An evolutionary approach to emotional communication

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Abstract

The study of pragmatics is typically concerned with ostensive communication (especially through language), in which we not only provide evidence for our intended speaker meaning, but also make manifest our intention to do so. This is not, however, the only way in which humans communicate. We also communicate in many non-ostensive ways, and these expressions often interplay with and complement ostensive communication. For example, fear, embarrassment, surprise and other emotions are often expressed with linguistic expressions, which they complement through changes in prosodic cues, facial and bodily muscular configuration, pupil dilatation and skin colouration, among others. However, some basic but important questions about non-ostensive communication, in particular those concerned with evolutionary stability, are unaddressed. Our objective is to address, albeit tentatively, this issue, focusing our discussion on one particular class of non-ostensive communication: emotional expressions. We argue that existing solutions to the problem of stability of emotional communication are problematic and we suggest introducing a new class of mechanisms—mechanisms of *emotional vigilance*—that, we think, more adequately accounts for the stability of emotional communication.
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1. Introduction

Communication is ostensive if, when we communicate, we not only provide evidence for our intended speaker meaning, but we also make manifest our intention to do so (Grice, 1989; Sperber and Wilson, 1995). Much human communication is ostensive—but we also communicate in many non-ostensive ways, such as body language and various expressions of emotion. Often, ostensive and non-ostensive behaviours complement one another. For example, fear, embarrassment, surprise, and other emotions are often expressed ostensively—with, say, linguistic expressions. At the same time, they are also expressed in non-ostensive ways with, among others, changes in prosodic cues (Frick, 1985), facial (Ekman, 1993) and bodily muscular configuration (James, 1932), pupil dilatation (Bradley et al., 2008) and skin colouration (Shearn et al., 1990). These ostensive and non-ostensive expressions are typically expected to be consistent with one another: we do not verbally express fear but at the same time produce the facial expressions associated with

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happiness, or vice versa. If such contradictions occur, observers have to reject one or the other observation as an unreliable guide to the focal individual's state of mind.

Although pragmatics is typically concerned with ostensive communication, non-ostensive behaviour also plays an important role in communication, and it often interacts with ostensive communication in non-trivial ways (e.g., in conversational contexts, see Proust, 2008). However this is not sufficiently reflected in the literature. Many fundamental questions about the role of non-ostensive behaviour in communication are unaddressed. In this paper, we specifically consider the *evolution* of non-ostensive communication. From an evolutionary perspective, a central question for any communication system is "what prevents dishonesty?". Although there is a substantial literature devoted to the evolution of the abilities that allow humans to produce and understand language (e.g., Pinker and Bloom, 1990; Bickerton, 1992; Jackendoff, 2003), the problem of honesty has not figured greatly in those discussions (but see Dessalles, 2007; Scott-Phillips, 2008a; Sperber et al., 2010). The 'honesty' of non-ostensive communication is even less studied, at least from an evolutionary perspective.

In this paper, our agenda is principally diagnostic: we wish to highlight the evolution of non-ostensive communication as a topic worthy of future research and suggest tentative answers intended to spur future research. Moreover, our discussion of non-ostensive communication will be focused on one particular type of non-ostensive communication: emotional signals. Note that we are specifically concerned with the involuntary use of emotional signals. Emotional expressions can also be used voluntarily, and this opens up an interesting current area of pragmatic research (see e.g., Wharton, 2009).

There are three reasons for our focus on emotional expressions.[1] First, as discussed above, they are frequently displayed alongside ostensive signals, which they complement and interact with (Proust, 2008). Second, the functioning of emotional expressions has been the focus of much previous research (e.g., Fridlund, 1994; Ekman, 2003a), and so our discussion can be informed by a wealth of previous work. Third, there have been tentative answers to the issue of the honesty of emotional communication (e.g., Mortillaro et al., 2012; Mehu et al., 2012; Owren and Bachorowski, 2001; Hauser, 1997; Ekman, 2003b) but none are wholly satisfactory, for reasons we shall document.

The paper is structured as follows: in the next section (section 2) we introduce a broad evolutionary framework, including definitions of key terms, providing the scaffolding for subsequent discussion; in section 3 we ask whether emotional expressions can be seen as communicative at all; in sections 4 and 5 we discuss the risks of deception in emotional communication, and how they can be avoided; in these sections, we also discuss and reject conventional hypotheses that have been proposed to account for the stability of emotional communication, and introduce a new class of mechanisms which, we think, may allow for the stability of emotional communication—mechanisms of emotional vigilance; in section 6, we discuss the question of why non-ostensive communication persists in humans; finally, in section 7, we discuss the question of interplay between the so-called emotional vigilance mechanisms, and those of epistemic vigilance that have previously been introduced by Sperber et al. (2010).

2. Communication and its evolution

We define communication in the following way: *communication* occurs when an action (a signal) produced by an individual organism causes a change (a reaction) in another organism, where both the signal and the reaction have been designed for these purposes (Scott-Phillips, 2008b; Table 1). If the action has been designed for these purposes, but the reaction has not, then the interaction is *coercive*; and if the reaction has been designed for these purposes but the action has not, then the interaction is a *cue*. The overall situation is summarised in Table 1.

Fig. 1 gives an everyday example of all three types of interaction. The example of signalling/communication in the figure is ostensive, but the definition applies equally well to non-ostensive communication. Indeed, this framework is a generalised version of one developed in evolutionary biology (Maynard-Smith and Harper, 2003; Scott-Phillips, 2008b), which is concerned with the communication systems of a wide variety of different species, almost all of which do not involve ostension. There are other approaches to defining communication (e.g., Hauser, 1997; Reboul, 2007; see Scott-Phillips, 2008b for a review). We adopt the definition that we do for two reasons. First, it is the only approach that works across a range of prima facie cases, in the sense that they correspond to our intuitions about what is and is not a signal/cue/coercive behaviour (Scott-Phillips, 2008b). Second, the clear functional distinction that it makes between cues and signals is particularly important for questions concerning the evolution and stability of communication systems.

From an evolutionary perspective, the classic question in the study of communication is stability (Maynard-Smith and Harper, 2003; Searcy and Nowicki, 2007). Signallers should presumably evolve to send signals leading to responses that are in their best interests. Yet, these interests may conflict with the receivers' best interests. If such is the case, receivers should in turn evolve not to attend to the signal, and this would then lead the system to collapse. The same logic can also

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[1] *Expressions* and *signals* are used as synonyms.

Table 1
Definitions of signal/response, cue and coercion (Y = yes; N = no). See main text for discussion.

	Function of action to cause reaction?	Function of reaction to be caused by action?
Signal/response	Y	Y
Cue	N	Y
Coercion	Y	N

Adapted from Scott-Phillips (2008a).

Fig. 1. Everyday examples of the distinction between signal/response, cue and coercion. (from Scott-Phillips and Kirby, 2013): this image depicts a young man (in the centre) pushing his colleague from her chair. This act involves three kinds of interaction with the audience: the first interaction involves the young man and the colleague he is pushing. This interaction is an example of *coercion*. The second interaction, involving the young man and the colleague he is laughing with, is a case of *communication*: the act of pushing is a signal whose purpose is to affect the female colleague who is witnessing: her smile is the response. Finally, in the third interaction – between the young man and his boss [this latter being at the left side of the image] –, the pushing is a *cue*: it informs the boss about the behaviour of his employee, even though this was not its function. Note that the example of signalling behaviour in this figure is ostensive but the definition also applies to non-ostensive communicative behaviours, as we will argue throughout the paper.

apply over individual lifetimes: if an individual's communication is regularly unreliable (for example, because she is dishonest), then others will learn not to pay too much attention, if any, to what the focal individual has to say. This is exactly the outcome described in Aesop's fable of the Boy That Cried Wolf.

The evolution and stability of communication thus presents a strategic problem: what prevents widespread deception, and the consequent collapse of the system? (Note that we are using 'deception' in functional terms. There is deception when one organism exploits another's organism sensitivity to certain signals to its own benefits. As such, and as long as it has to do with non-ostensive communication,[2] deception does not entail volition or consciousness from the sender.) Whatever the answers to these questions are in any particular case, the consequence of these strategic concerns is that stable communication systems should be beneficial for both parties (Scott-Phillips, 2010b). If they were not then one party would stop emitting or attending to the signal.

It is important to recognise that this is a problem for all evolved communication systems, and not just those where signal production is voluntary, or intentional. This is because it is a problem at the ultimate, rather than proximate, level of analysis. Ultimate explanations are concerned with why a behaviour exists; proximate explanations with how it works (see Scott-Phillips et al., 2011 for extensive discussion). The dynamic of natural selection leads to organisms whose behaviour is designed to maximise their inclusive fitness (Grafen, 2006), and ultimate explanations of behaviour explain how a particular behaviour contributes to that. For example, if lying is explained in terms of how it will lead to beneficial outcomes for the speaker, then that is an ultimate explanation if the beneficial outcomes eventually lead to positive fitness consequences, on average. If, on the other hand, lying is explained in terms of psychological motivations, then this is a proximate explanation: this sort of explanation is concerned with how the benefits are achieved, i.e., how behaviour operates. Both ultimate and proximate explanations are complementary and required for a proper understanding of behaviour (Mayr, 1963; Tinbergen, 1963; Scott-Phillips et al., 2011).

In the case of emotional communication, solutions to the problem of honesty and stability of emotional communication have often confused the proximal and ultimate level of explanation by suggesting that emotional expressions are honest

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[2] While deception in the context of non-ostensive communication does not presuppose any conscious intention to manipulate the receiver, it is not true of ostensive communication where senders often consciously intend to fool receivers (Maillat and Oswald, 2009).

because they are involuntary, being mandatorily associated with a corresponding emotional experience (e.g., the Duchenne smile[3] in Owren and Bachorowski, 2001). The issue is that a proximal mechanism (the involuntariness of emotional displays) is offered to answer an ultimate question (about the honesty of emotional communication). We detail below the more specific issues with this answer. Moreover, neglecting the ultimate/proximal distinction can also lead to other misunderstandings, such as equating signals defined at the ultimate level, as we have done, with signals that result from intentional, voluntary, and strategic decision-making (which are all proximate level phenomena).

With this in mind, we now turn to the question of what keeps human communication stable. For ostensive communication, this question receives relatively commonsensical answers. The ultimate reason it is stable is that the benefits to dishonesty are outweighed by the social costs of ostracism that will follow if one is perceived as a liar or an otherwise unreliable communicator (Lachmann et al., 2001; Scott-Phillips, 2010a) (this is indeed what happens to the boy in Aesop's fable). From a proximate perspective, a suite of cognitive mechanisms allows humans to be vigilant towards communicated information: we filter the information we receive via communication so that we are not unduly misled. These mechanisms have recently been termed *epistemic vigilance* (Sperber et al., 2010). However with regard to non-ostensive communication, and expressions of emotion in particular, the situation is less immediately clear. We will address this issue in section 4. However before we are able to do that, we must address an important preliminary question, about exactly what we mean by emotional displays, and whether they qualify as signals at all.

3. Are emotional expressions genuine signals?

Our goal is to apply the logic of the evolution of communication to emotional expressions. A first and necessary step must be to establish that emotional expressions are indeed signals, following the definition offered above. Although it intuitively seems as if the function[4] of at least some emotional expressions is communicative—to let others know we need them when distress is expressed, for example—this assumption will not always be justified. Behaviours often inform others only incidentally (i.e., they are cues). Indeed, Darwin (1872) suggested that this is exactly what emotions are. For example, the widening of the eyes created by fear could allow the individual to enlarge her visual field and be better prepared to react to potential threats (Susskind et al., 2008). The question is whether these pre-existing behaviours underwent later selection *because of any informative function they might have*.

How can we show this? A signal entails specific adaptations *for the signal* in both senders and receivers. The sender must do more than merely coerce the receivers and the receivers must do more than merely respond to a cue. Unfortunately, it is extremely difficult to provide conclusive arguments for either of these claims. Instead, two weaker types of evidence are usually provided in support of the claim that emotional expressions are genuine signals.

The first argument is simply that some traits of emotional expressions are difficult to account for without recourse to their role in communication. This is quite commonsensical in the case of sadness and joy for instance. Other cases are more ambiguous. As suggested above the expression of fear could have adaptive effects as action preparation (Susskind et al., 2008; Vermeulen and Mermillod, 2010). Similarly, the facial features of disgust can have direct adaptive consequences, such as narrowing the eyes to prevent exposure to potentially toxic substances (Susskind et al., 2008). Yet it has been argued that these potential benefits are slight and unable to account for the whole expression. For instance, Susskind et al. (2008) have shown that the functional importance of sensory acquisition in fearful expressions is limited to the upper visual field. For the individual producing the display, the benefits in terms of sensory acquisition enhancement might then be relatively small compared to the costs involved in making the display highly discriminable. If this is the case, it would be more likely that fearful expressions would have ultimately been selected for a signalling purpose by virtue of their high discriminability. More generally, the difficulty in accounting for the configuration of emotional displays in terms of efficient action preparation suggests that action preparation might not be their function (Fridlund, 1994).

It does not follow from this first argument that emotional expressions are adaptive as signals; they could still be mere accidents. If emotional expressions are signals, they should be designed as such. In particular, they should be sensitive to the social context. It makes little sense to emit a signal if there is no one to receive it. More complex social modulations could also be expected: hiding distress from an enemy, concealing envy from a friend, etc. At a very broad level, Dobson has shown that, among non-human primates, facial mobility (namely, the set of facial movements a species can produce) is predicted by group size (Dobson, 2009). This result suggests that the evolution of facial mobility on the whole serves social functions. Other evidence from non-human animals indicates that the expression of fear is socially modulated (Sherman, 1977; Alcock, 1984; Chapman et al., 1990). In humans, it has been shown that the social context modulates

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[3] Duchenne smiles are considered as genuine smiles (Ekman et al., 1990), smiles that are associated with the experience of joy, and which differ from faked or 'polite' smiles that do not involve the activation of the palpebral part of the *orbicularis oculi*.
[4] Our use of the concept of function reflects that of *proper function*, following Millikan (1989).

the expression of pain and distress (Badali, 2008) and sadness (Zeman and Garber, 1996). Similarly, smiling has been shown to be very heavily socially modulated (Fridlund, 1994). For instance Kraut and Johnston (1979), observed the smiling behaviour of people in various social settings, and concluded that smiling was so strongly associated with social motivation that its link with an internal experience of positive feelings was tenuous.

The evidence that emotional expressions are socially modulated is very suggestive that they are indeed signals. However, prima facie, it is also compatible with the hypothesis that they are but a form of coercion. If emotional expressions have evolved to influence the behaviour of other individuals, they should be also expected to be socially modulated. For instance, observers may have started to respond to some purely accidental features of distress as cues that help was required. It would then have been beneficial to exaggerate distress cues in order to influence observers more easily, and the behaviour would have become merely coercive. If it was in the observers' best interest to specifically attend to these new, exaggerated behaviours, they could evolve specific mechanisms to do so. Thus to complete the demonstration that emotional expressions are signals, it would therefore be necessary to show that observers are not merely responding to cues. We know of no strong empirical evidence supporting this claim. However, in many cases the usefulness of the original cue, whatever that may have been, is limited. It would be extremely surprising if the mechanisms designed to detect and react to the emotional expression were still only targeting that cue. To take an example, the raising of the lips triggered by anger cannot be a reliable cue that we are about to be bitten. Clearly, the detection of the cue has evolved beyond its original function.

The arguments exposed here may fall short of a strong demonstration that emotional expressions are genuine signals. Yet we consider them to be sufficiently suggestive to at least shift the burden of proof to those who would claim that emotional expressions have no signalling function. It is now possible to turn to the challenges raised by emotional expressions due to their communicative character.

4. The risks of emotional signals and how to ward them off

Like all communication, emotional signals can be dangerous. In particular, receivers run the risk of being deceived by senders. An individual who would always submit to anger displays or help in response to signals of sadness would be easily abused. In section 2, we distinguished between proximate and ultimate answers to this question, and emphasised that both are needed for a proper understanding of a trait. As we will shortly discuss, previous psychological research on emotional displays has suggested and described a range of proximate mechanisms that may be involved. However the *ultimate* question of how these mechanisms maintain the stability of emotional communication has received less attention. More precisely, as detailed below, previous explanations are problematic as they are based on the dubious assumption that there is an unfakeable relationship between emotional display and emotional experience.

Evolutionary theory suggests three broad classes of ways in which communication systems can be kept evolutionarily stable at the ultimate level (Davies et al., 2011; Maynard-Smith and Harper, 2003): (i) individuals may share a common interest, such that there is no incentive to lie; (ii) there may be a causal, unfakeable relationship between signal form and signal meaning (an index); or (iii) there may be costs associated with the signal. These costs may in turn be either handicaps, where the costs are associated with the production of the signal itself, and are paid by honest signallers as a guarantee of honesty (Zahavi, 1975; Grafen, 1990; Godfray, 1991); or they may be deterrents, where the costs are associated with the consequences of the signal, and are hence paid by dishonest signallers (Lachmann et al., 2001). The question is: which of these most likely describes emotional communication?

The most common answer has been to rely on explanation (ii), stressing the fact that producing dishonest emotional signals can be very difficult (see Owren and Bachorowski, 2001, 2003; Hauser, 1997 for crying). At a proximal level of explanation, Ekman and his colleagues have tried to demonstrate that some emotional signals—such as the famous Duchenne smile—are practically impossible to voluntarily fake (Ekman et al., 1980). The logic behind this argument is that the honesty of emotional signals is guaranteed by the lack of voluntary control. Someone who would want to fake genuine joy, for instance, would simply be unable to do so. As a result, at the proximal level, receivers would be certain at least that when an emotion is expressed, it is genuine. By contrast, Ekman allows for the possibility that the suppression of (some) emotional signals can be learned in the form of 'display rules' (Ekman et al., 1969). Ekman may be right that the main danger faced by receivers is not the voluntary inhibition but the voluntary production of emotional signals. Still, even if we assume that he is right and emotional expressions are, most of the time, involuntarily produced, his answer is unsatisfying for at least three reasons.

The first reason is that this explanation lies at the proximal level of analysis and says little or nothing about the ultimate one. The problem of honesty occurs regardless of what the proximate mechanism is; that is precisely why it is the defining problem of animal signalling theory, where the vast majority of signals, if not all of them, are 'involuntary' (see Maynard-Smith and Harper, 2003).

The second reason that makes accounts relying on lack of voluntary control unconvincing is that they are not evolutionary plausible. As pointed out by Frank (1988) and Fridlund (1994), if the voluntary control of emotional signals

had brought fitness benefits, it would have evolved. Indeed, there appears to be no essential physiological constraint that would have prevented natural selection from selecting the ability to voluntarily produce emotional displays. The voluntary use of emotional displays is evolutionary plausible as it involves structures that already exist (neural and motor pathways for one's voluntary control over most of facial muscles (Rinn, 1984)). In fact, the ''involuntariness'' argument rests upon one single example, that only concerns facial expression and neglect other muscular events that play a crucial role in emotional attribution (such as bodily movements, see: De Gelder, 2006; Grèzes et al., 2007): the mention of the *orbicularis oculi*, a muscle that is involved in blinking and in the production of so-called Duchenne smiles, and whose palpebral part is considered to be impossible to activate voluntarily. Yet, this is one of the few examples of muscles that cannot be activated voluntarily and that play a substantial role in emotional communication. Moreover, as Ekman (2003b) acknowledges, the characteristics that may allow observers to distinguish between faked and spontaneous emotional expressions are subtle (i.e., morphology, symmetry, duration, speed of onset, apex overlap, ballistic trajectory and overall cohesion of the display given the context) and one has to carefully pay attention to them in order to detect liars. In fact, it is still to be shown that the non-credibility of a display, investigated in laboratory settings (e.g., Mehu et al., 2012) where participants are urged to pay a lot of attention to the emotional displays, can reliably and rapidly be detected in more ecological contexts. Together, these elements cast serious doubts on the idea that the difficulty to control emotional displays can be part of the explanation for the honesty of emotional communication.

The third (and probably the more serious) problem is that voluntarily faked emotional signals are not always the main threat to receivers. Take anger as an example. Let's assume that the function of anger expressions is to signal a readiness to inflict costs to another individual if that individual fails to submit in some way. If the response to anger displays were automatic submission, a receiver would clearly be at risk of senders voluntarily expressing anger to make them submit for no good reason. But the receiver would also be at risk if senders were actually angry, but not in a position to follow up on their threat. Just as evolution could have led to the development of voluntary control of emotions, evolution could have led to the development of 'fake' emotions. For instance, senders could become genuinely angry even when they are not really willing to engage in a potentially costly confrontation. The emotion, including its cognitive, physiological and expressive correlates would be exactly similar to anger, except that if the receiver failed to submit, the sender would not assault her.

We may note another implausibility in Ekman's account, one that relates to the costs potentially incurred by senders instead of receivers. As noted by Fridlund ''any reasonable account of signalling must recognise that signals do not evolve to provide information detrimental to the signaller.'' (1994, p. 132). For instance, if expressing distress in some circumstances could regularly hurt a sender's interests—by making enemies aware of one's weaknesses, say—then the expression of distress could not be automatic, it would have to be modulated, whether it is by voluntary control or not. We mentioned above that Ekman allows for the learning of display rules to inhibit the expression of emotions. Yet this is more likely to be a cultural innovation than the built-in mechanism we should expect.

Besides the explanation based on the involuntariness of emotional displays, another type of explanation can be found in the literature. It suggests that certain emotional signals are handicaps, and are, as a consequence, honest. Such an explanation has for instance been offered for tears (Hasson, 2009; Hauser, 1997) that are indeed difficult to produce spontaneously. Because they considerably handicap perception and are not easily fakeable, tears honestly signal one's distress. Such explanation face the same problem as above: evolution could have favoured the deliberate use of tears whenever it is in the interest of the signaller.

The alternative explanation we suggest is that receivers are endowed with a suite of mechanisms designed to modulate their responses to emotional signals. These mechanisms might be termed *emotional vigilance*, in order to emphasise that the functional role they play is equivalent to the role played by mechanisms for *epistemic vigilance* (see section 2) in ostensive communication. However, it should be emphasised that we do not mean to suggest that the mechanisms involved in the two processes are similar, nor even that defence against misleading emotional signals necessarily requires high level cognitive abilities. Our only objective with this term is to draw attention to the *functional* equivalence of the two sets of mechanisms.

Mechanisms of emotional vigilance are confronted with a complex task. Figuring out when it is beneficial to respond to any given emotional signal requires integrating numerous variables such as the type of signal, its intensity, its source, as well as many features of the specific context in which it is emitted (e.g., Barrett et al., 2007; Barrett and Kensinger, 2010). A child's extreme anger display when she is told that she cannot have a second serving of ice cream should not elicit submission; a raised eyebrow by a mafia Don may.

A complete analysis of the mechanisms of emotional vigilance would therefore require a lengthy emotion by emotion analysis, which is not within the scope of this article. Indeed, one of the strengths of an explanation based on mechanisms of emotional vigilance is that it does not rely on one or a few very specific examples, such as the Duchenne smile or tears. Instead, it can readily extend its logic to all emotional signals, even if we should expect different heuristics to be at play for different emotions.

Two general dimensions of vigilance, likely to be observed for all emotions to varying degrees, are delineated. In the case of epistemic vigilance, it has proven useful to distinguish between issues of competence and issues of benevolence

(e.g., Mascaro and Sperber, 2009; see also Sperber et al., 2010). An ostensive message can be misleading either because of the deceitful intent of the sender or because she is merely mistaken. In both cases caution should be exerted about the message. The same distinction can be applied to emotional vigilance, as a first step towards more specific characterizations.

In the case of epistemic vigilance competence can be seen as a relatively objective measure: did the sender form false beliefs by mistake? But it is far from clear what it means—if it even means anything—for an emotional state to be true. As a result, issues of competence have to be treated differently for epistemic and emotional vigilance. The closest equivalent of the notion of an incompetent sender would be an individual who expresses emotional signals that bear no adaptive relationship whatsoever to the context. The emotional expressions of an individual whose emotional systems would be highly dysfunctional should not be trusted. Such cases, however, should be relatively rare: severely emotionally impaired individuals face a steep evolutionary challenge. Moreover, if the disorder is consistent, it should be relatively easy to flag these individuals as being unreliable and either not pay attention to their emotional signals or at least not react to them in the typical way.

Other competence concerns that would have likely been more frequent stem from asymmetries between the incentives of the sender and the receiver. For instance, someone with a strong allergic reaction to bee stings should not be deemed incompetent for expressing a strong fear in the presence of a bee. This fear signal should not be discounted as it provides important information regarding the behaviour of that individual and the appropriate course of action to be taken. Yet it should not produce in observers what is usually thought of as being the automatic reaction to fear, which is fear. The asymmetry in competence does not need to be permanent or long lasting, as in the case of the allergy. For instance, someone can be confronted with a dominant individual whose anger she knows to be based on a mistaken belief. Even if the receiver would otherwise be inclined to submit, it may be worth in this case trying to correct the dominant's beliefs first.

The second broad issue that mechanisms of emotional vigilance have to deal with is the benevolence of senders. In rare occurrences the interests of senders and receivers are perfectly aligned, but in the vast majority of cases there will be some discrepancy. Some very general metrics can be useful to judge the level of interest alignment. Someone's interests are more likely to align with her in-group than her out-group, with a friend than a stranger, with a brother than a third cousin, etc. Yet even the interests of very close individuals can diverge. When a child expresses pain, there is usually little conflict of interest with her parents. When she expresses anger for not receiving the latest toys, the interests are much more poorly aligned. Similarly, couples often have an incentive to misrepresent their emotions to each other. The converse is also true: the interests of strangers can converge. If we find ourselves stranded on a boat that requires two people for rowing, our interests can become very much aligned with those of a perfect stranger from a group we may otherwise not deem trustworthy. Even if general metrics—in-group vs. out-group and the like—can be useful, they must be supplemented by an assessment of each situation's specificities.

A crucial difference between competence and benevolence issues is in their evolutionary dynamic. In the case of competence, there is no selection pressure to deceive receivers. The individual who is allergic to bee stings is not better off if others also experience fear. By contrast, a stranger who gets angry with us would benefit if we were automatically submissive. As a result, the latter individual has an incentive to deceive us, for instance with anger displays that exaggerate the actual threat. There can therefore be an arms race between senders and receivers, with senders trying to pass through the receivers' vigilance and receivers evolving more complex mechanisms of emotional vigilance. Such an arms race would not arise in issues of competence. Moreover, the costs incurred by the wrong response to an emotional signal are likely to be higher when the issue is one of benevolence rather than competence. A deceitful sender might purposefully try to inflict the maximum cost upon a receiver—by making her experience an emotion at the worst possible moment—which is not the case for incompetent signals. It is thus reasonable to assume that issues of benevolence rather than competence were the main driver behind the evolution of emotional vigilance.

5. Evidence of mechanisms of emotional vigilance

While it is not possible here to make precise predictions regarding the working of mechanisms of emotional vigilance, we can make some more general suggestions. At the most general level, reactions to emotional signals are very unlikely to be automatic, or reflex-like. Instead, they should be heavily modulated by the social context. The competence and benevolence of the source in each particular context should play a role in the response to emotional signals. If the competence or benevolence of the source is dubious, the reaction should be either dimmed or adapted to the specific circumstances.

Unfortunately, there is a dearth of relevant evidence. Importantly, the relative paucity of empirical evidence should not be taken as evidence that there is no or little contextual modulation. Simply, the issue has not received the attention it deserves. Instead, research has focused on showing that some reactions to emotional signals are automatic (as in cases of primitive emotional contagion, see Hatfield et al., 1994). Such research would seem to be in direct contradiction with the present predictions. Yet this contradiction is more apparent than real. Most studies on automaticity in this area bear on very quick and subtle reactions such as slight facial movements (e.g., Dimberg et al., 2002) or variations in skin

conductance (e.g., Esteves et al., 1994). Our predictions do not bear mainly on such reactions, but on potentially more costly behaviour. The danger stemming from an automatic reaction to a fear signal, for instance, is unlikely to come from a micro-contraction of some facial muscles. For these reactions to be evolutionarily relevant, they would have to have a substantial impact on behaviour. Another problem with most studies of automaticity is that the relevant contextual modulations are not introduced. Participants have no reason to question the competence or benevolence of the people depicted in the stimuli, so that claims of automaticity cannot be thoroughly tested.

It may be worth saying a quick word about the supposed cases of emotional contagion that involve seemingly costly behaviour such as the "laughter epidemics" (e.g., Ebrahim, 1968). If a whole school can start laughing uncontrollably because emotions spread from student to student, it seems as if the automaticity of emotional responses trumps emotional vigilance. Such a conclusion would be hasty, for three reasons. First, emotion epidemics are exceedingly rare—that is what makes them so startling. Evidently, a laughter epidemic is not started every time someone laughs. Second, this type of epidemic only spreads within a closely knit group. In terms of benevolence, these are among the people one should trust the most. Third, it is possible that expressing these emotions may in fact serve the individuals' interests at that particular time. Laughter epidemics can get students out of school for a few days. Other emotion epidemics have given factory workers a break (see Evans and Bartholomew, 2009). In some contexts, and for some people, emotional vigilance may therefore have no reason to break the spread of these epidemics. Far from undermining the idea of emotional vigilance, the characteristics of emotion epidemics are in fact better explained by postulating mechanisms of emotional vigilance than an automatic response to emotional signals (Mercier, 2013).

Some studies have directly tackled the question of the contextual modulation of reactions to emotional signals. Most of them bear on issues of benevolence while only a few results shed light on the treatment of competence. For instance, Zeifman and Brown (2011) have shown that tears are more efficient at conveying sadness when they are shed by adults than by children or infants. A possible interpretation is that infants and children are much more likely than adults to cry in situations that would not qualify as sadness, such as anger (for children) or hunger (for infants). In a way, they are treated as less competent. To the extent that this result would carry to parents' reactions to their children vs. adult strangers, it would offer a nice contrasting case with benevolence. In the vast majority of cases, a parent's interests are more in line with those of her child than that of a stranger. Yet, because children have emotional reactions that differ from those of adults, reactions to their emotional signals can be more heavily modulated. More generally, it is important to see caregivers as active in their interaction with crying infants (see Owings and Zeifman, 2004).

Another interesting piece of evidence comes from Hepach et al. (2012) who have shown that children, as early as 3 years old, modulate empathetic response towards others according to the appropriateness of their distress (where the target could have been genuinely harmed, could be over-reacting or could signal distress for no reason at all). This result is especially relevant as it shows that, from very early on, reactions to emotional expressions are not automatic but rather heavily modulated by contextual cues.

As argued above, competence is not the main issue that receivers have to deal with. Senders whose interests do not align with receivers generally pose a more critical threat. Determining whose interests align with hers is, for the receiver, an arduous task. Many types of cues are likely to be taken into account in order to yield an appropriate assessment. Some of these cues can cover large, fixed categories. Out-group members are less likely to have interests aligned with those of a receiver than her in-groups. It is thus not surprising that people show different responses to emotions expressed by members of these two categories. For instance, "*positive* responses to fear expressions and *negative* responses to joy expressions were observed in outgroup perceivers, relative to ingroup perceivers." (Weisbuch and Ambady, 2008:1; see also Xu et al., 2009; Gutsell and Inzlicht, 2010; Mondillon et al., 2007; Nugier et al., 2009). Other general markers can be used to modulate one's emotional responses. Attitude towards the sender modulates the receiver's response, such that when that attitude is negative, the receiver's facial mimicry can weaken or even become incongruent with the emotion expressed by the sender (Likowski et al., 2008). Similarity between the sender and the receiver is another important moderator of the response to emotional signals (Heider, 1982; Feshbach and Roe, 1968; Sullins, 1991; Epstude and Mussweiler, 2009).

Beyond these traits of the receivers, momentary features of the situation are also taken into account. When an individual who would otherwise be trusted—the experimenter—behaved extremely rudely towards the participants, they seemed to rejoice in his misery rather than empathize with it (Bramel et al., 1968). Similarly, Lanzetta and Englis (1989) told participants that they would be either cooperating or competing in a game. While those set to cooperate showed empathetic responses to displays of pleasure and distress, those set to compete showed either no reaction or displayed "counterempathy" (p. 534).

6. Why do we still have emotional signals?

So far we have considered "pure" emotional signals, as they are expressed for instance in facial expressions. Yet most emotional signals are in fact mixed with other types of communication—ostensive communication, mostly. The emotional

tone helps disambiguate "I'm scared" (that I won't find a job) from "I'm scared!" (someone is breaking into my house). Moreover, some of these emotional tones are likely to be universal (Scherer et al., 2001; Bryant and Barrett, 2008; Sauter et al., 2010). The linguistic context also plays an important role in disambiguating emotional signals (Barrett et al., 2007). These elements point to the co-evolution of emotional signals and ostensive communication in humans; for instance, if emotional signals are adapted to transmit information with the tone of voice used in spoken communication, they probably co-evolved with language.[5]

This essential interplay between ostensive and non-ostensive signals becomes very clear when one considers conversational situations. As suggested by Proust (2008), non-ostensive signals may play an important role in transmitting information about one's own uncertainty in conversational contexts: senders can communicative hesitation about the information they are conveying (e.g., by rolling one's eyes); recipients can signal their level of understanding (e.g., frowning when something that has been said is unclear). Yet it might not always be advantageous to provide a recipient with sensitive data such as one's doubts, or as Proust put it, "evaluations of [one's own] incompetence"; conversely, it might be advantageous for the recipient to communicate false information about one's own uncertainty. Both strategies may threaten the stability of communication and the use of meta-cognitive gestures. Proust's solution to this puzzle is to argue that the use of meta-cognitive gestures is highly flexible (by selectively restricting others' access to one's own meta-cognitive states), and that meta-cognitive gestures are used in situations where cooperation is a priori guaranteed. We think that such solution itself presupposes the combined use of epistemic and emotional vigilance mechanisms that continuously track, over the course of the conversation, possible divergence of interests between signalers and receivers, and regulate the use of meta-cognitive gestures accordingly. We therefore see Proust's proposal as also suggesting that such mechanisms are needed to explain the stability of emotional communication.

Given the continued importance of emotional signals in human communication, we feel entitled to ask a question that may seem whimsical: why do we still have emotional signals? Ostensive communication clearly has a far greater expressive potential. In conversational contexts, senders may well signal their uncertainty using appropriate words; conversely, recipients may signal their lack of understanding using adequate expressions. Yet, non-ostensive signals continue to play an important role in maintaining conversation. Why is it the case? The answer, we surmise, rests at least in part on the argument we have developed in the previous sections: the mechanisms of vigilance that help stabilise emotional signals also explain their continued relevance.

Intuitively, it may seem as if emotional signals still exist simply because they express some things better than, or at least differently from, ostensive communication. For instance, when someone tells you, in the course of a face-to-face discussion "I'm scared" with a relatively neutral tone, you don't infer that she is currently experiencing a high level of fear—maybe she's worried about her job prospects. It would be hard to convey the level of fear experienced in, say, a home invasion without using at least the fear tone, and probably the facial expression too: it seems that only emotional signals can adequately communicate some emotional states. This, however, may be an artefact of our habits. Imagine that you are chatting with a friend on an instant messaging service. You know she is alone in her house. Interrupting the conversation, she writes to you that she's hearing someone breaking in, and then "I'm scared." We suspect that you would have no trouble inferring her emotional state, just as if she had said it with the right tone and facial expression in a face-to-face discussion. The reason that a toneless "I'm scared" in face-to-face discussion is not effective at communicating fear is that the fear tone is expected; in its absence, we interpret the utterance differently.

Still, one could argue that a lot of context is necessary to disambiguate "I'm scared" in the absence of emotional signals. Emotional signals could therefore be necessary when the context is unclear and there is no time to make it explicit. Again, we suspect this is not a hard limitation of ostensive communication. It is difficult to imagine why a word or an expression with the primary meaning "I am experiencing a high level of fear" (and effective in conveying high levels of arousal) could not have appeared, had it been necessary. One last edge that emotional signals seem to have over ostensive communication is their speed: a simple facial expression can be sufficient to communicate fear. Maybe even a monosyllabic expression would have to take a few more milliseconds to be processed, giving indeed a small edge to emotional signals. Yet this would hardly be critical for most emotional signals such as joy or even anger. And even when speed is of the essence—in the case of fear maybe—the increased expressivity of ostensive communication would probably compensate for the slowdown.[6]

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[5] Note that this scenario is not incompatible with scenarios linking emotional communication to paralinguistic systems of communication (e.g., Deacon, 1997) that presuppose independent evolution between those systems of communication and those of linguistic communication. Yet, given their constant interplay in human communication (e.g., in conversational contexts; see Proust, 2008), it is most likely that linguistic and paralinguistic systems of communication have co-evolved more recently.

[6] Note that the arguments against emotional signals being preserved thanks to their communicative properties carries to Fridlund's hypothesis that they serve to convey social motives rather than reveal internal emotional states (Fridlund, 1994).

While it is still possible that the question of the continued relevance of emotional signals could be found in their communicative power, it is worthwhile to consider other potential explanations. One such explanation is that the mechanisms that help insure the stability of emotional signals are very specific and could not easily be replaced by those used to insure the stability of ostensive communication. In particular, the evaluation of ostensive communication relies to some extent on what can be called "coherence checking" (see Mercier, 2012). Coherence checking consists in pitting communicated information against background beliefs. If inconsistencies are detected, they make it less likely that the communicated information is accepted. The efficacy of coherence checking depends on the relative ease of access to knowledge in the relevant domain. If John tells Sarah something about someone she does not know at all, her coherence checking mechanisms will not have much to work with. Emotional states are likely to create such asymmetries in access to information: observers have less access to an individual's emotional states than the individual herself. This is also true of the social motives—willingness to aggress, etc.—that emotional signals may communicate (Fridlund, 1994). As a result, coherence checking is not a very practical way to evaluate emotional signals.

Given that we cannot easily rely on coherence checking to evaluate them, how do emotional signals manage to remain stable? A possibility is that emotional signals are indices. Their stability would be guaranteed by the unfakeability of the signals: emotional signals would simply be too costly to fake, making them intrinsically honest. While it is difficult to discount this hypothesis, as we pointed out earlier, the specific mechanisms that make emotional signals so hard to fake have remained elusive. The other possibility is that emotional signals remain stable because senders are deterred from sending too many dishonest signals. For deterrence to be possible, receivers must have some way of reacting appropriately to emotional signals. If their reactions were fully automatic, not modulated by source or context, all senders would be equally successful, precluding the possibility of deterrence. Following the arguments and evidence reviewed in sections 4 and 5, we argue that humans are endowed with mechanisms that allow them to appropriately react to emotional signals. These mechanisms make deterrence possible and contribute to the stability of emotional signals.

Whether emotional signals remain stable because they are indices or because dishonest signals are deterred, specialised mechanisms tailored to emotional signals are required. As a result, we surmise that they are in part responsible for the continued relevance of emotional signals.

7. The interplay between epistemic vigilance and emotional vigilance mechanisms

Sperber et al. (2010) have hypothesised that mechanisms of epistemic vigilance have evolved to protect people from deleterious communicated information. One possibility is that the term applies to all the mechanisms allowing humans to perform this function, whether the signals are ostensive or not, emotional or not, etc. In this case, emotional vigilance would be a special case of epistemic vigilance. Another possibility is that epistemic vigilance mostly refers to ostensive communication, in which case emotional vigilance could be seen as a companion set of mechanisms. In any case, this is a purely semantic point.

The more substantial issue is the following: can there be specialised heuristics to ward-off deception in non-ostensive (and, more specifically, emotional) vs. ostensive communication? If yes, then using the term 'emotional vigilance' to refer to the mechanisms that instantiate these heuristics seems warranted. While the issue is ultimately an empirical one, a strong a priori argument can be offered that such specialised heuristics exist, as so many parameters differ between non-ostensive, emotional communication and ostensive communication, from their phylogenetic history, to the format in which they are encoded, or the cues on which they are based. Moreover, it is even likely that there are heuristics that only apply to the signals associated with one emotion. While we do not deny that there might be heuristics that are valid for emotional and ostensive communication, they are likely to interact with more specific ones. Generally, the massively modularist point of view tacitly adopted by Sperber et al. (2010), supports the existence of distinct mechanisms of emotional vigilance.

8. Conclusion

Our goal in this paper has been to apply the logic of the evolution of communication to emotional expressions. If emotional expressions are genuine communicative signals, we need to explain what keeps them stable. In other words: what prevents senders from manipulating receivers, and how do receivers stay safe?

While there might exist a consensual explanation for what keeps ostensive communication stable (namely, that dishonesty is not a payoff strategy given the social costs of ostracism), it was not clear what could be the explanation for guaranteeing the stability of non-ostensive communication. This state of affairs, we think, is due to the popularity of Ekman's view among emotion psychologists: being involuntary, emotional expressions are honest and therefore safe for receivers to accept. As we have pointed out, this is a proximal account and does not explain why we would not have evolved the capacity to fake emotional signals. What we need is therefore an explanation at the ultimate level.

At an ultimate level, communication can either be kept stable (i) if senders and receivers share a common interest, (ii) if signals cannot be faked, or if (iii) signals induce costs. In the case of emotional communication, (i) and (ii) are unlikely. In

this paper, we have shown that the most likely option lies in the third kind of explanations: being equipped with mechanisms of *emotional vigilance*, receivers would be able to evaluate the signals they receive and to punish dishonest signallers who would provide them with false information. These mechanisms would act as deterrents: dishonest signaller would run a risk, at least that of losing their ability to influence receivers in the future. This, we believe, would have led to the stability of emotional communication.

This position can also have important implications at the proximal level: a broad range of phenomena in social psychology (e.g., emotional contagion, empathy) are often described as being automatic responses to some stimuli. What our position predicts, by contrast, is that receivers' reactions are heavily modulated by their source: being emotionally vigilant, receivers will selectively react to emotional signals. More empirical work will be needed to better understand mechanisms of emotional vigilance.

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