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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