and Henrich 2010). It follows that if ritual is a non-beneficial by-product of primary adaptive mechanisms, given that the main outlet for art is through ritual, then most of the arts may also be a non-beneficial by-product.

Discussion

As we have stipulated, although the arts may be viewed as culturally maintained by-products of enduring evolutionary



precursors, this does not therefore mean they do not have important consequences for human endeavor. Moreover, we have developed in detail a specific variant of the null hypothesis, which proposes that the arts are neither an adaptation nor an exaptation but rather sustained as a nonfunctional by-product of such factors. Gene-culture coevolution has, however, been cited as an explanation for the prevalence of the arts (De Smedt and De Cruz 2012; Killin 2013), which is not incompatible with the above analysis, as the cultural part of this interrelationship can also give rise to neutral and maladaptive tendencies. As stipulated, culture appears to have arisen as a means of swiftly adapting to novel and changing environments that required a long period of learning and a degree of flexibility, by providing a means of transmitting information from one generation to the next which, although adaptive, also came with maladaptive costs (Boyd and Richerson 1985, 2005). This also fostered a tendency for magical thinking whereby the inanimate and animate were liable to be regarded as an extension of human cognitive faculties (Helvenston and Hodgson 2010). Although some aspects of ritual-like behavior may seem to have been adaptively beneficial, these may have been more than offset by the many instances where ritual led to maladaptive outcomes, e.g., the many examples of ritualized infanticide carried out in pre-Columbian Central and South America, as well as other parts of the world, where the remains of children became ritualized art objects with many infants thought to have been voluntarily donated by biological parents to appease the gods (De La Cruz et al. 2008). In the last analysis, the "sapient paradox" of Renfrew (2008) in which complex culture, i.e., the arts, did not predominate until sometime after the speciation of *Homo sapiens sapi*ens, suggests that, in conjunction with limited population levels, the behavioral trait that may have hindered this centered on a continued reliance on ritual and magical/ animistic thinking thereby preventing a more considered assessment of real practical issues.

Conclusion

The above evidence suggests that the arts did not evolve as adaptations, but rather arose as a non-beneficial by-product of certain long-standing psychosensory biases, which were duly co-opted by the arts in the context of ritual as a result of cultural evolution. As the arts evolved culturally, this allowed their qualities to be exploited in either neutral or maladaptive ways depending on circumstances. Having said this, it needs to be emphasized that when "culture" is referred to in this context, we are referring to a *capacity* for culture (i.e., evolved social learning abilities) that was itself adaptive by way of individual or group selection, and

the arts are a product of this capacity. In this way, ritual behavior and the arts may have been an inevitable but costly non-functional by-product of such a capacity that was realized in culture. It may therefore be time to move away from explanations based on traditional evolutionary psychology and straightforward adaptive explanations that do not take cultural evolution as an independent force in human evolution seriously, and concentrate on more fruitful avenues of research based on a coevolutionary framework involving culture. In view of the above observations, accounts based on traditional evolutionary psychology that have sought to explain the arts have not met the robust requirements that are essential for such claims to be verified. In coming to this conclusion, it has been necessary to examine evidence from diverse fields including neuroscience, cognitive evolution, archaeology, behavioral ecology, and related disciplines, which strongly suggest that alternatives to adaptation, especially the by-product hypothesis offered here, cannot currently be refuted.

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