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Scratching Beneath the Surface: Intentionality in Great Ape Signal production

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Abstract:

Despite important similarities having been found between human and animal communication systems, surprisingly little research effort has focussed on whether the cognitive mechanisms underpinning these behaviours are also similar. In particular, it is highly debated whether signal production is the result of reflexive processes, or can be characterised as intentional. Here, we critically evaluate the criteria that are used to identify signals produced with different degrees of intentionality, and discuss recent attempts to apply these criteria to the vocal, gestural, and multimodal communicative signals of great apes and more distantly related species. Finally, we outline the necessary research tools, such as physiologically validated measures of arousal, and empirical evidence that we believe would propel this debate forward and help unravel the evolutionary origins of human intentional communication.

Keywords: Intentional communication, signal production, vocalisations, gestures, language evolution

Introduction

The evolution of language remains one of the biggest unsolved puzzles in human origins. The complexity of human language far exceeds the complexity seen in the communication systems of any other extant primate species. However, we don't know nearly enough about the cognitive underpinnings of non-human communication to determine what changed in our early hominin ancestors. Because behaviour does not fossilise, it is imperative to look to the behaviour of other species and take a comparative approach in the study of language evolution. In recent decades, a growing focus on communication in non-human great apes, monkeys, and more distantly related species has started to reveal a variety of shared abilities.

The study of animal behaviour has a long history of considering non-human species as "automatons", machines that take input from their surroundings and automatically produce an output. Sensory input enters the black box, and behaviour comes out. For many research purposes that is an entirely adequate approach, but in comparative psychology the question should be "what is happening inside the black box?" (1). In order to understand the evolution of language, researchers must ask questions about the cognitive abilities involved in other species' communication. This is a real challenge, and hence many animal communication studies focus on describing the signals and signal sequences that are produced on a purely behavioural level. One danger of this approach is that behaviour in non-humans and humans can appear similar, but if the surface similarity in behaviour is underpinned by very different cognitive processes, then they may not tell us much about how human language evolved (2). We need to start to scratch beneath the surface and ask questions about the cognition that underpins signal production. One of the first questions that arises when we start to look deeper is whether signals are produced intentionally in non-humans.

Human language is intentional – we do not produce sentences as automatic responses to stimuli, rather we intend to alter the behaviour or mental state of other individuals (3,4). Intentionality is a difficult concept to define and operationalise, and researchers studying gestural, vocal, and facial signals have tackled this challenge in different ways. So we start this review paper by offering some definitions of intentional signal production and outlining the criteria that are most commonly used to identify intentional communication in other species. We then give an overview of evidence for intentional communication in non-human primates and other more distantly related species. Next, we critique current approaches to assessing intentional communication discussing (i) the inconsistency in the application of intentionality criteria; and (ii) the validity of the criteria themselves. Finally we suggest future directions for research, including the need for physiologically validated behavioural measures for arousal, and the potential benefits of refocussing attention back on experimental assessments of second-order intentionality.

Traditionally, researchers across different species and different communication systems have tended to tackle similar problems from different angles. We aim to bring together approaches from research on vocalisations, gestures, and facial expressions, across a number of species, and propose ways forward for the study of intentionality in non-human communication.

Defining intentional communication

To begin with, we have the problem of defining intentional communication in a way that can be operationalised and tested in non-verbal species. Varying definitions of intentional signal production have hindered the progression of our knowledge in this domain. The term 'intentionality' originated in philosophy, introduced by Franz Brentano, referring to puzzles of representation, linking together the philosophies of mind and language (5). Brentano believed that intentionality was a prevalent property in all mental states, from beliefs and hopes to love and hatred, with these always being about or referring to a specific target, property, or matter of fact (real or imagined). Notably Brentano's thesis suggested that intentionality is *only* a mental phenomenon, and cannot exist in non-mental constructs such as sentences of natural languages. However, Searle (6) and Grice (4,7) reinterpreted intentionality as it might apply to actions and communication, moving it beyond Brentano's original formulation. Grice's early conceptualisations of intentional signalling require sophisticated meta-representation from both the recipient and the signaller (4,7,8). He proposed that when producing an intentional signal, it is explicitly clear that the signaller is communicating *something* to the recipient (also known as ostension), and the fact that the signal is communicative is mutually understood by both participants (7,8). That this is ubiquitous in (adult) human communication is uncontroversial, but it is debated to what extent non-linguistic communication systems can be deemed intentional based upon Gricean views (2,9).

Questions have recently been raised about the appropriateness of using Gricean intentionality and meaning as a way of assessing non-human communication, given that Grice's definitions were rooted in linguistics rather than including any form of expressive communication (10,11). However the Gricean approach remains the dominant approach in animal communication, with most researchers using Dennett's intentionality framework (4) which offers more graded steps towards the complex meta-representation required for full-blown Gricean intentional communication. According to this framework, zero-order intentionality requires no mentality involved in signalling, whilst first-order requires that the signaller intends to signal in order to change the *behaviour* of the recipient, and second-order requires that intentions to signal are combined with mental state attributions (12). Using food calls as an example, zero-order intentional communication would be that the signaller calls on arrival at a food patch as a result of increased arousal or excitement triggered by food discovery. For first-order intentional communication, the signaller would call to affect their audience's behaviour, i.e. to recruit group members to join the signaller at the food patch. Finally, for second-order intentional communication, the signaller would call to inform ignorant audience members about the food patch, thus altering their mental state from ignorant to knowledgeable.

Because Dennett's framework offers tractable definitions for differing levels of intentionality, that can be operationalised, it has found popularity among animal communication researchers (12–14). Focussing on first-order intentionality (altering of behaviour) loosens previously strict criteria for mental state understanding, and offers a valuable stepping stone from no intention to higher levels of intention. However, many researchers still believe that second-order intentionality (requiring attribution of mental states) is the most relevant cognitive precursor to the evolution of language. Both lab and field experiments have been designed to try and identify second-order vocal production in primates, where researchers have tested whether the knowledge state of the audience mediates call production in the signaller (15,16). However, before second-order intentional signal production is tackled, the first logical step seems to be to distinguish first-order from zero-order intentional signal production. This approach has been recently advocated (9,12), particularly as children can struggle with high-order meta-representations (17), yet do not struggle with language, and communication in adults does not always rely on such high-order representations (18). In order to identify first-order intentional signal production a clear framework with observable behavioural criteria is required.

Townsend et al. provide such a framework (12), bringing together markers that have previously been used to identify first-order intentional communication in prelinguistic humans and non-human animals. They propose that an animal has communicated with first order-intentionality if the following three conditions are met: i) a signaller acts with a goal when communicating to a recipient; ii) the signaller exhibits volitional control over recipient-directed signal production to obtain their communicative goal; and iii) that the recipient alters their behaviour in a way that is in line with the signaller's goal. The value of this framework lies in its ability to define the intentionality of a signal using directly observable behaviour. The main limitation of the framework is that, as highlighted in the original paper and discussed in more depth later in this article, all the behavioural markers designed to diagnose first-order intentional signal production could also be explained by zero-order intentional processes. Thus the validity of the criteria used is unclear. In order to meaningfully discuss the validity and use of the criteria, we will first outline the criteria and the empirical evidence currently used to claim first-order intentionality in different communicative modalities.

To test Townsend et al.'s first criterion that signals are produced to meet a goal, the signaller should continue to signal until a 'stopping rule' has been satisfied and the goal met. That is, when a recipient does not respond to a signal immediately, the signaller should persist or elaborate in signalling in pursuit of their goal. In such a case, the recipient response that terminates these communicative attempts can be identified as the putative goal of the initial signal (19–21).

A broader range of behaviours centred on social use of a signal are suggested to help identify the production of volitional and recipient-directed signals (criterion (ii)). The most rudimentary marker concerning social-usage is the presence or absence of potential recipients. While humans sometimes produce signals in private, for non-humans, signals that are produced in the absence of an audience are presumed to be a product of underlying arousal-based mechanisms. For instance, if a monkey sees a snake and produces an alarm call when no other monkeys are around, it is assumed that the signal was produced as a result of elevated arousal or fear triggered by predator discovery.

Building from the simple presence of a potential recipient, researchers also search for complex audience effects, where the composition of the audience can mediate both the rate and structure of signals. For instance, vervet monkeys alarm call more frequently in the presence of kin than non-kin (22), and chimpanzees alter the structure of their victim screams given to severe aggression if high ranking bystanders are in the audience (23). These more complex audience effects show selective control over signal production, indicating that they are voluntarily produced and directed at specific recipients.

Decisions regarding when and what type of signal to produce can also be affected by the attentional state of the recipient(s). Visual signals produced to inattentive recipients are likely to be ineffective, because the recipient cannot see the signal. If the signaller intends to communicate to the recipient, they should produce a signal that is perceptible to the recipient – avoiding silent-visual signals when the recipient is inattentive and relying on audible or tactile signals in these circumstances. This selectivity indicates not only that the signaller may be engaging in basic perspective taking, but also that they understand the most effective means by which to achieve their goal. Before selecting the appropriate signal, the signaller should check where the recipient is looking, and then continue to visually monitor the recipient for a response. Together these behaviours are commonly known as "audience checking", which is a frequently used marker of first-order intentional communication, as it seems to indicate that the signaller is directing the signals at a recipient and then expecting a response.

The final criterion shifts focus from signal production, instead requiring a consistent behavioural response from the recipient that is appropriate for the signal given (e.g. moving away from the perceived threat that elicited the signaller's alarm calls). The recipient response needs to be consistent across multiple signalling events, and needs to occur immediately after a signal more frequently than at other times (chance level of response behaviour occurring), in order to show that the response is connected to the signal. This criterion is important to demonstrate that signals are effective, and that recipients seem to understand the signal or the signaller's goal in some manner.

To date, studies have focused on identifying behavioural indicators of intentionality (e.g. persistence, gaze alternation or social usage) without reaching a consensus on how these should be applied in methodology. Surprisingly, there is no established acceptable number of behavioural indicators required to classify a signal as intentional (24). The definition offered by Townsend et al. likewise does not specify this (12), but instead requires that a signal demonstrates at least one behaviour from each of the three broader criteria in order to be deemed intentional. Defining intentionality in these terms has the benefit of being conservative enough to avoid claims for intentionality with only one behavioural indicator, and at the same time is still empirically viable and inclusive across taxa.

Primate Evidence

Traditionally, primate vocalisations, gestures, and facial expressions have been studied in isolation with researchers specialising in just one of these types of communication (17, but see 18), and perhaps as a result have followed different approaches to looking at intentionality. Gesture researchers have been the most explicit in their treatment of intentional communication. Intentional gestures were first observed in captive chimpanzees (27,28), and have now been observed in all four species of non-human great apes (Table 1). Following this early work on chimpanzees, intentional production has been routinely used as a prerequisite for a body movement to be identified as a gesture. As it is difficult to define the onset and offset of gestures based on physical properties, researchers used intentional production as a way to differentiate communicative movements from non-communicative movements that are produced for other purposes. This is in stark contrast to vocal and facial signals which are defined in terms of their physical properties, with the degree of intentionality underpinning a signal a matter for separate investigation. Claims of intentionality in gestures are therefore rather circular, as gesture researchers are a-priori selectively focussing on body movements that appear intentional and therefore it is not surprising that these signals go on to meet behavioural markers for intentionality.

To be classified as a gesture, some of the following behavioural criteria must be met: it should be directed towards a specific recipient, the signaller should check the attention of the recipient and adjust their signal to match that attention, signallers should wait for a response, and if they do not receive a response they should continue to produce more signals (29–32). These criteria originate from early attempts to identify intentional gesture production in preverbal human infants (33), and attempt to distinguish first-order from zero-order intentional signal production. Different researchers require different numbers of criteria to be met before assigning intentionality to the signal or class of signals in question (Table 1), but it is widely claimed that great ape gestures are produced with first-order intentionality.

In contrast, vocalisations have traditionally been viewed as automatic, zero-order intentional signals elicited by specific environmental events (e.g. presence of a predator (34)). It is only in recent years that markers of first-order intentionality have been applied to vocal behaviour to challenge this stance (Table 1). On the other hand, experiments testing second-order intentional signal production have only been conducted in the vocal domain, not in the gestural domain. Capitalising on the fact that in many species alarm calls function to refer to predators, experiments have been designed to test whether alarm calls are produced selectively to ignorant group members, to change their mental state from ignorant to knowledgeable. Whilst captive macaques do not mediate their alarm or food calls as a function of their offspring's knowledge about a predator or food source (15), more promising results suggest that wild chimpanzees may be more likely to alarm call to individuals who know less about an ambush predator model (16). There is mounting evidence that both gestures and (some) vocalisations meet behavioural criteria for first-order intentionality, and that some may even show evidence of second order intentionality (35).

Of the three types of communication, facial expressions have received the least attention from researchers in terms of their intentional production. The traditional view of facial expressions is that they are zero-order intentional signals that are the product of emotional processes. However, although humans produce facial expressions automatically, we can also produce them intentionally, and so it is important to ask whether other primates share this ability. Hopkins et al. argue that chimpanzees have some volitional control over their facial expressions (36), and more recent studies have demonstrated that great apes modify their facial expressions if their audience is visually attending to them (37,38). More research is, however, needed to determine whether facial expressions meet other intentionality criteria.

-Table 1-

Intentional signal production in other species

Although most research has focussed on intentional signal production in non-human primates, other species have also been the subject of investigation. Identifying intentional communication in species more distantly related to humans is important, as it may help us to understand the selection pressures that give rise to intentional control over communicative signals, as well as helping us to evaluate the validity and utility of the behavioural criteria being used to identify first-order intentional signal production.

Social usage of signals, the first of the behavioural markers that is said to indicate voluntary control and recipient-directed signal production, is widespread in the animal kingdom. For instance, seminal work on audience effects demonstrated that female ground squirrels produce more alarm calls in the presence of direct kin as opposed to non-kin (39). Similarly, male domestic chickens were found to increase the frequency of food calls when a female was present compared to when they were alone (40), and male Siamese fighting fish produce fewer aggressive signals towards other males, when there is a female audience (41). In fruit flies, the genotypic composition of the social group significantly impacts the overall levels of pheromone signal production, as well as when chemical signals are produced (42,43). Such findings show that complex audience effects are found across taxa, with signals being affected not just by the presence of an audience, but by that audience's composition. We therefore need to question whether volitional control over signal production is in fact widespread in the animal kingdom, or whether audience effects are not strong markers of volitional control.

Miklosi and colleagues (34), move away from basic audience effects and argue that dogs produce intentional 'showing' signals to human owners to indicate the location of a hidden toy. 'Showing' was defined as a communicative action involving both a directional 'pointing' component (head orientation towards the hidden toy) and an attention-getting component (barking and gazing at owner). When the dogs observed an experimenter hiding a toy in one of three inaccessible locations in the room, and the naïve owner then entered, the dogs exhibited gaze alternation between the owner and hidden toy and attention getting behaviours, significantly more than when they were simply in the room with the owner in the absence of a hidden toy. While the authors claim that this demonstrates intentional referential communication, more evidence is required to confirm the intentional nature of these signals, certainly according to the Townsend et al. framework (12).

Similar claims of intentional showing behaviour have been made for ravens. Pika and Bugnyar argue that ravens 'show' objects to conspecific partners (44). Showing is defined as "picking up a non-food item, holding it up in the beak, head straight or tilted upwards, and staying in this position" (pg. 2; 44). They report that such showing 'gestures' were always recipient-directed, and produced at a significantly higher frequency to attending than non-attending partners, showing sensitivity to the partner's attentional state. The authors claim that these signals were goal-directed, based on the signaller looking at the recipient and showing response waiting. However, without subsequent persistence or elaboration in the face of an unresponsive partner, there would be insufficient evidence to show that these gestures were produced in a goal-directed manner according to Townsend et al.'s criteria (12). These gestures seemed effective in eliciting a positive response from recipients, in terms of partners orienting towards the signalling bird or object and subsequently engaging in affiliative, rather than agonistic behaviour, but chance levels of these responses within these dyads occurring are unclear. In summary, although this showing behaviour seems under voluntary control and is recipient-directed, more evidence is needed before the other criteria of goal-directed production and consistent recipient responses can be confirmed. On the surface, there seem to be commonalities between this 'showing' behaviour in ravens and courtship displays involving objects in a variety of avian species, so future research could usefully apply the intentionality criteria to such displays in non-corvids to see whether other avian species demonstrate first-order intentional signal production.

In terms of satisfying all three of the intentionality criteria for signal production proposed by Townsend et al. (12), perhaps surprisingly, some of the strongest candidates are two species of fish. Grouper fish and coral trout perform a 'headstand' to signal the location of prey to cooperative hunting partners, and this is considered to be referential communication (45). This signal meets the main criteria for intentional signalling, including being seemingly goal-directed (showing persistence, elaboration, and cessation when goal is met), recipient-directed, and eliciting a response from the recipient that is in line with the goal. It is one of the few empirical demonstrations that meets all of the intentionality criteria set by Townsend et al. in a single communication system (12), providing more solid evidence than most primate species to date. More recently, convincing evidence of intentional communication has also been found in Arabian babblers (46), and it is likely that the wider application of Townsend et al.'s criteria will reveal more intentional communication across a broader range of species.

These studies suggest that a diverse range of species deploy some form of intentional signalling and that intentional signal production may not be restricted to large-brained mammals. It is therefore unclear whether first-order intentional signal production is simply widespread in the animal kingdom, or whether different processes are underpinning the same behavioural patterns in different taxa. Given that the behavioural markers are designed to probe specific underlying cognitive processes, the validity of these measures is questioned if we attempt to explain away the findings of first-order intentional signalling in distantly related, relatively small-brained animals by claiming that they might be the product of different underlying processes. The findings of first-order intentional signal production in distantly related species provide insights into the types of problems and pressures that drove intentional communication to evolve, but they also call into question the importance of first-order signal production as a stepping stone in the evolution of human language.

Current Limitations

Our understanding of intentional communication in non-humans is currently limited by two main issues: (i) the diversity of evidence used to claim intentional signal production and consequent lack of comparability between studies, and more importantly, (ii) the validity of the behavioural criteria used to distinguish first-order from zero-order intentional communication. For those who consider the current criteria to be valid, or the best tools currently available, the lack of rigorous application of these criteria across studies remains problematic, and this issue will be addressed first.

Lack of consistency in application of intentionality criteria

The claim of intentional signal production can be based on highly variable types and amounts of data. As Table 1 shows, the number of criteria examined is very inconsistent across studies; some studies only require 1/3 or 1/4 criteria to be met to count as an intentional signal, while other studies require that 1/1 or 3/3 criteria are met. Some variation should be expected, as not all criteria are relevant to each species (e.g. a standard 1-2s “response waiting” period that was designed around chimpanzee data may be too short or too long for other primate species) or modality (several criteria are specific to visual signals). However, it also seems that there is additional variability in the stringency with which the behavioural criteria are used by different researchers before accepting a signal as intentionally produced, and such variability is problematic.

A better approach may be to use all criteria and list how many signals were eliminated at each stage: for example, the study started with 400 gesture instances, but 12 had no audience checking, 23 had no response waiting, and 15 had no persistence, which left 350 gestures that met all criteria for intentionality. One problem with this approach is that goal-directedness can often only be tested when the recipient does not immediately respond and provides the opportunity for the signaller to persist or elaborate to achieve their goal; so what to do with signals that elicit an immediate appropriate response is unclear, as we can’t use the established markers for goal-directedness in these cases.

There is also an important difference between studies that collect systematic data to test whether a certain signal or class of signals meet specific criteria for first-order intentionality (e.g. (38,47,48)) and studies, most of them gestural, where intentional production criteria are used as pre-conditions to screen potential gestures, so that only body movements that are produced intentionally are considered in later analysis (e.g (20,21,49)). When systematic data is presented, there is variation in whether baseline data on the behaviours of interest are associated with communicative signals at a level significantly above chance. For instance looking at group members is a common behaviour that, when produced in temporal association with a signal, we interpret as ‘audience checking’, and this is sometimes used as the sole criterion for identifying first-order intentional signalling (Table 1). However, we first need to know the chance level of these two behaviours co-occurring to be able to say that looking at group members really is related to signal production. One approach is to statistically compare the likelihood of the intentional behaviour marker occurring with signal production events and non-signal production events (e.g. (50)). In cases where inferential statistics are applied to the data, one can infer that on average, intentionality markers are likely to co-occur with signals at above chance rates, but it is much harder to interpret purely descriptive data. For instance, Gruber and Zuberbühler report 9 events where a chimpanzee vocal signal was repeated in the face of an unresponsive audience 0-13 minutes after the original call (40). Unfortunately, without comparison to signaller behaviour in all events with unresponsive and responsive audiences, it is hard to conclude from these data that chimpanzees generally persist with this call type until they meet their goal.

When the behavioural criteria for intentional signal production are used as preconditions to identify 'true' gestures, there is also variability with the number of criteria that a gesture instance has to meet. Many researchers only require a signal to meet one of a set of criteria that often includes 'response waiting', which typically means that after a signal, no subsequent signals are produced by the signaller for at least 2 seconds (13 out of 27 papers in Table 1 use "response waiting" as a criterion, and 10 out of those 13 studies required no other criteria to be met). Response waiting can be relevant to identifying intentionality when combined with persistence if the recipient is unresponsive, but response waiting in isolation (producing a single signal rather than a sequence of signals) has many explanations, most unrelated to intentionality. Thus response waiting on its own is not adequate to demonstrate intentional communication, but often that is exactly what researchers are using.

There is also variability in whether each individual signalling event is assessed against intentionality criteria (20,21,49), or whether one instance of intentional use of a specific signal by a specific individual is then extrapolated to all signals of the same type produced by that same individual (30). To summarise, there is a large amount of variability in the rigour with which researchers ensure their signals meet the behavioural criteria for intentionality, and whilst some variation is inevitable, we argue that the current degree of variation makes comparisons across studies, species, and modalities extremely difficult.

Trying to understand the cognitive processes in the signal producer, with a view to informing theories of language evolution, is a difficult endeavour and in terms of examining different signal types produced in different modalities, in different contexts, and across species, we have barely scratched the surface. Thus comparability across studies is really important, as an individual research team can only make small contributions to this substantial challenge. Even when comparisons are possible, interpretation of results from different studies can also be challenging.

A prominent example of conflicting interpretations about the same signal comes from claims of zero- to second-order intentional production made for the same type of chimpanzee alarm call. These alarm calls, called either 'soft huus' (47) or 'alert hoos' (16,51), were elicited by snake models presented by two different research groups. Schel et al. (47), presented wild chimpanzees with a moving python model, and found that the calls were given in the absence of an audience, whilst visually fixating on the snake (little audience checking), and with a calling rate unaffected by the arrival of new potentially ignorant individuals. When considered in bouts with other types of alarm calls (alarm huus and waa barks), positive evidence for persistence towards a goal and gaze alternation was found, but the contribution of soft huus within these mixed call type bouts is unclear. Thus Schel et al. concluded that soft huus, at least in immediate response to the snake, were best characterised as zero-order intentional individualistic expressions of fear (47). In contrast, experiments with the same community of wild chimpanzees using a static model of a snake, showed that the relative knowledge state of the receivers mediated the production of alert hoos and the researchers concluded that these calls were produced with second-order intentionality (16).

It is not at all clear what to make of this pattern of results: the same call type tested with a snake presentation experiment to the same community of chimpanzees within the space of a few years, yet despite these commonalities, the data point to very different conclusions. One way to reconcile these differences is to accept that there is variability in the degree of intentional control involved in the production of a signal, depending on the precise context (e.g. species and movement of predator model). Anecdotally, humans also experience varying degrees of voluntary control over their signal production. For instance, a normal ability to inhibit swearing in front of senior colleagues can be lost in a situation of extreme fear, such as almost crashing a car. If we accept this, however, it indicates that the intentionality of signal production must be assessed on an event by event basis, and extrapolation of intentional production of one instance of signal production to another, as is sometimes done in gesture research (e.g. (30)), is likely inadvisable. These conflicting findings demonstrate the value of replication and multiple groups working on the same questions, but wider discussion of how to make sense of seemingly contradictory findings such as these is needed.

In conclusion the variability across many dimensions in how the current behavioural criteria for first order intentionality are applied, means that valid comparisons across studies and modalities is essentially impossible. If we are to continue to use these criteria, a more rigorous and uniform approach is required.

Validity of the behavioural markers for first-order intentional signal production

Perhaps the most serious issue that requires attention is the validity of the behavioural criteria used to identify instances of first-order intentional communication and distinguish them from zero-order intentional communication. Whilst the behavioural criteria all make intuitive sense, they are all also open to lower level, zero-order intentional explanations (12,24), which means they may not be measuring first-order intentionality at all. First, let's consider goal-directedness as measured by persistence or elaboration in signalling when faced with an unresponsive recipient or an inappropriate audience response. It is sometimes easiest to imagine how a behaviour may be driven by a lower-level mechanism if you imagine an example with a signal that is assumed to be driven by zero-order intentional processes. Rightly or wrongly, we have traditionally assumed that primate facial expressions are read-outs of emotional arousal. In a case where a subordinate chimpanzee is fearful of approaching a dominant, they may produce a silent bared teeth face and both this signal and the fearful emotion presumed to underpin it, persist until the dominant individual reassures the subordinate, at which point the fearful emotion decreases and the silent bared teeth face disappears. In this scenario, the production of the silent bared teeth face would meet the criterion for persistence until the goal of eliciting reassurance from the dominant was met, but it may have been driven by purely zero-order intentional processes. A high level of emotional arousal may not only trigger the production of a single signal, but a number of signals that share similar functions. If a number of closely related signals share a common arousal based production mechanism, then this could also account for elaboration, where more than one signal type is used until the goal is achieved. To return to the above example, the arousal state associated with fear of approaching a dominant may

498 trigger submissive crouching behaviour, or pant grunt vocalisations, in addition to the
499 silent bared teeth facial expression, and this constellation of behaviours would meet
500 the criteria of elaboration of signals to meet a goal.
501 There is equal uncertainty as to the mechanisms underpinning the
502 behavioural criteria for a signal being produced voluntarily and in a recipient-directed
503 manner. Producing a communicative signal selectively in the presence of an
504 audience (social use), may be driven by arousal. Research with a range of species
505 indicates that arousal levels are higher when in a social group compared to alone
506 (52) and thus it is plausible that in an arousal-based system, the threshold for signal
507 production is usually only met when an audience is present and base levels of
508 arousal are elevated. More complex audience effects, such as only producing
509 signals in the presence of kin, friends, or higher ranking individuals may be more
510 compelling, but it is also possible that the presence of certain individuals differentially
511 affects arousal. The evidence for arousal increasing differentially with the presence
512 of different individuals is less apparent, but this possibility needs testing and ruling
513 out before we can say with certainty that complex audience effects do not arise from
514 an arousal based signal production system. Equally, cases where signals are
515 contingent on the behaviour of the audience (e.g. individual alarm calls until all other
516 group members have alarm called) could also arise from changes in arousal. In
517 humans we know that heartrate in a speaker can be increased by negative
518 behavioural responses in the audience (e.g. (53)) and behaviour in audience
519 members may affect autonomic arousal levels in signal producers across species.
520 Sensitivity to the recipient's attentional state, in terms of only producing visual
521 signals when a partner is attending, appears to be a strong marker of intentional
522 signal production, as it may involve perspective taking, however this behaviour could
523 also be a result of learned discriminations. Individuals may learn over their lifetime
524 that the face of a recipient is one of the necessary eliciting stimuli for effective
525 production of visual signals, possibly in a similar way to infant vervet monkeys
526 learning to narrow the type of stimuli that elicit their eagle alarm call (24). If this
527 scenario is correct, then looking for the stimulus of a conspecific face before
528 signalling (like visual examination of an aerial object in vervet monkeys before alarm
529 calling) would also result in what has been described as 'audience checking'
530 behaviour.

Although audience checking where the signal producer looks at the signal recipient before or during signal production, may have a low-level conditioning explanation for visual signals, there doesn't seem to be an obvious lower-level explanation for why primates should look to audience members before emitting a vocal signal, as visual attention in the recipients is not necessary for vocal signals to be effective.

In summary, as has been previously highlighted, each of the criteria has an alternative zero-order intentional explanation, however the empirical evidence supporting these alternative explanations is highly variable and many remain simple theoretical possibilities. It has been previously argued that providing convergent evidence from diverse markers, provides more robust evidence and more likely attributable to a single mental ability (intentionality) than a series of arousal and conditioning based explanations (12,24), and whilst we agree that convergent evidence across markers is stronger than evidence from a single marker, more discussion of the validity of these criteria is needed.

The way forward

While there are extensive claims of first-order intentional communication in other animal species, our current ability to rigorously assess such intentionality is sadly limited, and we need to look for new alternatives. We provide two main suggestions for moving forward: (1) directly assessing arousal during communication, which would allow us to determine the degree to which high levels of arousal elicit certain signals; and (2) focussing experimentally on second-order intentionality, as evidence for second-order intentionality implies the existence of first-order.

It is worth noting that although there are plausible emotional arousal based explanations for the behavioural criteria for first-order intentional signal production, few of them are underpinned by hard evidence. Unlike our understanding of conditioning, which is built on decades of experimental data and theoretical models, our understanding of how and when arousal affects behaviour is relatively poor. Despite this, arousal is often offered as a post-hoc explanation for a startlingly wide array of behaviours and phenomena, and because the tools we have for assessing arousal are currently inadequate, it is very difficult to rule out arousal accounting for interesting behaviours. Yet, because arousal is the lower level of explanation for behaviour, the onus is on the researcher wanting to claim a higher level mechanism to rule out the lower level explanation. In most cases this is impossible, because the current tools for evaluating emotional arousal in primates are inadequate: they are either prohibitively expensive and work on a timescale incompatible with understanding individual signal production events (e.g. hormone analysis), require minimal movement in the animal (thermal imaging), or need expensive specialist equipment (pupilometry via eyetracking equipment).

Current techniques for measuring dynamic changes in arousal levels are therefore incompatible with freely-moving, naturally-behaving primates interacting with one another and, unfortunately, that is the only kind of primate who will produce the meaningful social signals that we are seeking to understand. This means that most researchers interested in signal production (including ourselves) have not been able to address the contribution of arousal to signal production, and have essentially ignored it. This has led us to the situation in which we currently find ourselves, where considerable research effort is being invested in trying to establish whether signals are produced with first-order intentionality, with no certainty that any of our measures are valid.

Research to produce physiologically validated behavioural measures of arousal are sorely needed if we are to change this situation, so that we can make and test differential predictions for patterns of behaviour that would be primarily arousal driven or intentionally driven. This is not to say that these options are mutually exclusive; in fact it is likely that arousal plays a complementary role to intentional processes, as it does in humans, but we need to try and disentangle the relative contribution of affective arousal and higher cognitive processes on communicative behaviour.

Technological advances allowing us to test signaller arousal, as well as finding that more distantly related species are meeting criteria for first order intentionality (e.g. fruit fly courtship behaviour; Shuker, personal communication), may lead us to conclude that the behavioural criteria for first-order intentionality are not particularly useful for informing understanding of language evolution. In that eventuality, we may have to reconsider the virtues of trying to find evidence of second-order intentional signal production in non-human species. Despite its disadvantages (12), it may be the best approach we have left. As second-order intentional signal production builds on first-order intentional processes (voluntary goal-directed signal production), if second–order communication is demonstrated, this also provides evidence for first-order intentionality, but bypassing the need to rely on criteria with questionable validity. Second-order intentional signal production requires attribution of mental states, and this has been most commonly tackled by looking to see if signal production is mediated by the knowledge state of the recipient. This is a promising approach, at least in chimpanzees, as there is convergent evidence from a number of paradigms that chimpanzees understand what other chimpanzees have seen and know (44, but see 45) and it is clear that such theory of mind skills are necessary for second-order intentional signal production (35). Whether the understanding of others' mental states influences signal production is still currently unclear: it has been claimed that chimpanzees are more likely to alarm call in the presence of individuals that have partial knowledge rather than full knowledge of a model snake (16), but it is not clear that lower level behaviour reading explanations have been excluded (47).

What is clear is that further investigations focussed on whether signal production is mediated by an understanding of others' knowledge or ignorance are likely to focus on the vocal domain. There is good evidence that vocalisations function to refer to external objects and events, so it is possible to probe whether these calls are influenced by receivers' knowledge of those objects or events. In contrast, gestures to conspecifics seem to have less potential to be influenced by knowledge of mental states, as they are predominantly dyadic requests for certain behaviours from another individual (e.g. give me X; do X; stop that; come here; (20,21)). There are only a handful of potential cases of triadic gestures that have ever been observed in wild chimpanzees or bonobos, in many decades of continual field observations (56,57). In captivity many apes will point for human caretakers, but these points still seem to share the same imperative motivation as their naturally occurring gestures, in that they point to request things that they want, but do not gesture with an informative intention (58), where experimental manipulations of receiver knowledge could be usefully deployed. Thus, future investigations of second-order intentional signal production are likely to focus on whether the knowledge state of listeners mediates the production of functionally referential vocal signals. And as regards current debates, independently of whether or not it is best to take a Gricean approach to intentionality (10,11), testing second-order intentionality in great apes has the potential to inform us about their capacity for meta-representation and contribute more broadly to the field of animal cognition.

In conclusion, in order to further our understanding of language evolution it is vital that we move beyond surface similarities between human language and primate communication, and search for commonalities and differences in the cognitive processes driving the production and reception of signals. The degree of intentional control in non-human signal production is a central and important question, and although first–order intentional communication has been widely claimed, the current tools we have to detect intentional signal production are limited. The validity of the behavioural criteria for distinguishing first-order from zero-order intentional signal production is questionable and inconsistency across studies in how and which intentionality criteria are applied limits comparability. Looking ahead, we need to be able to detect first-order intentional communication with greater accuracy to understand how widespread it is in the animal kingdom and what selection pressures facilitated the evolution of this type of communication. The development of physiologically validated behavioural measures of arousal is essential if we are to truly understand the relative contribution of zero-order and first-order intentional processes to signal production in non-human species. Until those tools are available, however, productive steps may include individual researchers explicitly acknowledging the zero-order alternatives to the first-order behavioural markers they use, and a renewed focus on second-order intentionality in vocalisations produced by species with established Theory of Mind skills (35).

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References:

1. Heyes C. Blackboxing: Social learning strategies and cultural evolution. Philos Trans R Soc B Biol Sci. 2016;371(1693).

2. Scott-Phillips TC. Speaking our minds: how human communication is different, and how language evolved to make it special. London: Palgrave Macmillan; 2015. 195 p.
3. Dennett DC. Intentional systems in cognitive ethology: The "Panglossian paradigm" defended. Behav Brain Sci [Internet]. 1983 Feb 4;6:343–90. Available from: http://www.journals.cambridge.org/abstract_S0140525X00016393
4. Grice HP. Utterer's meaning and intention. Philos Rev [Internet]. 1969 [cited 2013 Sep 23];78(2):147–77. Available from: http://www.jstor.org/stable/10.2307/2184179
5. Brentano F. Psychologie vom empirischen Standpunkt. Leipzig: Duncker & Humblot; 1874.
6. Searle JR. Intentionality: An Essay in the Philosophy of Mind. Cambridge: Cambridge University Press; 1983.
7. Grice HP. Meaning. Philos Rev. 1957;66(3):377–88.
8. Grice HP. Meaning revisited. In: Smith N V, editor. Mutual knowledge. New York: Academic Press; 1982. p. 222–43.
9. Moore R. Meaning and ostension in great ape gestural communication. Anim Cogn [Internet]. 2016;19:223–31. Available from: http://link.springer.com/10.1007/s10071-015-0905-x
10. Bar-on D. Origins of Meaning: Must We 'Go Gricean'? Dorit Bar-On. Mind Lang. 2013;28:342–75.
11. Sterelny K. From code to speaker meaning. Biol Philos [Internet]. 2017;32:819–38. Available from: https://doi.org/10.1007/s10539-017-9597-8
12. Townsend SW, Koski SE, Byrne RW, Slocombe KE, Bickel B, Boeckle M, et al. Exorcising Grice's ghost: an empirical approach to studying intentional communication in animals. Biol Rev. 2017;92(3):1427–33.
13. Byrne RW, Cartmill EA, Genty E, Graham KE, Hobaiter C, Tanner J. Great ape gestures: intentional communication with a rich set of innate signals. Anim Cogn [Internet]. 2017;20(4):755–69. Available from: http://link.springer.com/10.1007/s10071-017-1096-4
14. Call J, Tomasello M. The Gestural Communication of Apes and Monkeys [Internet]. Manhaw, NJ: Lawrence Erlbaum Associates; 2007 [cited 2013 Nov 19]. 256 p. Available from:

http://books.google.co.uk/books/about/The_Gestural_Communication_of_Apes_and_M.html?id=hZQ-4vn3tWsC&pgis=1

15. Cheney DL, Seyfarth RM. How Monkeys See the World [Internet]. Chicago: University of Chicago Press; 1990 [cited 2013 Dec 4]. 377 p. Available from: http://books.google.com/books?id=QbWTd85eHUgC&pgis=1
16. Crockford C, Wittig RM, Mundry R, Zuberbühler K. Wild chimpanzees inform ignorant group members of danger. Curr Biol [Internet]. 2012 Jan 24 [cited 2013 Nov 12];22(2):142–6. Available from: http://www.ncbi.nlm.nih.gov/pubmed/22209531
17. Liddle B, Nettle D. Higher-order theory of mind and social competence in school-age children. J Cult Evol Psychol. 2006;4(3–4):231–46.
18. Moore R. Gricean communication and cognitive development. Philos Q [Internet]. 2017;67(267):303–26. Available from: https://web-a-ebscohost-com.nomade.univ-tlse2.fr/ehost/pdfviewer/pdfviewer?vid=1&sid=23e1226a-3745-46c6-a406-682a376aa982%40sdc-v-sessmgr05
19. Leavens DA, Russell JL, Hopkins WD. Intentionality as Measured in the Persistence and Elaboration of Communication by Chimpanzees (Pan troglodytes). Child Dev. 2005;76(1):291–306.
20. Hobaiter C, Byrne RW. The Meanings of Chimpanzee Gestures. Curr Biol [Internet]. 2014 Jul 21 [cited 2014 Jul 4];24(14):1–5. Available from: http://dx.doi.org/10.1016/j.cub.2014.05.066
21. Graham KE, Hobaiter C, Ounsley J, Furuichi T, Byrne RW. Bonobo and chimpanzee gestures overlap extensively in meaning. PLoS Biol. 2018;16(2):e2004825.
22. Cheney DL, Seyfarth RM. Vervet Monkey Alarm Calls: Manipulation through Shared Information? Behaviour. 1985;94(1/2):150–66.
23. Slocombe KE, Zuberbühler K. Chimpanzees modify recruitment screams as a function of audience composition. Pnas. 2007;104(43):17228–33.
24. Liebal K, Waller BM, Slocombe KE, Burrows AM. Primate communication: a multimodal approach. Cambridge: Cambridge University Press; 2013. 294 p.
25. Slocombe KE, Waller BM, Liebal K. The language void: The need for multimodality in primate communication research. Anim Behav [Internet]. 2011;81(5):919–24. Available from: http://dx.doi.org/10.1016/j.anbehav.2011.02.002

26. Wilke C, Kavanagh E, Donnellan E, Waller BM, Zarin P, Slocombe KE. Production of and responses to unimodal and multimodal signals in wild chimpanzees, Pan troglodytes schweinfurthii. Anim Behav. 2017;123:305–16.

27. Tomasello M, George BL, Kruger AC, Farrar MJ, Evans A. The development of gestural communication in young chimpanzees. J Hum Evol [Internet]. 1985 [cited 2013 Sep 23];14:175–86. Available from: http://www.sciencedirect.com/science/article/pii/S0047248485800051

28. Tomasello M, Gust D, Frost GT. A longitudinal investigation of gestural communication in young chimpanzees. Primates [Internet]. 1989 Jan [cited 2013 Sep 24];30(1):35–50. Available from: http://link.springer.com/10.1007/BF02381209

29. Bates E. Language and context: The acquisition of pragmatics. New York: Academic Press; 1976.

30. Cartmill EA, Byrne RW. Semantics of primate gestures: intentional meanings of orangutan gestures. Anim Cogn [Internet]. 2010 Nov [cited 2013 Sep 23];13(6):793–804. Available from: http://www.ncbi.nlm.nih.gov/pubmed/20563619

31. Gomez JC. Mutual awareness in primate communication: A Gricean approach. In: Parker ST, Mitchell RW, Boccia ML, editors. Self-awareness in animals and humans: Developmental perspectives. New York: Cambridge University Press; 1994. p. 61–80.

32. Liebal K, Pika S, Call J, Tomasello M. To move or not to move: How apes adjust to the attentional state of others. Interact Stud. 2004;5(2):199–219.

33. Bates E, Benigni L, Bretherton I, Camaoni L, Volterra V. The emergence of symbols. New York: Academic Press; 1979.

34. Tomasello M. Origins of human communication [Internet]. Cambridge, MA: MIT Press; 2010 [cited 2016 Aug 27]. 393 p. Available from: https://books.google.com/books?hl=en&lr=&id=T3bqzIe3mAEC&oi=fnd&pg=PR7&dq=tomasello+ontogenetic+ritualization+of+gestures&ots=3GwC_jfELs&sig=NvAmTp9DFRVwLcJnLIIzqJ4Cx7g

35. Zuberbühler K, Gomez J-C. Primate Intentional Communication. Int Encycl Anthropol. 2018;1–10.

36. Hopkins WD, Taglialatela JP, Leavens DA. Do chimpanzees have voluntary control of their facial expressions and vocalizations? In: Vilain A, Schwartz J-L,

Abry C, Vauclair J, editors. Primate Communication and Human Language - Vocalization, gestures, imitation and deixis in humans and non-humans [Internet]. Amsterdam, Philadelphia: John Benjamins Publishing Company; 2011. p. 71–88. Available from: http://sro.sussex.ac.uk/13565/

37. Demuru E, Ferrari PF, Palagi E. Emotionality and intentionality in bonobo playful communication. Anim Cogn. 2015;18:333–44.

38. Waller BM, Caeiro CC, Davila-Ross M. Orangutans modify facial displays depending on recipient attention. PeerJ [Internet]. 2015;3:e827. Available from: https://peerj.com/articles/827

39. Sherman PW. Nepotism and the Evolution of Alarm Calls. Science (80-). 1977;197(4310):1246–53.

40. Evans CS, Marler P. Food calling and audience effects in male chickens, Gallus gallus: their relationships to food availability, courtship and social facilitation. Anim Behav. 1994;47(5):1159–70.

41. Doutrelant C, McGregor PK, Oliveira RF. The effect of an audience on intrasexual communication in male Siamese fighting fish, Betta splendens. Behav Ecol [Internet]. 2001;12(3):283–6. Available from: https://academic.oup.com/beheco/article-lookup/doi/10.1093/beheco/12.3.283

42. Krupp JJ, Kent C, Billeter JC, Azanchi R, So AKC, Schonfeld JA, et al. Social Experience Modifies Pheromone Expression and Mating Behavior in Male Drosophila melanogaster. Curr Biol. 2008;18:1373–83.

43. Kent C, Azanchi R, Smith B, Formosa A, Levine JD. Social Context Influences Chemical Communication in D. melanogaster Males. Curr Biol. 2008;18:1384–9.

44. Pika S, Bugnyar T. The use of referential gestures in ravens (Corvus corax) in the wild. Nat Commun [Internet]. 2011 Jan [cited 2013 Oct 21];2:560. Available from: http://www.ncbi.nlm.nih.gov/pubmed/22127056

45. Vail AL, Manica A, Bshary R. Referential gestures in fish collaborative hunting. Nat Commun [Internet]. 2013;4:1765. Available from: http://www.ncbi.nlm.nih.gov/pubmed/23612306

46. Mocha Y Ben, Mundry R, Pika S. Joint attention skills in wild Arabian babblers (Turdoides squamiceps): A consequence of cooperative breeding? Proc R Soc B Biol Sci. 2019;286(20190147).

47. Schel AM, Townsend SW, Machanda Z, Zuberbühler K, Slocombe KE.

Chimpanzee alarm call production meets key criteria for intentionality. PLoS One [Internet]. 2013 Jan [cited 2013 Oct 31];8(10):e76674. Available from: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3797826&tool=pmcentrez&rendertype=abstract

48. Roberts AI, Vick S-J, Buchanan-Smith HM. Communicative intentions in wild chimpanzees: persistence and elaboration in gestural signalling. Anim Cogn [Internet]. 2013 Mar [cited 2014 Jul 28];16(2):187–96. Available from: http://www.ncbi.nlm.nih.gov/pubmed/23053796

49. Graham KE, Furuichi T, Byrne RW. The gestural repertoire of the wild bonobo (Pan paniscus): a mutually understood communication system. Anim Cogn. 2016;20(2):171–7.

50. Gruber T, Zuberbühler K. Vocal Recruitment for Joint Travel in Wild Chimpanzees. PLoS One. 2013;8(9):1–9.

51. Crockford C, Gruber T, Zuberbühler K. Chimpanzee quiet hoo variants differ according to context. R Soc Open Sci. 2018;5(172066).

52. Zajonc RB. Social Facilitation. Science (80-). 1965;149(3681):269–74.

53. Bassett R, Behnke RR, Carlile LW, Rogers J. The effects of positive and negative audience responses on the autonomic arousal of student speakers. South Speech Commun J. 1973;38(3):255–61.

54. Call J, Tomasello M. Does the chimpanzee have a theory of mind ? 30 years later. Trends Cogn Sci. 2008;12(5):187–92.

55. Povinelli DJ, Vonk J. Chimpanzee minds: suspiciously human? Trends Cogn Sci [Internet]. 2003 Apr [cited 2013 Sep 20];7(4):157–60. Available from: http://linkinghub.elsevier.com/retrieve/pii/S1364661303000536

56. Hobaiter C, Leavens DA, Byrne RW, Leavens DA. Deictic gesturing in wild chimpanzees, (Pan troglodytes)? some possible cases. J Comp Psychol. 2014;128(1):82–7.

57. Vea J, Sabatier PJ. Spontaneous pointing behaviour in the wild pygmy chimpanzee (Pan paniscus). Folia Primatol. 1998;69:289–90.

58. Bullinger AF, Zimmermann F, Kaminski J, Tomasello M. Different social motives in the gestural communication of chimpanzees and human children. Dev Sci. 2011;14(1):58–68.

Table 1. Studies examining intentional signal production in non-human primates. Papers selected for relevancy from an initial search for 'intentional communication' & 'primate' on Web of Science that were published in journal articles from 1980-2018.

Paper Details			**Empirical details**				
Author	**Year**	**Intentionality Criteria used**	**Criteria explicitly tested with data**	**A priori criteria signals met to be classed as intentional**	**Order of intentionality claimed**	**Type of signal**	**Species**
Bard	1992	Social use	No	N/A	First	Gestural	Bornean orangutan
Brockett et al.	2004	Goal-directed	No	1/1	First	Gestural	Black howler monkey
Cartmill & Byrne	2010	Social use, Gaze alternation, Persistence, Elaboration, Flexible use, Response-waiting	No	Not specified	First	Gestural	Bornean & Sumatran orangutans
Crockford et al.	2012	Calling behaviour modified when audience is ignorant vs knowledgeable of predator	Yes	N/A	Second	Vocal	Eastern chimpanzee
Demuru et al.	2015	Social use, Attentional state [secondary = eye contact, body orientation, response waiting, persistence]	No	Not specified	First	Gestural, Facial	Bonobo
Fröhlich et al.	2016	Attentional state, Response waiting, Persistence, Satisfaction with goal	No	Not specified	First	Gestural	Eastern & Western chimpanzees
Fröhlich et al.	2018	Audience checking, Attentional state, Persistence	No	N/A	First	Gestural, Vocal	Eastern & Western chimpanzees

Genty & Byrne	2010	Social use, Attentional state, Persistence, Elaboration	No	Not specified	First	Gestural	Western gorilla
Genty et al.	2009	Social use, Attentional state, Attention-getters, Persistence, Elaboration, Flexible use, Response-waiting	No	3/3	First	Gestural	Western gorilla
Gruber & Zuberbühler	2013	Social use, "Checking" (Attentional state), Persistence, Response-waiting	Yes	N/A	First	Vocal	Eastern chimpanzee
Graham et al.	2018	Attentional state (audience checking), Persistence, Response-waiting	No	1/3	First	Gestural	Bonobo, Eastern chimpanzee
Gupta & Sinha	2016	Persistence	No	1/1	First	Gestural	Bonnet macaque
Halina et al.	2013	Persistence, Satisfaction with goal	No	2/2	First	Gestural	Bonobo
Hobaiter & Byrne	2011a	Social use, Attentional state, Persistence, Flexible use, Response-waiting	No	¼	First	Gestural	Eastern chimpanzee
Hobaiter & Byrne	2011b	Social use, Attentional state, Attention-getters, Persistence, Elaboration, Response-waiting	No	¼	First	Gestural	Eastern chimpanzee
Liebal et al.	2004	Social use, Attentional state, Attention-getters, Persistence, Elaboration, Flexible use	No	2/2	First	Gestural, Vocal, Facial	Chimpanzee
Liebal et al.	2004	Social use, Attentional state, Persistence, Elaboration, Flexible use, Response-waiting	No	2/2	First	Gestural, Facial	Siamang
Liebal et al.	2006	Social use, Attentional state, Persistence, Elaboration, Flexible use, Response-waiting	No	2/2	First	Gestural, Facial	Sumatran orangutan

Roberts et al.	2013	Attentional state	No	1/1	First	Gestural	Eastern chimpanzee
Scheel & Edwards	2012	Goal-directed	No	1/1	First	Gestural	Spider monkey
Schel et al.	2013	Social use, Gaze alternation, Attentional state (specifically audience checking), Persistence	Yes	N/A	Zero & first	Vocal	Eastern chimpanzee
Sueur & Petit	2010	Flexible use, Goal-directed	Yes	N/A	First	Body posture/ movements	Tonkean & rhesus macaques
Tempelmann & Liebal	2012	Social use, Attentional state, Attention-getters, Persistence, Elaboration	No	1/1	First	Gestural	Orangutan
Tomasello et al.	1985	Social use, Gaze alternation, Response-waiting	No	1/3	First	Gestural	Chimpanzee
Tomasello et al.	1994	Social use, Gaze alternation, Attentional state, Attention-getters, Persistence, Elaboration, Flexible use, Response-waiting	No	Not specified	First	Gestural	Chimpanzee
Waller et al.	2015	Attentional state	No	1/1	First	Facial	Orangutan