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What the face communicates: clearing the conceptual ground

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Facial displays such as smiles and angry expressions appear to promote and maintain cooperation, raising the possibility that they evolved in part for signaling functions. Research programs designed to test signaling functions for these facial displays (or any others) should be organized in light of two interlocking conceptual tasks. The first task is to consider whether the display is a genuine signal, or whether it might instead be a cue or a coercive display. The second task — assuming that the display really is a signal — is to consider the evolutionary route by which the signaling system has maintained its reliability over deep time. We conclude by encouraging researchers to consider the degree of mismatch between the experimental environment and the environments in which facial displays putatively evolved to operate as signals when designing experiments to test hypotheses regarding their signaling functions — particularly in cooperative contexts.

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Introduction

Throughout history, many thinkers have surmised that facial displays can reveal something useful or interesting about the person making the display [1]. There is intuitive appeal to the idea that facial displays exist *in order to* reveal the displayer's inner state [2], but evolutionary signaling theories insist that the function of a facial display — to the extent that it has a function at all — must be in the interests of both the individual making the display and the individual who can comprehend its meaning [3,4•,5]. The distinction is subtle, but as we will explain below, it is important.

Our broad goal here is to clarify some conceptual issues that researchers should consider when seeking to evaluate whether a given facial display evolved via a communicative (or *signaling*) function. Below, we focus specifically how smiles and angry expressions might have evolved to communicate information that promotes cooperation [6], but the conceptual material here is quite general and could guide work on the possible signaling functions of many traits in many different social contexts.

Properly considering whether a given display evolved due to a signaling function requires two preliminary conceptual steps (see Box). The first task is to evaluate whether the display is in fact a signal. The second task is to identify the evolutionary pathway that has preserved the signal's information over evolutionary time.

Is it a signal?

Drawing on Maynard Smith and Harper [7], Scott-Phillips [8] defined *signal* as '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' (p. 388). By definition, signals contain information that could enable receivers to reduce their uncertainty about states of the world [9]. However, a trait is not a signal simply because it contains information [8]: Receivers must also possess evolved computational systems that enable them to extract the information from the display and then respond adaptively to that information. Correspondingly, signalers must have evolved to display that information to its intended audience.

These criteria help researchers to differentiate signals from two other modes by which facial displays might influence the behavior of perceivers (see Box 1). First, in contrast to signals, *cues* contain information about the individuals who bear them that perceivers might put to use, even though the cue did not evolve to broadcast that information [8]. Although a toothy grin contains information that enables perceivers to determine whether the grinning individual brushed her teeth, there is no implication that grinning evolved to communicate information about oral hygiene. Even though cues and signals are distinct, cues can evolve into signals occasionally through a process called sensory manipulation, and, more readily, through a process called ritualization [7,10,11]. The physiological arrangements of facial muscles that are associated with certain physiological responses to adaptively relevant environmental events can evolve into signals via ritualization if receivers are better off for decoding the information the display contains and if cue-emitters

Box 1

What are we saying when we say that a display is a signal? Two critical questions.

Many evolutionary psychologists invoke signaling theory to explain the evolution of particular facial displays, but such assertions are onerous ones that come with a heavy evidentiary burden (Williams, 1964). Appeals to signaling theory can be made more rigorous by dividing the assertion into two questions that researchers should seek to address—both theoretically and empirically. First, there is the question of whether the trait is a signal. Second—assuming the trait is indeed a signal—there is the question of how the signal achieved its reliability over evolutionary time.

Question 1: Is The Trait a Signal, or Is It Some Other Type of Trait?

Trait Type	Definition
Signal	An act or structure that (i) affects the behaviour of other organisms; (ii) evolved because of those effects; and (iii) is effective because the response has evolved to be affected by the act or structure (Scott-Philips, 2008)
Cue	A feature of another individual that can be used by an animal as a guide to future action (Hasson, 1994)
Coercion	A form of exploitation in which displayer creates a sensory stimulus that changes the behavior of a stimulus-perceiver, consequently a fitness benefit for the displayer, but not for the perceiver.

Question 2: If It Is producing Signal, Through what Evolutionary Pathway Did It Achieve Its Reliability?

Pathway	Definition
Indexing	A signal whose intensity is causally related to the quality being signaled, and which cannot be faked (Maynard Smith and Harper, 1995)
Handicapping	A signal whose reliability is ensured because its cost is greater than required by efficacy requirements (Zahavi, 1975)
Receiver-dependent responses	A signal whose reliability is maintained due to costs (e.g. reputational) incurred by dishonest signalers
Common Interest	When a signaler and receiver agree upon the rank order of possible outcomes of an interaction. Here, signalers have no reason to be dishonest and receivers have no reason to distrust.

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are consequently better off because of receivers' evolved responses to that information.

Signaling also differs from *coercion*, which involves agents' exploitation of a signal-decoding system within receivers that evolved to make use of other kinds of information [12•,13]. When anglerfish dangle their lures in front of prey, for instance, they are coercing their prey by exploiting their evolved responses to worm-like visual stimuli rather than signaling to them. In light of these differences, researchers interested in testing hypotheses about facial displays of emotion based on evolutionary signaling theory need to concern themselves from the outset with explaining how signalers enjoyed better fitness than non-signalers, and how signal-decoders enjoyed better fitness than non-decoders as the signaling system was evolving [10].

If a given display is a signal, how did it achieve its reliability?

Above, we alluded to the fact that signals cannot evolve to provide beneficial information to receivers at a net cost to signallers. Both parties must benefit on average [3]. Otherwise, signal recipients will evolve to ignore them, and signal users will consequently evolve to stop using them [12•]. Thus, if a particular facial display is claimed to

constitute a signal, the second conceptual task is to determine which of four known evolutionary processes might have guaranteed the signaling system's informativeness by garnering net benefits for both signalers and receivers over deep time [14•].

Reliability via indexing. A frequently invoked explanation for the honesty of emotional signals is that physiological or anatomical constraints make them impossible to fake. Signals with this property are called *indices* [7] or *assessment signals* [15]. Often, indices are built upon non-signaling design features, which reduces the costs of evolving the signaling system. For instance, aggressive animal displays in which a signaler brandishes a weapon (e.g., a claw or an antler) could be an index because the size of the brandished weapon is causally related to the weapon's formidability [16,17]. As others have noted [3,12•,18], most human facial displays probably do not obtain their evolutionary stability by indexing. Unlike the important strategic information encoded by the size of a weapon, the physical characteristics of the neural and motor systems that produce smiles and snarls are unlikely to be of strategic interest to others. Note, however, that there might be exceptions to this rule of thumb. For example, individual differences in humans' tooth sizes or facial bone structure might be particularly well-revealed by angry facial displays. If so — and if those individual differences also cause individual differences in fighting ability (or, are caused by physiological influences that *also* cause individual differences in fighting ability) — then such expressions could turn out to be indices after all.

Reliability via handicap. Explanations for the reliability of emotion displays based on costs come in two varieties. First, if a signal is a *handicap* [19,20], traditional theory leads us to expect that high-quality individuals will pay greater costs to produce the signal than will low-quality individuals, but will also receive greater net fitness benefits from producing the signal. Arguing against the notion that it is costs per se that maintain the reliability of handicaps, recent amendments to theory suggest that high–quality individuals produce greater displays because they reap greater marginal benefits for incremental investment in signal production [23,24]. As a result, high-quality individuals are more than repaid for their large investments in signaling [21–24]. Similarly, signals of need — for example, infants' cries (and associated visual displays) associated with hunger — can be productively analyzed as handicaps whose costs and benefits cause the hungriest infants to get the most food, thereby promoting the inclusive fitness of both offspring and parents [22]. Although handicap-based theorizing certainly has its place in theorizing about facial displays, we remain somewhat dubious of recent proposals to conceptualize as smiles as quality-based handicaps that honestly signal willingness to cooperate (via the fitness costs that honest signalers pay in terms of visual acuity [25]) because we remain unconvinced that there are actual fitness costs to be paid by smile-induced reductions in visual acuity.

Reliability via receiver-dependent responses. We do think that there is a form of cost-based reliability that is potentially relevant to facial displays — particularly in social interactions that are characterized by strong conflicts of interest. So-called *conventional signals* [26,27] typically obtain their stability via the costs they impose on dishonest signalers. Suppose an angry facial display, when directed toward a cooperation partner, contains the information, 'I expect you to increase the rate at which you provide benefits to me' [28]. Such a display should cause recipients to proceed to assess its veridicality on the basis of its consistency with other available information about the signal and the signaling context (e.g., the sender's physical formidability and social status, existing allegiances, ability to exclude the signal recipient from vital resources, or the ability to enforce ultimatums in bargaining [29•,30]). If the signal recipient's subsequent assessments of the signaler reveal that the angry display was genuine, then the receiver benefits by acceding to the signaler's implied demands for more cooperation and thereby avoiding more costly sanctions [31,32]. Likewise, the signaler benefits both by the receivers' accelerated benefit delivery and by having avoided an aggressive encounter (fights typically have fitness costs even for victors [33]).

But what if the signal recipient's subsequent assessments reveal that the signaler was bluffing (i.e., he or she appears upon further assessment to lack the qualities and social position that would enable him or her to behave consistently with signal's implication)? Under such circumstances, the signal receiver could increase his or her fitness by refusing the signaler's implied demands, perhaps even imposing retaliatory costs upon the signaler instead. These retaliatory costs can come in the form of direct aggression [34], or, in a highly social species such as humans, via reputational damage or ostracism directed against the dishonest signaler that plays out within the larger group, or via exclusion from partner choice in the future by the recipient (also called individually directed skepticism; [27]). Thus, the dishonest signaler loses fitness (i.e., he or she would have been better off by not signaling) and the fitness of the receiver either is unchanged or increases via enhanced status or new resources obtained from the signaler [35].

Reliability via common interests. When signalers and receivers' fitness interests diverge, the evolutionary history of the signaling system should resemble an arms race in which signalers appear to be seeking to innovate the means to deceive signal receivers (thus turning their signals into uninformative 'cheap talk') and signal receivers seek to acquire the capacity to 'mind-read' the inner

states of signaler [36]. However, when signalers and receivers agree upon the rank order of the possible outcomes of an interaction, signalers have no incentive to be dishonest and receivers have no incentive to distrust the signal (provided the signal is consistent with other information that might be obtained from the signaler and the signaling context). The regular use of smiles when sharing resources [37–39] or making decisions about whether to trust others [40], and people's tendency to cooperate more with people who are smiling than with people who are not smiling [38,41,42], suggest that the reliability of smiles (at least in cooperative contexts) might be maintained via common interests. Because both parties are better off by obtaining the good than by not obtaining it, and because collaboration is essential to obtain the good, there is no incentive to cheat [43]. The two parties must collaborate, and the smile might therefore signal a willingness and readiness to do so. Indeed, the real information contained in the smile in such instances might be that the signaler has recognized the mutually beneficial nature of the upcoming opportunity and therefore intends not to act stupidly (i.e., in an impulsively selfish way that would leave both the signaler and the receiver worse off).

Although the reliability of smiles in such contexts could be guaranteed exclusively via common interests, it is conceivable that the dishonesty of smiles is also mitigated over evolutionary time through receiver-dependent costs [44]. The dishonest smiler might gain the benefits associated with the short-term exploitation of a duped smile-recipient, but in choosing to exploit a social partner he or she also loses the benefits of establishing a friend or long-term collaborator, which could have a higher lifetime fitness value in a social world in which partner choice is an active element of the adaptive social landscape [35]. The dishonest smiler might also incur the costs associated with any direct or indirect retaliation on the duped smile-recipient's part (as might be the case with anger [32], but cf. [44]).

Summary

With this conceptual material in hand, we hope researchers will be better equipped to plan programs of research to evaluate the possible signaling functions of facial displays (and, by extension, vocal or postural displays) — not only in cooperative contexts, but others as well. In designing such experiments, we would encourage researchers to consider the potential mismatches between the lab and the world — and not only the modern world, but also the ancestral world in which our adaptations evolved.

In cooperation research, for instance, researchers often study interactions between anonymous strangers for whom the scope for action (e.g., defect or cooperate) and the shadow of the future are extremely limited. Rating one's reactions to photos of strangers' facial displays and choosing how much of a monetary endowment to send to a recipient in a dictator game, for instance, are surely quite removed from the natural ecology in which humans evolved to respond to information that facial displays might ordinarily contain. To be sure, such constraints often improve experimental rigor, but they can also make the laboratory setting quite unlike both the current and the ancestral worlds [45]. This is particularly problematic because many emotional displays (e.g., smiles) are supremely sensitive to social context [46•]. If the critical contextual features that ordinarily elicit facial displays in the real world (be it modern or ancestral) are absent from the experimental setting, the external validity of the conclusions drawn about the signaling value of the display might be compromised in important ways. We do not have an easy solution to the dilemma of optimizing the tradeoff between experimental rigor and conceptual proximity to the sorts of phenomena to which researchers would want their theories to apply, but we do think the field will be better off for pondering the dilemma.

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Conflict of interest statement

None declared.

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