From animal signals to art: manipulative animal signaling and the evolutionary foundations of aesthetic behavior and art production

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Abstract: As humans are evolved animals, we propose a non-anthropocentric framework based on animal signaling theory to understand the evolutionary foundations of human art, instead of a classical anthropocentric approach based on sociocultural anthropology that may incorporate evolutionary thinking but does not start with it. First, we provide a concise review of the basics of the evolutionary theory of animal communication or signaling. Second, we apply this theory to specifically human aesthetic behavior and art and provide four empirical arguments or factors that reduce the conceptual gap between nonhuman animal signaling and human aesthetic-artistic behavior (two from the nonhuman and two from the human side) and that, as such, grant a conceptual integration of human aesthetic behavior and art production within animal signaling theory. And third, we explore the theory's explanatory power and value when applied to aesthetic behavior and art production, through proposing four valuable insights or hypotheses that it may contribute or generate: (i) on art's operation within multiple functionally adaptive signaling contexts, (ii) on the basic evolutionary economics of art or what art is (for), (iii) on why art is functionally adaptive rather than a non-functional byproduct, and (iv) on how art is functionally rooted in competitive-manipulative animal signaling and – unlike language – only to a lesser extent in cooperative-informative signaling. Overall, animal signaling theory offers a potentially integrating account of the arts because humans and their signaling behaviors are conceptually situated within a broader, trans-human field that also comprises nonhuman species and their behaviors, thus allowing an identification of deeper commonalities (homologues, analogues) as well as unique differences. As such, we hope to increase insights into how acoustic, gestural/postural, visual, olfactory, and gustatory animal signaling evolved into music, dance, visual art, perfumery, and gastronomy respectively.

Key words: sociocultural anthropocentrism *vs.* evolutionary non-anthropocentrism; animal communication or signaling theory; competition and cooperation; manipulation *vs.* assessment/information; aesthetics/art and symbolism/language

1. Introduction

From a classical sociocultural-anthropological perspective, the most *parsimonious null-hypothesis* on the origins and nature of the human arts is that they have a purely sociocultural origin and history which do not require (evolutionary) biology as a non-trivial explanatory tool (Boas 1927; Lévi-Strauss 1966; Geertz 1973, 1976; Davies 2012; Killin 2013). Hence, from this perspective the *burden of proof* is to provide explicit evidence that

(evolutionary) biology would be involved in a non-trivial way, which is definitively the case according to several present-day evolution-minded philosophers of art (e.g., Dutton 2009; De Smedt & De Cruz 2012; Davies 2012, 2014; Killin 2013, 2018; Richards 2019). However, a research strategy starting from a sociocultural-anthropological null-hypothesis or zero-background and subsequently – insofar deemed necessary – adding input from (evolutionary) biology is typically *anthropocentric*. By contrast, in the present paper we defend and elaborate on an explicitly *non-anthropocentric stance on the evolutionary foundations of aesthetic behavior and art production* (cf. Prum 2013). We follow Darwin and adopt a continuity principle that asserts we should explain human behavior in terms of the same general processes that explain the behaviors of other animals, based on the fact that humans are evolved animals and products of the same evolutionary processes. While this might also plausibly be characterized as a parsimony principle, what truly justifies it is that we have good reason to believe in it on empirical grounds about the natural processes that produced humans.

We start from the following three background assumptions:

- Just like language, art is subject to abundant sociocultural variation. But also like language, the presence *per se* of aesthetic behaviors and art products transcends sociocultural boundaries and specifications: artistry is a cross-cultural, panhuman, and arguably even pre- and nonhuman behavioral phenomenon, or perhaps even a behavioral phenotype (Dutton 2009; De Smedt & De Cruz 2012; Davies 2012; Richards 2019).
- Again like language, art may involve or belong to the broader category of *communication or signaling* in which there is by definition always a signal transfer from a signaler (an actor or sender) to an observer (resp. a reactor or receiver) (Maynard Smith & Harper 2003; Bradbury & Vehrencamp 2011). That is, although art may involve more than solely signaling, most scholars agree that artistic behavior and art production always imply the roles of an 'actor' or 'artist' and an 'observer' or 'audience' (Dutton 2009; De Smedt & De Cruz 2012; Davies 2012; Richards 2019).
- It is an *evolutionary-biological fact* that 'humans' incl. their neuropsychology and communication/signaling behavior evolved from and belong to the broader or more comprehensive category of 'animals' and their neuropsychology and communication/signaling behavior (cf. Darwin 1871; Dawkins 2016).

Put together, these three background assumptions allow one to conceptualize human language and art as communication or signaling behaviors that evolved from, and belong to the broader or more comprehensive category of, animal communication/signaling in general (Maynard Smith & Harper 2003; Bradbury & Vehrencamp 2011). Obviously, this does not exclude the possible addition of human-specific neurocognitive and sociocultural complexities to or upon this broader or more general foundation of animal signaling.

While the details about the evolutionary origin of language are still not entirely clear, we have a pretty good understanding of the adaptive function of language and 'what language is', i.e., that it evolved from *cooperative* animal (social mammal and primate) signaling to underpin and allow for efficient *information transfer* among large numbers of individuals in socially complex societies (cf. Cheney & Seyfarth 2005; Seyfarth et al. 2005; Tomasello 2008; Scott-Phillips et al. 2012; Scott-Phillips 2015). By contrast, as yet there is no such clear understanding of the – if any – adaptive functionality of art and on the question what art is (Davies 2012; Seghers 2015; Richards 2019). According to classical sociocultural anthropology, art thrives on socioculturally transmitted symbolical information or meaning, thus ultimately on language (Boas 1927; Lévi-Strauss 1966; Geertz 1973, 1976). This is also the default position in archaeology and evolutionary anthropology: in line with the sociocultural-anthropological approach, art is usually supposed to be part of the human symbolism/language cluster (Mithen 1996, 2005; Lewis-Williams 2002; Henshilwood & d'Errico 2011) which in turn, then, evolved from cooperative mammal and primate signaling in which (pre-symbolical) information transfer is central (Cheney & Seyfarth 2005; Seyfarth et al. 2005; Tomasello 2008; Scott-Phillips et al. 2012; Scott-Phillips 2015; Seyfarth & Cheney 2017).

In the present paper, we question this default or standard position, as it does not fit well with at least two bodies of empirical research. First, there is increasing evidence from the *cognitive and affective neurosciences* that the aesthetic experience of morphological core aspects of art engages or manipulates our biologically evolved nervous, sensory, affective, emotional and motivational systems (Aiken 1998; Voland & Grammer 2003; Panksepp 2009; Chatterjee 2014; Huston et al. 2015; Kapoula & Vernet 2016; Westphal-Fitch & Fitch 2018; Hodgson 2019). And second, there is a growing body of literature in the field of *evolutionary or bio-aesthetics*

that demonstrates that *aesthetic signaling behavior* has its evolutionary roots in *competitive-manipulative* – mainly courtship but also territorial, ritualized combat, and coalitional – animal signaling (Darwin 1871; Dawkins & Krebs 1978; Eibl-Eibesfeldt 1988; Voland & Grammer 2003; Welsch 2004; Hagen & Bryant 2003; Hagen & Hammerstein 2009; Endler 2012; Heinrich 2013; Mandoki 2014; Prum 2012, 2013, 2017; Ryan 2018; Westphal-Fitch & Fitch 2018; Nüsslein-Volhard 2019).

The present paper is divided into two parts. In the first part (i.e., section 2), we provide a concise review of the basics of the behavioral-ecological evolutionary theory of animal communication or signaling. First (2.1), we provide a general definition of an animal signal. Second (2.2), we explain why the term 'manipulation' is to be preferred over 'influence' to denote signaling. And third (2.3), we explain more thoroughly different types of competitive-manipulative and cooperative-informative signaling. In the second part (i.e., section 3), we explore the explanatory potential of animal signaling theory when applied to human artistry. First (3.1), we formulate an operational animal signals-based definition of aesthetic behavior and art production as well as provide four empirical arguments or factors that decrease or reduce the conceptual gap between nonhuman animal signaling and human aesthetic-artistic behavior (two from the nonhuman and two from the human side) and that, as such, grant such a conceptual integration of human aesthetic behavior and art production within the definitional framework of animal signaling theory. Next, we explore the latter's explanatory power and value when applied to aesthetic behavior and art production, through proposing four valuable or interesting insights or hypotheses that it may contribute or generate: (3.2) on art's operation within multiple functionally adaptive signaling contexts, (3.3) on the basic evolutionary economics of art or what art is (for), (3.4) on why art is functionally adaptive rather than a non-functional byproduct, and (3.5) on how art is functionally rooted in competitive-manipulative animal signaling and – unlike language – only to a lesser extent in cooperative-informative signaling.

Like other evolution-informed philosophers of art before him (e.g., Dutton 2009; Davies 2012), Richards (2019) points in his review essay to the multiple potentially adaptive functions behind the evolutionary origins of art behaviors, and also to the failure of such evolutionary hypotheses to account for the rich sociocultural (symbolical and normative) spatiotemporal diversity in art genres, styles, periods, cultures, contexts, and so on. To explain this sociocultural diversity he proposes a sociocultural-ecological *niche-construction* framework, the diversity of niches accounting for the symbolical and normative diversity in aesthetic and artistic styles and genres. In the present paper, we propose the behavioral-ecological theory of animal signaling as a unifying or universal evolutionary theory or framework for explaining aesthetic and artistic behavior, within which multiple adaptive signaling functions or contexts can be integrated (such as courtship, territorial, ritualized combat, coalition, and social-bond and group-cohesion signaling), but upon which also a niche-construction theory on the sociocultural (symbolical and normative) specifics and diversity of art styles (cf. Richards 2019) could be built. These latter are, however, not the focus of the present paper. We only focus on the evolutionarily universal features of art for which, so we claim, animal signaling theory provides the suitable unifying framework. While Richards (2019) proposes niche construction theory as a unifying framework on the sociocultural (symbolical, normative, spatiotemporally confined) 'superstructures' of art, we propose animal signaling theory as a unifying framework on the evolutionary-biological 'substructure' or 'groundwork' of aesthetic and artistic behavior.

Overall, whereas classical sociocultural anthropology and philosophy of art, due to their anthropocentrism or exclusive focus on the human species, have failed to provide a satisfying definition or account of what art is (for), trans-human animal signaling theory offers a potentially integrating account precisely because humans and their signaling behaviors are conceptually situated within a broader field that also comprises nonhuman species and their behaviors, thus allowing for an identification of deeper commonalities (homologues, analogues) as well as unique differences. As such, we hope to increase insights into how acoustic, gestural/postural, visual, olfactory, and gustatory animal signaling evolved into music, dance, visual art, perfumery, and gastronomy respectively.

2. The basics of animal communication or signaling theory

2.1 Defining animal communication and signaling

The empirical study of animal communication and signaling behavior was pioneered by classical ethologists such as Karl von Frisch, Konrad Lorenz, and especially Niko Tinbergen (1952, 1964). Given some naïve – by now obsolete – assumptions in classical ethology about cooperation and group and species selection, there was a kind of general tendency to take for granted that animal signals had evolved to carry a benefit to conspecifics (for the ultimate good of the group and/or the species) in the form of useful information. However, the evolutionary

study of animal behavior was forever changed by three landmark theoretical innovations which gave rise to the modern field of behavioral ecology: the theories of 'kin altruism' (Hamilton 1963, 1964; Maynard Smith 1964), 'reciprocal altruism' (Trivers 1971), and 'evolutionary games' (Maynard Smith & Price 1973; Maynard Smith 1974). All three start from the *Darwinian-competitive zero-background or null-hypothesis* on a world in which there are *limited resources* and in which individual organisms are forced to *compete* for these resources in order to *survive and reproduce*. All three also provide theoretical explanation on how, against this null-hypothetical competitive zero-background, complex behaviors like kin and reciprocal altruism and other behavioral strategies may evolve. Evolutionary game theory in particular (Maynard Smith & Price 1973; Maynard Smith 1974) provided the insight that, in a Darwinian-competitive world with limited resources, natural selection is expected to favor individuals who *conceal* information about their motivational or intentional states and, hence, that a selective pressure to *abstain* from signaling or, at most, produce *uninformative and/or non-costly* signals is to be expected (thus in contradistinction to the abovementioned classical-ethological assumption). This left the question on the origin and nature of animal communication and signals largely unanswered. However, two conceptual solutions were formulated already soon afterwards: Zahavi's (1975, 1977) 'handicap principle' (i.e., animal signals are selected 'not despite but because' of their informative costs) and Dawkins & Krebs' (1978) 'manipulative' definition of signaling (i.e., animal signals are selected not to carry information/benefit to a reactor but to manipulate a reactor to the signaler's benefit).

Zahavi (1975) reasoned that, as *courtship signals* (e.g., the long tail of a male peacock) are costly items or 'handicaps' according to the logic of evolutionary game theory, they can only be afforded by high-quality signalers, as such 'honestly' reflecting or advertising the latter's fitness. That is, the more costly the signal (e.g., the longer the male peacock's tail), the higher the signaler's fitness, the more likely a sexual partner will be impressed and seduced. Hence, courtship signals as costly handicaps may evolve through sexual selection (cf. Darwin 1871). Zahavi (1977) and Zahavi & Zahavi (1997) also extended or generalized the handicap principle to other *assessment signals* like ritualized aggression signals and territorial markings or signals. They, too, may 'honestly' reflect the signaler's fitness (e.g., its size, strength, health). That is, the more costly the signal (e.g., the louder a call, a whistle, or a roar; the showier or more strenuous a gesture or posture), the higher the signaler's fitness, the more likely an opponent will be intimidated and retreat. Grafen (1990) provided mathematical game-theoretical proof of honest and costly signaling as a possible 'evolutionarily stable strategy' (ESS). However, notwithstanding claims made by Grafen (1990) and Zahavi & Zahavi (1997), the handicap principle presumably cannot serve as a general principle or definition of animal signaling, as it only applies to honest signals and not or, at least, less to dishonest or deceptive signals (e.g., bluffing). Furthermore, as signals are assumed to 'honestly' reflect the signaler's fitness (its strength, size, health, etc.), a central claim of the handicap principle is that signals would be selected 'not despite but because' of their potential costs – thus in contradistinction to how natural selection is usually assumed to operate, viz., driving the evolution of traits 'not because but only despite' of their costs (Számadó & Penn 2015). As this claim remains contested (e.g., Dawkins & Guilford 1991; Hurd 1995; Getty 1998; Lachmann et al. 2001; Maynard Smith & Harper 2003; Számadó 2011; Számadó & Penn 2015), we will not further make use of the handicap principle here.

A more general definition of animal communication or signaling was provided by Dawkins & Krebs' (1978) *manipulation*-based account. They wrote:

> "When an animal seeks to manipulate an inanimate object, it has only one recourse – physical power. A dung beetle can move a ball of dung only by forcibly pushing it. But when the object it seeks to manipulate is itself another live animal there is an alternative way. It can exploit the senses and muscles of the animal it is trying to control, sense organs and behavior machinery which are themselves designed to preserve the genes of that other animal. A male cricket does not physically roll a female along the ground and into his burrow. He sits and sings, and the female comes to him under her own power. From his point of view this *communication* is energetically more efficient than trying to take her by force." (p. 282)
>
> "Communication is said to occur when an animal, the actor, does something which appears to be the result of selection to influence the sense organs of another animal, the reactor, so that the reactor's behavior changes to the advantage of the actor." (p. 283)
>
> "It may happen that both parties benefit by the arrangement […]. But as far as our definition of communication is concerned, whether the reactor benefits or not is incidental". (p. 285)

> "[…] actors do sometimes succeed in subverting the nervous system of reactors, and adaptations to do this are the phenomena that we see as animal signals." (p. 309)

That is, according to Dawkins & Krebs (1978) an animal signal is

1. a ***phenotypic feature*** (a morphological structure or behavioral pattern) of a signaling organism (not necessarily an animal, e.g., a flower producing a visual or olfactory signal),
2. which evolved by natural selection to ***manipulate*** the behavior of a reactor (always an animal) to the advantage of the signaler's fitness,
3. ***not*** through trivial (i.e., non-signaling) ***direct physicochemical influence, manipulation, coercion or brute force*** on another organism's physiological constitution (e.g., not through chemical poisoning, pushing away, fighting, eliminating an opponent, prey-catching, outrunning, etc.),
4. but through ***energetically less strenuous-costly indirect – via the sense organs – manipulation and exploitation of the reactor's evolved nervous (sensation, arousal, emotion, motivation) system***, as such transforming an 'unwilling' reactor into a 'willing' (e.g., approaching and falling into a trap, retreating or fleeing, giving up chasing, mating, cooperating) one.

Further relying on Dawkins & Krebs (1978), Maynard Smith & Harper (2003) provided the following stripped-down definition of a signal:

> "any act or structure which alters the behavior of other organisms, which evolved because of that effect, and which is effective because the receiver's response has also evolved.'' (Maynard Smith & Harper 2003, p. 3; see also Stegmann 2005, p. 1014)

The only notable difference with Dawkins & Krebs' (1978) account is that this definition offers an abstract generalization of the above 4th specification: according to Dawkins & Krebs (1978) the thing that is being manipulated and exploited is the reactor's *evolved nervous system*, whereas according to Maynard Smith & Harper (2003) the thing that is being manipulated and exploited is the reactor's *evolved response*. As such, following Maynard Smith & Harper's (2003) suggestion, the 4th specification in the above 4-step scheme becomes:

> 4. but through an ***energetically less strenuous-costly exploitation of an evolved response*** in the reactor.

This abstract generalization allows us to generalize the theory of signaling to non-animals – thus organisms lacking a nervous system (i.e., bacteria, archaea, protists, plants, and fungi). As such, Maynard Smith & Harper's (2003) definition could take into account that non-animals like plants and bacteria could – apart from being trivially physicochemically influenced, manipulated or coerced – also be manipulated non-trivially through signaling, i.e., through the elicitation and exploitation of an evolved response in them (cf. Brenner et al. 2006; Shinar et al. 2007). Furthermore, Maynard Smith & Harper's (2003) definition also provides the opportunity to exclude *camouflage* from the category of signaling, as there is no elicitation of an evolved response in the reactor here (cf. Stegmann 2005).

Relying on Maynard Smith & Harper (2003), Scott-Phillips (2008) offered the following definition of a signal:

> "any act or structure that (i) affects the behavior of other organisms; (ii) evolved because of those effects; and (iii) which is effective because the effect (the response) has evolved to be affected by the act or structure."

Again, the only difference is in the 4th specification in the above 4-step scheme, which now becomes:

> 4. but through the exploitation of a reactor's response that is ***specifically evolved to be affected by the signal***, i.e., that is ***adaptively evolved to the presence of the signal***.

As Scott-Phillips (2008, p. 388) confirms:

> "The only substantial difference between this definition and Maynard Smith and Harper's wording is the explicit requirement that the response not simply be adapted but be adapted to fulfil its half of the communicative dynamic."

However, this *coadaptation between signaler/signal and reactor/response* is arguably too demanding as a requirement for signaling in general: although a signal by definition always elicits and exploits an evolved response, the latter is not necessarily an evolved adaptation to that signal. For example, the response (e.g., flee, approach) could equally have been evolved for some other purpose or for no purpose at all (in case of a byproduct), but is now elicited and exploited by a signal. That is, signals may evolve through exploitation of *pre-existing* biases in a reactor's (neuro)physiological system, i.e., biases and responses that are not adapted to – and do not benefit from – the occurrence of the signal. Hence, Scott-Phillips' (2008) *coadaptation* criterion would not apply to signaling in general (e.g., not to deceptive and parasitic signaling where the reactor's response is not adapted to – and does not benefit from – the signal), only to signaling systems where the reactor is also adapted to – and benefits from – the signal, such as assessment (courtship, ritualized combat, territorial) signaling. Of course, Scott-Phillips has a point when claiming that coadaptation and interdependent functionality (albeit often antagonistic) among signaler and receiver would be requirements for true communication (cf. Scott-Phillips et al. 2012). Yet, here we accept with Dawkins & Krebs (1978), Krebs & Dawkins (1984), Maynard Smith & Harper (1995, 2003), Rendall et al. (2009), Owren et al. (2010), and Rendall & Owren (2013) that signaling does not *per se* require the reactor to be specifically co-evolved with, co-adapted to, and benefit from the signal. That is, signals *as phenotypic features of a signaling organism* are always and primarily for the good of the signaler itself, and may or may not be for the good of the reactor. We return to this issue in the next sections.

2.2 Why prefer 'manipulation' over 'influence' to denote signaling: on 'signals', 'cues' and 'causes'

An important *evolutionary mechanism* behind the evolutionary origin of signals is a form of 'exaptation' (Gould & Vrba 1982; Andrews et al. 2002), which in the earlier literature was often referred to as 'derived activity' (Tinbergen 1952; Dawkins & Krebs 1978; Krebs & Dawkins 1984). That is, a pre-existing phenotypic morphological or behavioral adaptation (e.g., a bird's tail, canine biting) may carry with it initially inadvertent byproducts (e.g., length and color of the tail, tooth-bearing preceding biting) that have – as inadvertent 'cues' – an initially inadvertent effect on another animal's nervous system and behavior (e.g., inadvertently attract a mate; inadvertently frighten an opponent). However, such an *initially inadvertent* byproduct or cue may evolve into an amplified, exaggerated, ritualized and manipulative (e.g., attractive, repulsive, intimidating) spatiotemporal pattern, structure, design or signal *advertently manipulating* the reactor's nervous (sensation, arousal, emotion, motivation) system and behavior to the signaler's advantage (cf. Dawkins & Krebs 1978; Maynard Smith & Harper 1995, 2003; Rendall et al. 2009; Owren et al. 2010; Rendall & Owren 2013). It is important in this respect to clearly distinguish 'signals' from 'cues' (cf. Maynard-Smith & Harper 1995, 2003; Scott-Phillips 2008).

Maynard Smith & Harper (1995, p. 307) defined a cue as follows:

> "a cue is a feature of the external world used to decide what to do. In general, a cue is not a signal, for example it may be an inanimate object such as a landmark. If, however, a cue is a property of an organism, it may evolve into a signal."

And Scott-Phillips (2008, p. 388) defined a cue as

> "Any act or structure that (i) affects the behavior of other organisms; and (ii) which is effective because the effect has evolved to be affected by the act or structure; but which (iii) did not evolve because of those effects."

Note that Scott-Phillips (2008) – just like in his definition of a signal – requires the reactor's evolved effect or response to be specifically adaptively evolved to the cue. However, just like a signal (see supra), a cue may also elicit a *pre-existing* bias in a reactor that evolved for some other purpose and, hence, is not necessarily an evolved adaptation to that cue. Therefore, the only difference with causality in general, i.e., with a 'cause' in general, is that the latter refers to any kind of effect or influence from one factor on another factor, whereas a 'cue' is a more specific subcategory of causality in that it causes an *evolved effect or reaction* in a (biologically evolved) reactor. That is, causes, cues, and signals relate to each other as follows:

- a 'cause' is a factor that has an ***effect or influence*** on another factor;

- a 'cue' is more specific: it is a factor or pattern that has an ***inadvertent but evolved effect or influence*** on a (biotically evolved) reactor;
- a 'signal' is even more specific: it is always a biotic (more specifically, an adaptively evolved or phenotypic) factor or pattern that has an ***advertent/manipulative as well as evolved effect or influence*** on a (biotically evolved) reactor.

This is why we prefer the word 'manipulation' (cf. Dawkins & Krebs 1978; Krebs & Dawkins 1984) over 'influence' (cf. Rendall et al. 2009; Owren et al. 2010; Rendall & Owren 2013; Stegmann 2013) to define a signal, because influence may also be *inadvertent* whereas manipulation is always *advertent*. That is, influence is so broad that it also applies to cues and even to causes in general, whereas manipulation as 'advertent influence' really is a defining property of signaling.

Note that a signal may sometimes inadvertently act like a cue for some other animal towards which it is not directed. However, as a signal did not biologically evolve to act as such, this is of no further relevance for the present exposition. Of course, once the signaler starts to advertently exploit the changed behavior of that initially inadvertently influenced or informed reactor, the cue is being 'ritualized' into a manipulative signal specifically directed towards that new reactor (see supra).

2.3 Competitive-manipulative and cooperative-informative signaling and their links to art and language

There are several types of animal signaling. *Parasitic or deceptive signaling* is characterized by signaler benefit *vs.* reactor cost (e.g., all kinds of bluffing, the Venus flytrap, screaming cuckoo chicks begging for food) and can be an evolutionarily stable strategy or ESS if the costs the reactor pays in assessment (e.g., for developing more sophisticated neuropsychological assessment skills to better discriminate non-harmful from harmful signals) *exceed* the costs of being exploited (Dawkins & Krebs 1978; Krebs & Dawkins 1984; Owren et al. 2010). By contrast, when the costs the reactor pays in assessment *are lower than* the costs of being exploited, this may result in *coadaptation through co-evolutionary arms-races* among signalers (striving for maximal manipulative efficiency with minimal energetic and informational costs) *versus* reactors (striving for maximum assessment or information gain) (Dawkins & Krebs 1978, p. 309; Krebs & Dawkins 1984; Carazo & Font 2010). The evolution of many *assessment (courtship, ritualized combat, territorial) signals* could be interpreted this way, viz., between manipulating signalers (striving for reactors to, respectively, mate, retreat, or stay away) *versus* assessing or information-gaining reactors (increasingly assessing the signaler's fitness, health, quality or strength). Both signaler and reactor may benefit from this type of signaling, but due to conflicting or diverging fitness interests these are mainly antagonistic (as opposed to mutual or common) benefits (Krebs & Dawkins 1984; Searcy & Nowicki 2005). This contrasts, then, to *coadaptation through cooperation* which relies on reduced conflicting interests and/or increased common benefits among signaler and reactor, and which thrives on selection for:

- mutualism (i.e., immediate mutual benefits), which may lead to both inter- and intraspecific short-term cooperation. The evolution of assessment (courtship, ritualized aggression, territorial) signals may – apart from being driven by coadaptation through co-evolutionary arms-race dynamics (see above) – eventually result in an evolutionarily stable 'cooperative settlement' or 'compromise' in which *the immediate mutual benefit is conflict resolution by means of a circumvention of physical-energetic costs or damage through coercion, fight, or violence*.
- kin (and sometimes also reciprocal) altruism, which may lead to intraspecific cooperation. Seminal examples are the bee dance signaling the location of a food resource to conspecifics (von Frisch 1967) and alarm calls signaling the presence of predators to conspecifics (e.g., in marmots, meerkats, and primates – Seyfarth et al. 1980). Other examples include – often collective, intimate and playful – signaling to foster mammalian social bonding (e.g., among mother and infants) and mammalian group cohesion and robustness (e.g., collective howling and ritualized social play in wolf packs; dolphin and whale acoustics and ritualized social play; see de Waal & Tyack 2003; Whitehead & Rendell 2012; Yamagiwa & Karczmarski 2014; Cafazzo et al. 2018; Watson et al. 2018).

However, due to the fact that cooperation (mutualism, kin and reciprocal altruism) always ultimately takes place within a more basic Darwinian-competitive world or zero-background in which individuals have to compete for limited resources in order to survive and reproduce, competition and corruption between the two ultimately competing camps (signaler and reactor) always lurks in the background, even among kin and among sexual partners (cf. Trivers 1972, 1974). More specifically, due to natural selection acting on individual fitnesses, there is a *twofold corruption of information/honesty* possible through

- *a selection pressure on signalers* for strategic concealment or minimization of cue-style 'give-away' information about motivations and intentions and try less costly (i.e., less cue-style, less 'give-away', less informative, less honest) signaling for the same manipulative success (Dawkins & Krebs 1978; Krebs & Dawkins 1984; Guilford & Dawkins 1991; Maynard Smith & Harper 2003), i.e., an inclination to evolve into the direction of deception, exploitation and parasitism;
- *a selection pressure on reactors* to lower their assessment costs and to settle with cheaper, less costly and reliable indicators of quality "where the costs of fully assessing a signaler are high, in terms of energy, time, or risk, and the value of the extra information gained is low" (Dawkins & Guilford 1991, p. 865).

Therefore, a state of purely or 100% cooperative signaling is possibly never fully reached in nature. There is even a minimal amount of competition and conflicting interest among sexual partners and among kin (e.g., among siblings and even among parents *vs.* infants) (cf. Trivers 1972, 1974). However, the bee waggle dance is often considered as an example of pure cooperation without conflict of interest between signaler and reactor. This would then suggest that manipulative (e.g., spellbinding, hypnotic, seductive) power aimed at persuasion to overcome diverging interests is not really necessary here and, as such, that the waggle dance would be a non-manipulative, thus purely informative signal (indicating the location of food). This would indeed be the case if there was 100% genetic identity – and thus a 100% common genetic interest – among signaling and reacting bees. However, genetic diversity within bee colonies is common, and it has been demonstrated that such increased genetic diversity significantly increases signal production by waggle-dancing foragers (Mattila et al. 2008; Matilla & Seeley 2010). Intriguingly, this suggests that this increased waggle-dance signal production meets the demand for increased manipulative persuasion to overcome diverging interests. Put differently, decreased genetic diversity correlates to decreased waggle-dance signal production (Matilla & Seeley 2010), suggesting that manipulative signaling to overcome diverging interests would be less required here. The ideal of a colony with 100% genetic identity is probably never fully reached. Therefore, like any other animal signal the bee dance, too, seems to be a signal constituted *in the first place* by manipulative design aimed at a reactor to actually do something in favor of the fitness of the signaler (i.e., to fly off towards the desired location and get some food) in a Darwinian context or zero-background of competition and conflicting interests, and only *secondarily* by information transfer (about the location of food) in a cooperative setting.

Yet, in spite of the infeasibility of purely or 100% cooperative signaling systems in animals due to inevitable corruption in a basically Darwinian-competitive world – thus in spite of a continuum between competitive and cooperative signaling in nature, two overall types and/or styles of animal signaling are discernible in nature:

- **Competitive (like parasitic, deceptive, and co-evolutionary arms-race) signaling**, which is the Darwinian zero-background of animal signaling and which is driven by manipulation by signalers *versus* assessment by reactors or, more generally, by conflicting or diverging interests between signaler and reactor. Signal morphology is designed to be manipulative, and the nature of the reactor's neuropsychological apparatus that has to be manipulated by the signal, i.e., the so-called 'receiver psychology', constitutes a powerful selection pressure on signal design. As Guilford & Dawkins (1991, p. 1; see also Miller & Bee 2012; Rowe 2013) wrote: "three aspects of receiver psychology (what a receiver finds easy to detect, easy to discriminate and easy to remember) constitute powerful selective forces in signal design". As persuasive power is central in a competitive setting, there is a prevalence of manipulative design over informative content, i.e., a prevalence of manipulation of the receiver's neuropsychology over the sharing of information with the receiver (cf. Dawkins & Krebs 1978; Krebs & Dawkins 1984; Rendall et al. 2009; Owren et al. 2010; Rendall & Owren 2013; Prum 2017; Ryan 2018). That is, instead of being 'dry' informational-referential signs, competition-driven manipulative signals rather exhibit 'striking' or 'moving' – such as attractive *vs*. repulsive, intoxicating *vs*. disgusting, arousing-seductive, frightening-intimidating, hypnotic, haunting, spellbinding, aesthetic – 'design' or 'morphology' characterized by complex spatial and often temporal patterns and colors, or acoustic volume, texture, duration, pitch, and hypnotic repetition/rhythm (Darwin 1871; Dawkins & Krebs 1978; Krebs & Dawkins 1984; Owren et al. 2010; Rendall & Owren 2013; Prum 2017; Ryan 2018). There is a vast literature in the field of *evolutionary or bio-aesthetics* that demonstrates that aesthetic signaling behavior has its evolutionary origins in manipulative – mainly courtship but also territorial, ritualized combat, and coalitional – animal signaling (Darwin 1871; Dawkins & Krebs 1978; Eibl-Eibesfeldt 1988; Voland & Grammer 2003; Welsch 2004; Hagen & Bryant 2003; Hagen & Hammerstein 2009; Endler 2012; Heinrich 2013; Mandoki 2014; Prum 2012, 2013, 2017; Ryan 2018; Westphal-Fitch & Fitch 2018; Nüsslein-Volhard 2019). That is, aesthetic design or morphology of physiological and behavioral signals

originated and evolved as a means to affect or manipulate the nervous system and behavior of reactors to the advantage of in the first place the signaler's fitness. In the next section, we argue that it is here that the evolutionary origins or, at least, a crucial evolutionary pillar of art should be situated, for example, in the form of (co-evolutionary arms-race) competition between manipulating signaler-artists *versus* assessing and increasingly sales-resistant reactor-audiences, as such driving or fueling the bio-cultural evolution of human art production.

- **Cooperative signaling**, which may arise from or within the Darwinian competitive zero-background, only in case of reduced conflicting interests and/or increased mutual benefits among signaler and reactor, as such allowing for the evolution of mutualism, kin altruism, or even reciprocal altruism. If there are strong common benefits, the signaler has to *invest less into manipulative or persuasive design, and more into efficient information transfer and transparency*, thus allowing for *an economic saving on elaborated 'de-signs' in favor of the evolution of more stripped-down informative 'signs'*. Some researchers (e.g., Seyfarth et al. 1980, 2010; Seyfarth & Cheney 2003, 2017; Watson et al. 2018) have argued that cooperative animal signaling may also involve referential meaning and/or semantic content, which is heavily contested by other theorists (Rendall et al. 2009; Owren et al. 2010; Rendall & Owren 2013) as this would require the background assumption of a 'common referential code' among signaler and reactor, something which can only evolve in a highly cooperative setting. In the next section, we will see that it is here that a crucial evolutionary pillar of human symbolical behavior and language can be found (cf. Seyfarth et al. 2005; Tomasello 2008; Scott-Phillips et al. 2012; Scott-Phillips 2015; Seyfarth & Cheney 2017).

3. An application of animal signaling theory to aesthetic behavior and art production

3.1 An operational animal signal-based definition of aesthetic behavior and art production: decreasing the gap between animal signals and human aesthetic-artistic behavior

Now that we have sketched the elementary basics of animal communication or signaling theory, we will further explore the latter's explanatory potential in the evolution of human aesthetic behavior and art production. We start by repeating the above 4-part definition of an animal signal:

1. A ***phenotypic*** physiological-morphological structure or behavioral pattern of a signaling organism
2. which evolved by natural selection to ***manipulate*** the behavior of a reactor to the signaler's and possibly but not necessarily the reactor's advantage
3. ***not*** through ***trivial*** direct physicochemical ***coercion or force*** on another organism's physiological constitution
4. but through a ***less strenuous/costly exploitation of an evolved response*** in the reactor (Maynard Smith & Harper 2003), i.e., a ***less strenuous/costly indirect (via the sense organs) manipulation and exploitation of the reactor's evolved nervous (sensation, arousal, emotion, motivation) system***, as such transforming an 'unwilling' reactor into a 'willing' (e.g., approaching, retreating, mating, cooperating) one (Dawkins & Krebs 1978).

In order to evolutionarily ground or situate human aesthetic behavior and art production within nonhuman animal signaling, we use the above definition to formulate a 'null-hypothetical' (i.e., methodologically putting aside human-specific neurocognitive and sociocultural complexities required for a fuller explanation of human artistry) animal signals-based definition of 'aesthetic behavior' and 'art production':

1. A ***phenotypic*** behavioral pattern and/or its extra-somatic ('extended-phenotypic' – Dawkins 1982, 2004) material deposits or products
2. which evolved by natural selection to ***manipulate*** the behavior of a reactor (an audience) to the signaler's (the artist's) and possibly but not necessarily the reactor's (the audience's) advantage
3. ***not*** through ***trivial*** direct physicochemical ***coercion or force*** (e.g., not through direct musclepower-, artefact- or weaponry-based violence or enforcement)
4. but through a ***less strenuous/costly exploitation of an evolved response*** in the reactor/audience (cf. Maynard Smith & Harper 2003), i.e., a ***less strenuous/costly indirect (via the sense organs) manipulation and exploitation of the reactor/audience's evolved neuropsychology and mind***, as such transforming an 'unwilling' reactor-audience into a 'willing' (e.g., mating, allying, cooperating, money-paying) one (cf. Dawkins & Krebs 1978).

According to this definition, human aesthetic behavior and art production are a complex form of manipulative animal signaling or 'mind-manipulation' which *evolved like any other animal signal to avoid and circumvent more strenuous-costly physical coercion, force or violence.* Again, this operational definition does not exclude the possible requirement of human-specific neurocognitive and sociocultural complexities for a more complete explanation of human artistry. Notwithstanding, to grant such a conceptual integration or grounding of human aesthetic behavior and art production within this definition, it is crucial to acknowledge *four empirical factors – two from the nonhuman animal side and two from the human side – that conceptually decrease or reduce the gap that is often assumed between animal signals on the one hand and human aesthetic behavior and art production on the other*.

A first gap-reducing nonhuman animal factor is that although most if not all manipulative animal signals lack symbolism, they are not confined to the raw physiological-sensory level of attraction (arousal, pleasure, seduction) *versus* repulsion (pain, disgust), but also operate at higher, *neuropsychologically more sophisticated* levels, exhibiting haunting, hypnotic, spellbinding, aesthetic, intimidating or frightening, and comforting, reassuring or confidence-inspiring (in coalition, social-bond and group-cohesion signaling) design or morphology (Darwin 1871; Dawkins & Krebs 1978; de Waal & Tyack 2003; Welsch 2004; Bradbury & Vehrencamp 2011; Whitehead & Rendell 2012; Prum 2012, 2013, 2017; Mandoki 2014; Yamagiwa & Karczmarski 2014; Cafazzo et al. 2018; Ryan 2018; Watson et al. 2018; Westphal-Fitch & Fitch 2018; Nüsslein-Volhard 2019). Animal signals are not limited to, for instance, attractive-intoxicating *vs.* repulsive-disgusting olfactory signals or scents. Visual signals, for example, may be characterized by complex spatial and often temporal patterns, colors, postures and gestures, and acoustic signals may be characterized by volume, texture, duration, pitch, and hypnotic repetition/rhythm.

A second gap-reducing factor from the nonhuman animal side is that nonhuman animal signals may involve extra-genetic behavioral and cultural variation or local tradition. Although animal signals, as morphological structures and instinctive behavioral patterns, are often assumed to be strictly genetically based adaptations, in case of behavioral patterns many neurocognitively-complex and socially-intelligent animal species also exhibit

- extra-genetic *cognitive-behavioral plasticity, variability and/or creativity*, which is most striking in *play behavior* in higher animals like birds and mammals (Bekoff & Byers 1998; Burghardt 2005; Bateson & Martin 2013; Kaufman & Kaufman 2015);
- extra-genetic *behavioral inheritance or transmission and niche construction* sustained by imitation and social learning and supporting nonhuman *animal cultures and traditions* (de Waal & Tyack 2003; Laland & Galef 2009; Whitehead & Rendell 2012; Ramsey 2013; Jablonka & Lamb 2014, Ch. 5; Yamagiwa & Karczmarski 2014; Aplin 2019).

Animal signals comprise physiological-morphological structures but also postural, gestural, and acoustic incl. vocal behavioral patterns. Some animals also engage in the manufacturing of extra-somatic or 'extended-phenotypic' structures or artefacts (Dawkins 1982; 2004). Most of these are ordinary – non-signaling – functional adaptations, such as a spider's web, a beehive, a bird's nest, a beaver dam, and tool use and manufacturing by corvids and primates. But a prominent example of extra-somatic or extended-phenotypic adaptive structures with a truly 'ritualized signaling' function are the 'aesthetically' decorated bowers built by male bowerbirds to seduce females. These courtship signaling devices also exhibit extra-genetically inheritable behavioral or 'cultural' variation or 'local traditions' in design (Madden et al. 2004; Madden 2008; Aplin 2019), e.g., sometimes including the 'painting' of the inner walls with regurgitated fruit residues (Hicks et al. 2013). Another typical example of cultural evolution and tradition in animal signaling are vocal cultures and song dialects built on *complex vocal learning*, i.e., the capacity to flexibly add novel vocalizations to the repertoire, as seen in several bird and mammal species, which contrasts, for example, to unlearned or quasi-purely genetically based and/or 'fixed' cricket and frog acoustic signaling (cf. Arriaga & Jarvis 2013; Verpooten 2019). Overall, variation in animal signals is usually attributed to genetic variation with, in addition, sometimes extra-genetically inheritable behavioral and cultural variation on it. The chimpanzee culture debate (Laland & Galef 2009), too, is illustrative in this context. The evolution of local cultural traditions was further developed in the hominin lineage by Paleolithic social groups or tribes, eventually resulting in more 'institutionalized', i.e., by tradition governed, symbolical systems of aesthetics.

A first gap-reducing factor from the human side is that evidence from the *cognitive and affective neurosciences* demonstrates that our aesthetic experience of morphological core aspects of art, like aroma, timbre, color, line,

rhythm, and tonal pitch interval, involves a direct engagement or manipulation of our biologically evolved nervous, sensory, affective, emotional and motivational systems (Aiken 1998; Voland & Grammer 2003; Panksepp 2009; Chatterjee 2014; Huston et al. 2015; Kapoula & Vernet 2016; Westphal-Fitch & Fitch 2018; Hodgson 2019). This has prompted Mithen (2006) to distinguish, for example, between "a natural biologically based musicality" and music as a socioculturally evolved phenomenon built upon that biological basis (cf. Morley 2013). A similar distinction could be made for the visual realm and other sensory modalities and, thus, for aesthetics and art in general (cf. Westphal-Fitch & Fitch 2018). Therefore, *although this research does not deny that a lot of art contains socioculturally evolved symbolical information, it does demonstrate that several aesthetic core aspects of art are in fact biologically based rather than socioculturally constructed*.

And a second gap-reducing factor from the human side is that insights from the field of *evolutionary or bio-aesthetics* demonstrate that human aesthetic behavior and its underlying neuropsychology exhibit homologous or at least analogous (in case of more distantly related species) commonalities with the functional neuro-architecture and (courtship, territorial, ritualized combat, coalitional) signaling behaviors of nonhuman animals (Darwin 1871; Dawkins & Krebs 1978; Eibl-Eibesfeldt 1988; Voland & Grammer 2003; Welsch 2004; Hagen & Bryant 2003; Hagen & Hammerstein 2009; Endler 2012; Heinrich 2013; Mandoki 2014; Prum 2012, 2013, 2017; Ryan 2018; Westphal-Fitch & Fitch 2018; Nüsslein-Volhard 2019). Homologues are similarities among different species due to common ancestry, such as the four limbs shared among tetrapods (including amphibians, reptiles and birds, and mammals). Analogues are similarities among different species, not due to common ancestry but due to similar ecological niches selecting for similar or analogous ways of functioning, such as the wings of birds and bats (which evolved independently but share a similar function of flying). All mammals incl. humans share neuropsychological homologues of basic affects and emotions such as pain, fear, rage or anger, joy and playfulness, and even a capacity for affective empathy (Panksepp 1998; Preston & de Waal 2002). Both homologous and analogous commonalities in aesthetic appreciation and preferences for colors, sounds, structural symmetry and regularity, and so on, can be found – especially in signaling behaviors – to varying degrees in various species from disparate taxa (such as insects, fishes, amphibians, reptiles, birds, and mammals). Also the abovementioned capacity of complex vocal learning seems to be either homologously or analogously spread among particular, more or less disparate bird (songbird, parrot, and hummingbird) and mammal (bat, elephant, cetacean, pinniped, and human but not nonhuman primate) species (Verpooten 2019).

Together, these four gap-reducing factors between nonhuman and human aesthetic signaling behaviors grant a basic, broad or general definition (such as the 4-part definition provided above) of aesthetic behavior and art production in terms of – broader than human or trans-human – animal communication or signaling. Although such a trans-human definition of aesthetic behavior and art production might fail to explain a number of human-specific neurocognitive and sociocultural complexities and peculiarities of art (cf. Dutton 2009; Davies 2012; Richards 2019), it is useful as an *operational definition* in that it may contribute or generate the following four evolutionary hypotheses on art:

- It provides the opportunity to view human art – just like manipulative animal signaling in general – serving several disparate adaptive functions, that is, functioning in disparate adaptive signaling contexts (of courtship, territorial, ritualized combat, coalition, and social-bond and group-cohesion signaling) (3.2).
- It may contribute to a better understanding of the basic evolutionary economics of art and how art works or functions, i.e., what art is (for) (3.3).
- It may contribute an argument for, and understanding of, why art is functionally adaptive rather than a non-functional byproduct (3.4).
- It may contribute to an understanding of why art is predominantly competitive-manipulative and – in contrast to language – only to a lesser extent cooperative-informative (3.5).

3.2 The multiple adaptive functions or signaling contexts of aesthetic behavior and art production

Although the evolutionary origins of art are speculative, there are plausible claims with some evidential basis about art as aesthetic signaling behavior in several functionally adaptive contexts, such as *courtship signaling* (e.g., Darwin 1871; Kohn & Mithen 1999; Miller 2000, 2001; Voland & Grammer 2003; Dutton 2009; Varella et al. 2011; Prum 2017; Ryan 2018), between-group/tribe/nation *territorial, ritualized combat, and coalition signaling* (e.g., Hagen & Bryant 2003; Hagen & Hammerstein 2009), and within-group *signaling for social bonding and group cohesion* (e.g., Dissanayake 1974, 1979, 2000; Coe 2003; De Smedt & De Cruz 2012). However, as their focus is each time on just one or two types of manipulative signaling behavior (courtship signaling, ritualized combat and coalitional signaling, signaling to foster social bonds and group cohesion), they fail to explain the

multifariousness of aesthetic behavior and art production as a whole. For example, many manipulative animal signals such as bird and whale singing and wolf howling serve not just one but several adaptive functions (like courtship, territorial, ritualized combat, coalition, and signaling to foster social bonds and group cohesion) (e.g., de Waal & Tyack 2003; Yamagiwa & Karczmarski 2014; Watson et al. 2018; Verpooten 2019). Likewise, human aesthetic behavior and art production, too, fail to be reduced to just one or two adaptive signaling functions (cf. Menninghaus 2019; Richards 2019). Therefore, although we do not endeavor to explain every aspect of human aesthetics and art, we yet aim to evolutionarily ground and situate human aesthetic behavior and art production within a more comprehensive and unifying framework of animal signaling in general, thus without reducing it to only one or two adaptive signaling functions. The above 4-part definition allows to clarify a palette of several functionally adaptive signaling contexts in which hominin and human aesthetic and artistic signaling could have evolved and still evolve:

- **Courtship signaling** evolved as a less strenuous-costly alternative to physical sexual coercion. Animal courtship signals evolved to manipulate or seduce reactors' evolved (neuro)physiological system and mind towards mating. Aesthetics proves to be crucial: the animal world is rich of aesthetically pleasing postural and gestural signaling behaviors or 'courtship dances' (e.g., by several birds like the paradise bird), acoustic calls and 'love songs' (e.g., male cricket chirping, birdsong), visual physiological, morphological and colorful structures (e.g., the male peacock's tail), and even the manufacturing of aesthetically elaborated constructions (by male bowerbirds) (Endler 2012; Kelley & Endler 2012; Hicks et al. 2013). Likewise, many human aesthetic and artistic behaviors, signals and/or products have been suggested to function this way. As in the rest of the animal world, such artistic courtship signaling may involve all sensory modalities: visual, acoustic/music, olfactory/perfumery, gustatory/gastronomy (e.g., cooking for your partner to get him/her into bed), and even tactile (e.g., the cultivation of smooth skin texture, leather clothes and body accessories) (cf. Darwin 1871; Kohn & Mithen 1999; Miller 2000, 2001; Voland & Grammer 2003; Duttton 2009; Allen et al. 2016). In accordance to the above 4-part definition of an animal signal, artistic courtship signaling is aimed at transforming an 'unwilling' reactor-audience into a 'willing' – mating – one, while avoiding or circumventing more costly physical sexual coercion or rape.
- **Signaling 'for a living' (e.g., begging behavior and signaling for food and/or survival resources)** evolved as a less strenuous-costly alternative to physical coercion, fight or violence. Many animal signals evolved to obtain nonsexual resources (food and other survival resources) through manipulation and exploitation of a reactor's evolved nervous system and mind towards offering or sacrificing a resource (e.g., begging cubs signaling to obtain food from their parents, the Venus flytrap signaling to attract and catch flies, etc.). This principle of 'signaling for a living' to obtain food and other survival resources also – admittedly almost trivially – applies to human artists: most artists (whether they work in the visual, musical, gastronomical, or perfumery realm) 'signal for a living' in that they – *by means of their aesthetic art products* – try to manipulate, exploit and/or 'please' the evolved biases in the nervous system and mind of reactor-audiences to make them 'willing to pay', i.e., willing to offer or sacrifice a survival resource which, in our present time, is almost always money. To the same 'signaling for a living' category belong begging street artists and musicians or buskers, as well as the ancient widespread cultural tradition of rambling or wandering musicians and artists signaling or working for food and shelter as a less costly/strenuous alternative to physical violence and robbery. That is, it was and – in case of more recent artists – still is their way to make a living, i.e., their 'evolutionarily stable (survival) strategy' or ESS. In accordance to the above 4-part definition of an animal signal, artistic signaling 'for a living' is aimed at transforming an 'unwilling' reactor-audience into a 'willing' – sacrificing or money-paying – one, while avoiding or circumventing more costly physical coercion or violence.
- **Territorial, ritualized combat, and coalition signaling** evolved as a less strenuous-costly alternative to physical coercion or combat/war. Most animal territorial, ritualized combat, and coalition signaling relies on *intimidation and proving one's value or fitness, i.e., displaying physiological strength but also cognitive intelligence, creativity and trustworthiness* through bird song, wolf howling, postural and gestural signaling, and so on. The same applies to many human artistry: many ancient and traditional forms of *human impressive and intimidating* singing and shouting, war dancing, drumming and military music, intimidating hairstyle and ornamentation on the body, on weaponry and on military outfits, impressive and intimidating statuary, painting and architecture, and so on, are all performed in the contexts of territorial, ritualized combat, and coalition signaling among *competing groups, tribes, citystates, or nations* displaying their fitness, i.e., their military, economical and intellectual power and strength (cf. Hagen & Bryant 2003; Hagen & Hammerstein 2009). Assessment signaling like ritualized

combat and coalition signaling was and still is also used among competing noble families and religious and profane institutions and companies, using mostly visual art (e.g., hiring artists) incl. monumental and/or richly decorated architecture to signal or advertise their fitness, i.e., their strength, wealth and prestige (cf. Neiman 1998; Verpooten & Joye 2014). In accordance to the above 4-part definition of an animal signal, artistic territorial, ritualized combat, and coalition signaling are aimed at transforming an 'unwilling' competing group, tribe, citystate or nation into a 'willing' – e.g., staying off the property, retreating, or allying – one, while avoiding or circumventing more costly physical coercion, violence, battle or war.

- **Within-group social-dominance and reputation signaling** (which is a kind of within-group ritualized combat signaling) evolved as a less strenuous-costly alternative to physical coercion or combat. Many social mammals like lions, wolves, elephants, and primates signal (through postural, gestural and acoustic signaling) to gain social dominance and reputation within their troop, herd, pride, pack or gang, for the ultimate benefit of gaining primary access to sexual mates, food and other survival resources (e.g., de Waal & Tyack 2003; Wittemyer et al. 2007; Mech & Cluff 2010; Cafazzo et al. 2018). Likewise, many human artists signal or work for *reputation, fame and 'stardom'* for the ultimate benefit to gain easy access to sexual partners and wealth (Miller 2000, 2001; Verpooten & Dewitte 2017). In accordance to the above 4-part definition of an animal signal, artistic social-dominance and reputation signaling is aimed at transforming an 'unwilling' reactor-audience into a 'willing' – subordinating, idolizing, following, mating, money-paying, etc. – one, while avoiding or circumventing more costly physical coercion, violence or combat.
- **Social-bond and group-cohesion signaling** evolved as a less strenuous-costly alternative to physical coercion or enforcement. Many signaling in social mammals evolved to foster social bonds and group cohesion, strength, robustness and identity. Examples are mammalian mother-infant intimate signaling (whispering, humming, singing), collective howling and ritualized social play in wolf packs, and dolphin and whale acoustics and ritualized social play (e.g., de Waal & Tyack 2003; Whitehead & Rendell 2012; Yamagiwa & Karczmarski 2014; Cafazzo et al. 2018; Watson et al. 2018). To this category of signaling to foster social bonding and group cohesion also belong many instances of human social play and rituals, dance, music, storytelling, poetry, religious art, etc. (cf. Dissanayake 1974, 1979, 2000; Coe 2003; De Smedt & De Cruz 2012). Even gastronomy, such as a 'ritualized meal' or dinner in group, in community or among friends, may function as a kind of coalitional gustatory signaling to foster social bonds (comradeship, friendship), group cohesion, and alliances like political or business deals. In accordance to the above 4-part definition of an animal signal, artistic social-bond and group-cohesion signaling are aimed at transforming an 'unwilling' reactor-audience into a 'willing' – thrusting, allying, cooperating – one, while avoiding or circumventing more costly physical coercion or enforcement.

Overall, just like many animal signals such as bird and whale singing and wolf howling may serve not just one but several adaptive functions (e.g., courtship, territorial, ritualized combat, coalitional, signaling to foster social bonds and group cohesion) (e.g., de Waal & Tyack 2003; Yamagiwa & Karczmarski 2014; Watson et al. 2018; Verpooten 2019), human aesthetic signaling and art production, too, has served and still serves many adaptive functions.

3.3 The basic evolutionary economics of aesthetic signaling behavior and art production: how art works or what art is (for)

The foregoing suggests that just like an animal signal, no human aesthetic-artistic signal is 'for free' – no artist signals or 'works for free'. Like all other cases of animal signaling, there is always a Darwinian fitness interest or benefit ultimately serving survival and reproduction involved. That is, the Darwinian background of competitive-manipulative signaling arguably always continued to constrain the way how human aesthetic behavior and art production functioned and evolved. Without reducing art to manipulative animal signaling, i.e., without excluding the possible addition of human-specific neurocognitive and sociocultural complexities to or upon the broader or more general foundation of manipulative animal signaling, the operational definition and situation of human artistry within this more basic framework thus contributes to our insight in 'how art works' or 'what art is (for)'. According to this definition, *aesthetic signaling behaviors and its art products are human-specific forms of manipulative animal signaling or design, evolved to avoid or circumvent more strenuous-costly direct physical coercion, force, violence, battle or war, through or by means of pushing a reactor's sensory buttons and/or manipulating his neuropsychology and behavior, always and primarily to the advantage of the signaler-artist's fitness, and often but not per se to that of the reactor-audience* (cf. Dawkins & Krebs 1978; Owren et al. 2010). Indeed, it does not seem excluded to us that deceptive or parasitic aesthetic signaling – thus signaler-artist

benefit *vs.* reactor-audience cost (cf. bluffing, the Venus flytrap, the cuckoo chick) – may sometimes also thrive in human aesthetic behavior and art production (e.g., gastronomically delicious but unhealthy or even poisonous food and drinks; magical voodoo art to intimidate or frighten thus *mislead* audiences).

In this context we have to return to Scott-Phillips' (2008) earlier-mentioned (at the end of section 2.1) requirement for an animal signal that the reactor's response should be *coadapted or coevolved* with the signal. Prum's (2013, p. 818) animal signal-based definition of art – "art consists of a form of communication that has coevolved with its evaluation" – is in line with Scott-Phillips' coadaptation criterion of a signal. Yet, although in both animal signals and art, coevolution and coadaptation between signaler-artist and reactor-audience are very often the case, we do not regard it as mandatory. As explained at the end of section 2.1, animal signals may evolve through exploitation of *pre-existing* – thus pre-evolved but not co-evolved and, as such, vulnerable to deception – biases in a reactor's neurophysiological system, i.e., biases and responses that evolved for some other purpose or for no purpose at all (in case of byproducts) but are now elicited and exploited and possibly deceived by a signaler (cf. Dawkins & Krebs 1978; Owren et al. 2010; Ryan 2018). Similarly, art (e.g., cheesecake, voodoo art, gardening art and landscape painting), too, may have evolved through exploitation of *pre-existing* – thus pre-evolved but not co-evolved and, as such, vulnerable to deception – aesthetic biases and preferences that evolved for some other purpose (e.g., respectively, for the functionally adaptive appreciation of nutritious food; for the functionally adaptive fear of dangerous spiders, snakes, carnivores, and the like; for the functionally adaptive appreciation of particular landscape features by our ancestors in search of suitable habitats) and that are now elicited and exploited (and deceived in case of truly health-undermining or poisonous food or truly misleading voodoo art) by signaler-artists to affect, move or manipulate (and possibly mislead or deceive) the evolved neuropsychology of reactor-audiences. This also brings us to the next section.

3.4 The average cost of art: an argument for art as functionally-adaptive signaling behavior rather than a non-functional byproduct

While an adaptationist approach in terms of animal signaling does not exclude a further addition of human-specific neurocognitive and sociocultural complexities for a fuller explanation of human artistry, it does seem to conflict with non-functional byproduct hypotheses on art. The main rationale behind the latter explanations or hypotheses is that they would be generally or 'ceteris paribus' *more parsimonious* than adaptationist ones and should therefore always deserve *first consideration* (Williams 1966; Gould & Lewontin 1979), which is why they are often invoked to explain the evolutionary origins of the arts (Pinker 1997; Patel 2008; Panksepp 2009; Verpooten & Nelissen 2010, 2012; Hodgson & Verpooten 2015). According to Pinker's (1997) 'psychological cheesecake' hypothesis, for instance, the neuropsychology involved in aesthetic experience (e.g., in the gustatory enjoying of cheesecake) predates human art (such as gastronomy) and evolved for non-artistic adaptive purposes (e.g., gustatory preferences for nutritious food). This rationale is also applied to other sensory modalities like the visual, acoustic (music) and olfactory (perfumery) arts, as such allowing for a conceptualization of the arts as non-functional byproducts exploiting or thriving on our pre-existing functionally-adaptively evolved neuropsychology (cf. Patel 2008; Panksepp 2009). According to Verpooten & Nelissen's (2010, 2012) 'sensory exploitation' hypothesis on the arts, the latter are non-functional byproducts that exploit and thrive on our pre-evolved "adaptive sensory biases" as well as "byproduct hidden preferences" that drive the gradual accumulation of cultural innovations (skills, knowledge) for making ever more enticing art. However, while it is true that byproduct explanations are in general more parsimonious than adaptationist ones, they can also only account for relatively 'parsimonious' or 'low-cost' morphological and behavioral structures. It has been argued before that art is too costly (in terms of energy, time, and material) to be a byproduct, instead requiring some fitness benefit 'in return' to flourish and be maintained (De Smedt & De Cruz 2012). More specifically, if our above-proposed hypothesis is correct, then human art – as an instance of animal signaling – falls within a *spectrum range of average cost*:

- on the one hand: animal signals incl. human art are *too costly* to have evolved and maintained as non-functional byproducts (i.e., without receiving compensating fitness benefits in return from the effects they have);
- on the other hand: animal signals incl. human art evolved by natural selection to avoid and circumvent *even more costly* direct physical-physiological coercion and violence (rape, fight, combat, war).

The appeal and contribution of byproduct (such as cheesecake and sensory exploitation) hypotheses sits in the deeper insights they provide on how art exploits and thrives on our pre-evolved neuropsychology, sensory biases and byproduct preferences. But this is exactly what animal signals (as adaptations primarily for the good of the

signaler) do: they exploit and thrive on a reactor's *evolved* nervous (sensation, arousal, emotion, motivation) system (see 4th specification in the above definition of animal signals), i.e., they exploit biases in a reactor's nervous system that in many cases were already present, either as a pre-existing adaptation for some other purpose or as a byproduct of such a pre-existing adaptation. For example, pre-existing aesthetic landscape preferences, once a functional adaptation of our ancestors in search of suitable habitats (Orians & Heerwagen 1992; Dutton 2009; Falk & Balling 2010), were later exploited in art (e.g., in gardening and in landscape painting) by signaler-artists to affect, move or manipulate the evolved neuropsychology of reactor-audiences. Think of the central role of *reactor/receiver psychology* in animal signal design (Guilford & Dawkins 1991 p. 1; Miller & Bee 2012; Rowe 2013): "three aspects of receiver psychology (what a receiver finds easy to detect, easy to discriminate and easy to remember) constitute powerful selective forces in signal design". The latter term 'signal design' could equally be replaced by 'aesthetic/art design'.

Thus, an animal signaling approach to aesthetic behavior and art dismisses the problematic, i.e., too parsimonious, aspect inherent to the byproduct hypothesis, offering instead an adaptationist alternative that accords to and even supports the byproduct hypothesis' correct insight on how aesthetic behavior and art thrive on (pre-)evolved features of the reactor's or audience's neuropsychological apparatus. Moreover, the argument or reason why art would not be a byproduct (i.e., due to its costs) is the same why animal signals are not byproducts, and this is itself also an argument why human art would be a subcategory of animal signaling.

3.5 Why aesthetic behavior and art production are functionally rooted in competitive-manipulative animal signaling and – unlike language – only to a lesser extent in cooperative-informative signaling

According to classical sociocultural anthropology, art thrives on socioculturally transmitted symbolical information or meaning, thus ultimately on language (Boas 1927; Lévi-Strauss 1966; Geertz 1973, 1976). This is also the default position in archaeology and evolutionary anthropology: in line with the sociocultural-anthropological approach, art is usually supposed to be part of the human symbolism/language cluster (Mithen 1996, 2005; Lewis-Williams 2003; Henshilwood & d'Errico 2011) which, in turn, belongs to and evolved from cooperative mammal and primate signaling in which (pre-symbolical) information transfer is central (Cheney & Seyfarth 2005; Seyfarth et al. 2005; Tomasello 2008; Scott-Phillips et al. 2012; Scott-Phillips 2015). However, there is the aforementioned evidence from the cognitive and affective neurosciences on our aesthetic experience of morphological core aspects of art, like aroma, timbre, color, line, rhythm, and tonal pitch interval, involving the engagement or manipulation of our biologically evolved nervous, sensory, affective, emotional and motivational systems (Aiken 1998; Voland & Grammer 2003; Panksepp 2009; Chatterjee 2014; Huston et al. 2015; Kapoula & Vernet 2016; Westphal-Fitch & Fitch 2018; Hodgson 2019). And second, there is also the aforementioned evidence in the field of evolutionary or bio-aesthetics on the functional evolutionary roots of aesthetic signaling behavior in *competitive-manipulative* – mainly courtship but also territorial, ritualized combat, and coalitional – animal signaling (Darwin 1871; Dawkins & Krebs 1978; Eibl-Eibesfeldt 1988; Voland & Grammer 2003; Welsch 2004; Hagen & Bryant 2003; Hagen & Hammerstein 2009; Endler 2012; Heinrich 2013; Mandoki 2014; Prum 2012, 2013, 2017; Ryan 2018; Westphal-Fitch & Fitch 2018; Nüsslein-Volhard 2019). As such, this seems to suggest that unlike human symbolism and language the aesthetic basis of art would not – or at least far less – be evolutionarily rooted in cooperative-informative animal signaling (i.e., animal signaling in which information transfer is central; cf. Seyfarth et al. 1980, 2005, 2010; Seyfarth & Cheney 2003, 2017; Scott-Phillips et al. 2012; Seyfarth & Cheney 2017) but rather in competitive-manipulative animal signaling (i.e., animal signaling in which the signaler's manipulation of a reactor's nervous system and behavioral response stands central; cf. Dawkins & Krebs 1978; Krebs & Dawkins 1984; Rendall et al. 2009; Owren et al. 2010; Rendall & Owren 2013; Prum 2012, 2017; Ryan 2018). This demands some deeper analysis.

As explained in section 2.3 on animal signaling theory, competitive (such as courtship, territorial or ritualized combat) animal signaling, although seldom entirely cue-free or information-free, holds a prevalence of manipulation over information transfer, whereas cooperative animal signaling (e.g., the bee waggle dance indicating the location of a food resource; three distinguishable alarm calls made by vervet monkeys to refer to the presence of three different predators), although never entirely manipulation-free, holds an increased amount of information transfer and informative transparency. The hypothesis that art would be evolutionarily rooted in rather competitive-manipulative animal signaling, and language in rather cooperative-informative animal signaling, may then explain the following eye-catching difference between art and language. Art, although seldom entirely non-informative or non-symbolical, holds a prevalence of aesthetics, i.e., of a *direct aesthetic manipulation of our neuropsychology*, over informational-semantic-symbolical transparency. And language, although arguably seldom entirely manipulation-free and/or aesthetics-free, i.e., often involving some kind of

aesthetic-manipulative feel or expression, holds an obvious prevalence of informative-semantic-symbolical transparency over aesthetic manipulation. That is, although language has been used from its very origins to manipulate and command other people (cf. plausible Paleolithic equivalents for shouts like 'look', 'stop', 'move' and so on) and possibly evolved from more aesthetic-manipulative gestural and vocal song-like signaling (cf. Darwin 1871; Mithen 2005), there is – when compared to aesthetic behavior and art – an undeniable focus on informative transparency, i.e., an undeniable *economic saving on elaborated 'de-signs' in favor of more stripped-down abstract-informative 'signs'*. Art, on the other hand, with its focus on a direct aesthetic manipulation of our neuropsychology (cf. most nonhuman animal signals), kept on investing rather heavily in aesthetic-manipulative design. Hence, these signaling aspects, i.e., the *relative prevalence* of direct aesthetic manipulation of our neuropsychology in art and of informative-semantic-symbolical transparency in language, or the relative prevalence of 'design' in art and of 'signs' in language, enable us to conceptualize art as distinct from language rather than to consider it as a kind of language as some theories of art do.

Notwithstanding, the preceding hypothesis thus takes into account that a lot of art is not solely characterized by basic manipulative-aesthetic design but also by a significant informational-symbolical meaningfulness. But unlike manipulative-aesthetic design, informational-symbolical meaningfulness does not have to be considered a basic or pre-conditional property of art, but rather something that is 'co-opted' in art in cooperative *sociocultural contexts or niches* (cf. Richards 2019): it allows to make art *socioculturally relevant* within a specific *sociocultural group or community* with a *common sociocultural history*. That is, socioculturally transmitted symbolical content is *spatiotemporally limited or confined* to particular sociocultural contexts or niches, which contrasts to the 'timeless' aesthetic core aspects of art (e.g., taste, aroma, timbre, color, line, rhythm, tonal pitch interval) which may *directly*, i.e., without the explicit requirement of symbolical interference, affect or manipulate our biologically evolved nervous system and neuropsychology (cf. Aiken 1998; Voland & Grammer 2003; Panksepp 2009; Chatterjee 2014; Huston et al. 2015; Kapoula & Vernet 2016; Westphal-Fitch & Fitch 2018; Hodgson 2019). The latter evolved on an evolutionary-biological, i.e., geological, timescale, which makes it 'timeless' compared to the relatively short-term spatiotemporality of socioculturally transmitted symbolical meaning or content. Overall, the preceding hypothesis predicts that increased complexity of sociocultural organization and history during human evolution would correspond or lead to an increased relative – but not absolute or essential – importance of the symbolic-semantic dimension in art.

Indeed, even art in highly cooperative and symbolized societies is presumably never purely cooperative and, as such, never purely informationally transparent and symbolically-semantically meaningful, i.e., always retaining a basic or elementary competitive-manipulative aesthetics. Recall (from section 2.3) that in most cases of cooperative animal signaling, competition, corruption and co-evolutionary arms-race dynamics among the two cooperating but ultimately competing camps – manipulating signalers *vs.* assessing reactors – always lurks in the background, even among kin and among sexual partners, as such driving or fueling the evolution of new signal variation and design (Trivers 1972, 1974; Krebs & Dawkins 1984; Dawkins & Guilford 1991; Maynard Smith & Harper 2003; Searcy & Nowicki 2005). In art and art history, too, co-evolutionary arms-race competition between manipulating signaler-artists *versus* assessing and increasingly sales-resistant reactor-audiences, as well as between competing artists themselves, always lurks in the background and, even more, drives or fuels the sociocultural evolution of art into ever new styles and idioms (cf. Verpooten & Dewitte 2017). Art thus refuses to fully trade in its 'defining' (according to the definition in section 3.1) competitive-manipulative-aesthetic design aspect for the full cooperative-informative transparency that characterizes language.

Pre-modernist art, whether hunter-gatherer art made by nomadic tribes, rural art made by agricultural societies, or urban 'high' art made by city and nation based societies, contain both aesthetic design and symbolical content which are highly constrained by overall sociocultural group institution or tradition. Although competition among individual artists is presumably as old as art itself, between-group (tribe, citystate, nation, diocese, guild, corporation, etc.) territorial, ritualized combat and coalition signaling as well as within-group (*ibidem*) social-bond and group-cohesion/identity signaling were highly developed (see also section 3.2). Artists during the Antiquity, Middle Ages, Renaissance and Baroque all worked on commission for competing citystates, nations, religious institutions, noble families, guilds, corporations, and so on. Aesthetics, of which the elementary foundations are biologically evolved (see supra), were institutionalized through sociocultural transmission and evolution into by tradition governed culture-specific symbolical and normative systems.

Following the demise of the Ancient Regime and the dawn of the Industrial Age and of secularity, *modernist art* was an explicit reaction against such institutionalized and/or 'academic', by tradition governed and culturally

inherited symbolical and normative systems of aesthetics, that is, a systematic rejection of and liberation from these symbolical and normative systems in favor of more pure, liberated or original forms of aesthetics (Arnason et al. 1998). Although academic art was still widely produced during the 19th century, Romanticism, roughly starting around 1770, was an early reaction against institutionalized academic style prescriptions, although still retaining strong commitment and support to nationalistic symbolical traditions (Palmer 2019). Modernist art started off in earnest from around 1850 onwards, with a series of relatively rapidly following movements, such as – in roughly chronological order – realism, impressionism and post-impressionism, symbolism and expressionism, cubism and futurism, Dadaism and surrealism, and abstract expressionism. Some focused on the external material world (of nature and society) such as realism, impressionism, post-impressionism, cubism, futurism and Dadaism, whereas others focused on the internal psychological world (of spirituality, feelings and emotions) such as symbolism, expressionism, surrealism, and abstract expressionism. While it is not the place here to delve deeper into the characteristics of these and other styles and movements, it should be mentioned that the transition from pre-modernist to modernist art marked a transition from strong between-group (tribe, citystate, nation, religious institution, noble family, etc.) arms-race competition towards increasing competition among 'individual' artists themselves as well as between manipulating signaler-artists *versus* assessing and increasingly sales-resistant reactor-audiences, driving or fueling the increasingly rapid sociocultural evolution of art into ever new aesthetic styles and idioms.

At the one hand, *postmodernist art* (roughly starting after 1950) presented a continuation of the modernist trend to reject and react against traditionally-institutionally governed symbolical systems of aesthetics (Arnason et al. 1998). At the other hand, it also presented a rejection of any modernist pretention to create an (non-academic, more pure or liberated) aesthetic-artistic idiom or discourse. It was a self-conscious questioning of the aesthetic and artistic practice and art world in itself. Although postmodernism as a whole did not endorse an anti-aesthetic stance *per se*, conceptual art did or, at least, aimed to do so. But what happens when art becomes purely 'conceptual', i.e., only presenting 'an idea'? Does it really lose entirely its competitive-manipulative-aesthetic design aspect? Does it really entirely 'put offside' our evolved neuropsychology containing all those basic aesthetic preferences? Early forerunners of conceptual art were Marcel Duchamp's *ready-mades*, the most famous being *Fountain* (1917), a porcelain urinal presented on its backside, signed "R. Mutt", and submitted to an art exhibition in New York. Another example was his *Trap (Trébuchet)* (1917), a wood and metal coatrack he submitted to a show at the Bourgeois Art Gallery and asked to be placed near the entryway. It went unnoticed as art during the event. However, as Duchamp himself has acknowledged, during the *act of choosing* a particular object to put at display as an artwork, aesthetic taste or preferences cannot be entirely put aside (Cabanne 1979). As such, ready-mades are still 'aesthetic-artistic creations' to some extent. Even more radical but much lesser known (because destroyed – which was the whole point), was Max Ernst's 'creation' and presentation of an art object with an axe attached to it, at a Dada exhibition or event in Cologne (1920), with the explicit invitation to destroy it (Waldman 1975). In a somewhat similar vein, but more than 30 years later, Robert Rauschenberg 'created' his *Erased de Kooning Drawing* (1953), an almost blank piece of paper in a simple gilded frame. And one year before, John Cage 'created' his *4'33"* (1952), a four minutes, thirty-three seconds 'composition' for any instrument or combination of instruments, with the score instructing performers not to play their instruments during the entire duration of the piece, the latter thus only consisting of the sounds of the environment that the listeners hear while it is 'performed'.

These and many 'artworks' that followed in the 1950s, '60s and '70s presented clever or captious tricks incl. the use of text (e.g., by the artists group *Art & Language*) to put offside aesthetic design and creative-performative skill as much as possible. That is, the artists aimed to present a purely conceptual and linguistic idea, devoid as much as possible of material aesthetic design. However, it can be argued that, in spite of an omission of material aesthetics, these artists' conceptual ideas – in their humor, cleverness, captiousness or trickiness – are still aesthetic. Narratives and even non-narrative texts can also be aesthetic, yet they do not exhibit material design but only immaterial or idealistic design. Moreover, cleverness, captiousness and trickiness are all signs or symptoms of *intelligence and creativity* and, as such, are also displayed in a 'ritualized manner' in more sophisticated forms of nonhuman animal signaling (e.g., birdsong, cetacean acoustics, bowerbird constructions) to attract mates (in courtship signaling), to intimidate competitors or opponents (in territorial and ritualized combat signaling), or to prove one's value and trustworthiness (in coalitional signaling). As such, co-evolutionary arms-race competition among competing conceptual artists as well as between increasingly sophisticated (clever, captious, tricky) signaler-artists *versus* assessing and increasingly sales-resistant reactor-audiences, remains fully in charge and, as such, does not represent a break with pre-conceptual, more traditional art, not even with competitive-manipulative animal signaling (cf. Verpooten & Dewitte 2017). That is, conceptual

artworks are – like so many, more sophisticated nonhuman animal (courtship, territorial, ritualized combat, coalition) signals – *ritualized displays of creativity and intelligence* used to manipulate (attract, impress, overawe, intimidate, prove one's value and trustworthiness to) potential mates, competitors, allies, or money-paying audiences.

4. Conclusion

A conceptual integration of human aesthetic behavior and art production within the broader-than-human or trans-human evolutionary framework of animal signaling theory, incl. an explicit animal signal-based definition of human aesthetic and artistic behavior and production, may contribute or generate at least four valuable or interesting hypotheses and insights:

1. Just like many animal signals such as bird and whale singing and wolf howling may serve not just one but several adaptive functions (like courtship, territorial, ritualized combat, coalition, social-bond and group-cohesion signaling) (e.g., de Waal & Tyack 2003; Yamagiwa & Karczmarski 2014; Watson et al. 2018; Verpooten 2019), human aesthetic behavior and art production, too, show a similar wide palette of adaptive functionality.
2. Situating aesthetic behavior and art production within animal signaling theory contributes to our understanding of 'how art works' or 'what art is (for)', viz., a human-specific form of manipulative animal signaling or design, evolved to avoid or circumvent more strenuous-costly direct physical coercion, force, battle or war, through or by means of pushing a reactor-audience's sensory buttons and/or manipulating its neuropsychology and behavior, always and primarily to the advantage of the signaler-artist's fitness and often but not *per se* to that of the reactor-audience (cf. Dawkins & Krebs 1978; Owren et al. 2010).
3. An adaptationist evolutionary framework based on animal signaling theory explains the costs and benefits of art better than byproduct hypotheses on the origins of art. Like animal signals, art falls within a *spectrum range of average cost*: on the one hand animal signals incl. human art are *too costly* to have evolved and maintained as non-functional byproducts, whereas on the other hand, animal signals incl. human art evolved by natural selection to avoid and circumvent *even more costly* direct physical-physiological coercion and violence.
4. Aesthetic behavior and art production are primarily functionally rooted in competitive-manipulative animal signaling and – unlike language – only to a lesser extent in cooperative-informative signaling.

Overall, without denying the role of human-specific neurocognitive and sociocultural complexities in art, the evolutionary background of competitive-manipulative animal signaling has arguably always continued to form the basis of human aesthetic behavior and art production and has arguably always continued to determine or, at least, constrain how art functioned and evolved. As such, while Richards (2019) proposes niche construction theory as a unifying framework on the sociocultural (symbolical, normative, spatiotemporally confined) 'superstructures' of art, we propose animal signaling theory as a unifying framework on the evolutionary-biological 'substructure' or 'groundwork' of aesthetic behavior and art production.

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Conflicts of Interest

None.

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