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Communication without language

How great apes may cover crucial advantages of language without creating a system of symbolic communication

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Great apes do not possess language or any comparable system of symbolic communication. Yet they communicate intentionally and possess cognitive competencies like categorization and decontextualization. These provide the basis for mental concepts and the *meaning* side of linguistic symbols. The arbitrarily linked and conventionalized *forms* for expressing these meanings, however, seem to be largely missing. We propose two strategies that may allow great apes to communicate a wide array of meanings without creating numerous arbitrarily linked forms. First, we suggest the existence of 'population-specific semantic shifts': within a population a communicative signal's meaning is modified without changing its form, resulting in a new 'vocabulary item'. Second, we propose that great apes, in addition to possessing sophisticated inferential abilities, intentionally display behaviors without overt communicative intent to provide eavesdropping conspecifics with 'natural meaning' (in the Gricean sense) and thus to influence their behavior.

Keywords: great apes, symbolic communication, intentionality, auditory gestures

Introduction

Human language is a system of intentional communication that plays a crucial role in human social interaction. Its functions include the informing and helping of others, the establishment and maintenance of social bonds, and the manipulation of others' psychological states and resulting behavior (Enfield, 2010). Human language in its spoken, written or signed forms can be defined as a system of linguistic symbols, and rules that govern their combination and hierarchical structure (morphology, syntax, discourse). Linguistic symbols are based on

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mental abstractions (which in the following we will refer to as 'meanings') that by convention are linked arbitrarily with forms (that is, usually — but not necessarily — with sound shapes) within a speech community. Contrary to non-symbolic communication systems, language provides its users with these advantages: (i) the possibility of referential *temporal and spatial displacement*, that is, the possibility of making reference to objects, events, or ideas etc. that are distant in space and/or time, and (ii) *open-endedness*, that is, the possibility of creating new symbols and an unlimited number of symbol combinations (e.g., Hockett, 1960). These properties make language an immensely powerful means of communication.

Great apes do not possess language or any other comparable system of symbolic communication, although they do possess symbolic competencies (see below). They communicate via intentional gestures and vocalizations. Gestures, i.e., goal-directed and mechanically ineffective limb or head movements and body postures directed toward a recipient (Pika & Mitani, 2008), in great apes fall into three sensory modalities: auditory, visual and tactile. They are a means of intentional communication and have been described for great-ape populations in the wild (e.g., Bard, 1992; Genty, Breuer, Hobaiter, & Byrne, 2009; Goodall, 1986; Hobaiter & Byrne, 2014; Jaeggi, van Noordwijk, & van Schaik, 2008; MacKinnon, 1974) as well as in captivity (e.g., Liebal, Pika, & Tomasello, 2006; Pika, Liebal, & Tomasello, 2003; Pika, Liebal, Call, & Tomasello, 2003, 2005; Tomasello, Gust, & Frost, 1989). Gestures are used flexibly and are adjusted to the attentional state of the potential recipient. It is still unclear though whether they are aimed at manipulating just the behavior of conspecifics or their mental state and resulting behavior.[1]

Compared to gestures, the production and usage of great ape and other non-human primate vocalizations is limited (e.g., Hammerschmidt & Fischer, 2008; Seyfarth & Cheney, 2010), apparently due to neural and socio-cognitive constraints that influence, for instance, the apes' ability of vocal imitation (for a comprehensive review see Fitch, 2005). Moreover, vocalizations until rather recently have been regarded as being tightly connected to emotional states (e.g., see the review by Owren, Amoss, & Rendall, 2010). However, there is evidence for the presence of social learning processes in their acquisition, resulting in a certain acoustic variation of calls between groups (Crockford, Herbinger, Vigilant, & Boesch, 2004). There is also evidence that they can be under volitional control (e.g., Byrne,

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[1] Note that Moore (forthcoming) argues that great apes (and young children) not only act with communicative intent and perceive the potential recipient as intentional agent, but that they also mark their intentional gestures by an act of ostension (for example, positioning themselves in front of the potential recipient when presenting a body part for grooming), and thus provide the recipient with the possibility of recognition of communicative intent. They thus would be capable of "Gricean communication", which so far has been attributed exclusively to adult humans as it supposedly requires so-called higher-order meta-representations.

1993, 2010; Hauser, 1990; Watts & Mitani, 2001; Wilson, Hauser, & Wrangham, 2007). Intentional usage of context-specific vocalizations in great apes has been reported as well (e.g., Crockford, Wittig, Mundry, & Zuberbühler, 2012; Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013; Slocombe et al., 2010). The level of intentionality in the production and usage of different vocalizations seems to vary, however, and is still debated.

Thus, compared to open-ended language, the great apes' repertoires of intentional communicative signals seem to be limited. They are adjusted to the apes' specific needs of informing, helping and manipulating conspecifics in the areas of, for instance, foraging, mating, predator evasion, and traveling. The apparently stable sets of ecological challenges that great apes are facing do not seem to result in any selective pressures strong enough to enhance language evolution (Boesch, 2012b).

However, great apes do possess symbolic competencies. Studies in captive settings confirm that great apes not only are able to spontaneously acquire and apply linguistic symbols provided by humans (for example, symbolic gestures based on signs from ASL, or lexigrams). They also show abilities of categorization, that is, the mental grouping of objects, subjects etc. according to specific properties and for specific purposes; they invent new signs for novel objects by combining known signs; they decontextualize signs, that is, they isolate and generalize a mental representation from the original context; and they combine signs to form short utterances (e.g., Greenfield & Savage-Rumbaugh, 1990; Miles, 1990; Patterson, 1978; Savage-Rumbaugh, McDonald, Sevcik, Hopkins, & Rubert, 1986). The use of human-provided symbols moreover enables great apes to express spatial and temporal displacement (Call, 2011; Lyn et al., 2014), one of the advantages provided by human language as mentioned above that seems to be absent in great ape natural communication.[2]

That is, in great apes there must have been a selection for abilities to entertain mental concepts (including concepts of absent objects or individuals and of past or future events, see e.g., Boesch & Boesch, 1984; Janmaat, Ban, & Boesch, 2013; Mulcahy & Call, 2006; Normand, Ban, & Boesch, 2009; Osvath, 2009; Osvath & Osvath, 2008; van Schaik, Damerius, & Isler, 2013). This seems logical, given the complexity of nonhuman primate social systems (e.g., Cheney & Seyfarth, 2007) or the complexity of their material environment (e.g., Milton, 1981; Russon & Begun, 2004). These mental concepts would provide the cognitive basis for the *meaning* side of linguistic symbols, at least on a rudimentary level.

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[2] The only candidate for displacement in great ape gestural communication in the wild so far reported is the *buttress-drumming* observed by Boesch (1991a) in one individual of the Taï chimpanzee community in the travel context. Drumming was used to announce resting periods as well as changes in travel direction. The latter included changes that would not happen before one hour of resting had passed.

On the other hand, there do not seem to have been selective pressures on great apes for evolving a correspondingly extensive arbitrarily linked *form* side (be it vocal or gestural) that would be necessary for forming a system of symbolic communication. A large proportion of the great apes' rich mental activity thus does not appear to be intentionally communicated (Cheney & Seyfarth, 2007; Fitch, 2005).

But is this really the case? Or are there alternative communicative means that great apes use to express a wide array of meanings for effectively informing, helping, and manipulating each other without considerably enlarging their repertoires of intentionally communicative signals? In the following we propose two such means, namely (a) population-specific semantic shifts and (b) the provision of natural meaning (in the Gricean sense) without overt communicative intent. We suggest that these means, to a certain extent, can provide the advantages offered by language as outlined in the introduction, that is, displacement and open-endedness.

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Population-specific semantic shifts

In several wild chimpanzee populations it has been observed that the meaning of an established communicative signal can be modified (shifted) within a population without changing the signal's form. This, of course, can be observed also in human language; the important point for us is that it can occur outside language.

In the following, we describe the evidence available for such semantic shifts in the auditory gesture of *leaf-clipping* in several wild chimpanzee populations and we propose a scenario for the shift's emergence.

Leaf-clipping is a gesture that is performed by taking off bits of leaves with the mouth or fingers, thereby causing a distinctive sound. It can be observed in the wild chimpanzee communities of Bossou (Guinea), Budongo (Uganda), Kibale (Tanzania), Mahale (Tanzania), and Taï (Côte d'Ivoire) (e.g., Boesch, 1995; Whiten et al., 1999, 2001). It has, however, never been observed in the Gombe chimpanzees despite four decades of observation (Goodall, 1986). While in all communities it serves as an attention getter, in some communities its usage in adult individuals is restricted to a specific context, as described by Boesch (1995, 2003, 2012a, 2012b). Thus, leaf-clipping is used by the chimpanzees of Bossou as an invitation to play (Sugiyama, 1981), while in Mahale it can be observed in adult male chimpanzees to attract females to mate (Nishida, 1980). In Budongo it is used by adult male and female chimpanzees for sexual solicitation (Hobaiter & Byrne, 2014). Taï adult male chimpanzees signal their intention to display[3] by leaf-clipping, the

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[3] A display may involve buttress-drumming, branch-shaking, loud vocalization etc.

signal here is never used in the context of play or courtship (Boesch, 1995, 2003, 2012a, 2012b). Thus, the same form (sound shape) is linked to different meanings in different populations.

Conversely, for sexual solicitation, the chimpanzees in Mahale leaf-clip while the Taï chimpanzees knuckle-knock (Boesch, 1995, 2003, 2012a, 2012b; Nishida, 1980, 1987, 1997). Thus, the same meaning is expressed by different forms (sound shapes) in different populations. See Table 1 for this contrast.

Table 1. Evidence for arbitrary relations between form and meaning in auditory gestures in different chimpanzee populations as a result of semantic shifts

	Taï	**Bossou**	**Budongo, Mahale**	**Taï**
form	leaf-clipping	leaf-clipping	leaf-clipping	knuckle-knocking
meaning	intention to display	invitation to play	invitation to sex	invitation to sex

Observations of this sort suggest that the link between leaf-clipping and its meaning may be arbitrary and established through social learning as a convention (see also Boesch, 2012b, for a discussion on the acquisition of leaf-clipping). The fact that the same form is combined with different meanings respectively in different populations safely excludes mere emotional triggering.

Given the arbitrary and conventionalized connection between form and meaning, the gesture of leaf-clipping (and knuckle-knocking) might qualify as a strong candidate for symbolic signal use or at least represent a first step in a process towards symbolic communication.[4]

In the following we suggest a scenario for the emergence of the above described semantic shifts. The attention getter (AG) leaf-clipping, serving originally merely to direct one or more individuals' attention to its sender in several contexts, could be used exclusively (and successfully) by one individual with a context-specific intentional communicative signal (S_{cs}) like for instance *presenting signs of sexual arousal* to invite females to mate (Mahale). The attention getter

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[4] Note that in different human populations of Indonesia the same click vocalization is used for expressing different meanings. In Riau province it is used to communicate an invitation to (a specific type of) sexual intercourse, in Kupang (East Nusa Tenggara province) it is used to make the driver of a bus stop so that passengers can alight (David Gil, personal communication). While the click still contains a semantic component of attention getting, its exclusive usage in one specific context per population makes additional cues unnecessary for understanding its meaning. It qualifies as symbolic.

thus would become context-specific (AG_{cs}) for this individual. Over time, through social learning processes, its context-specific use would spread within the community. The original context-specific signal S_{cs} itself (*presenting*) on the other hand, though still being used, would become obsolete for understanding the sender's communicative intent. Thus, AG_{cs}, keeping its original form (the sound shape of leaf-clipping), within a specific population would undergo a semantic shift from a general attention getter to a context-specific attention getter. It being arbitrary and conventionalized through social learning processes would make it a strong candidate for being symbolic (AG_{symb}). (Also see the left column in Figure 1.)

The attention getter leaf-clipping could thus acquire an additional semantic component (*play, mating,* or *display* respectively) by being used in connection with a context-specific communicative signal. This additional semantic component then could be conventionalized within the given population through social learning processes and over time 'override' the attention getter's primary (general) meaning. The former attention getter thus keeps its form (the sound shape of leaf-clipping), but the underlying meaning would shift. As a result, the form would be completely unrelated to the new meaning (arbitrary relation), but linked to it by convention through social learning within a population (basic criteria for symbolic signal). The same process may underlie the emergence of the other potentially symbolic signal mentioned above, namely knuckle-knocking (see Table 1).

Unfortunately, it is unclear, which social learning strategies were applied in the different populations and contexts. Given the richness of social learning mechanisms (e.g., Heyes, 1994, 2012; Hoppitt & Laland, 2008, 2013; Laland, 2004), it is hard if not impossible to pin them down retrospectively.

However, one possible answer as to why the members of a population copy and thus conventionalize the usage of such a semantically modified signal would be the following. The limitation of usage of these auditory gestures to specific contexts is advantageous in environments with constrained vision, because the visual component of the original context-specific signal (S_{cs}) would become dispensable for understanding the new signal's meaning. If, for instance, knuckle knocking and leaf clipping in Taï were used interchangeably, it would be necessary to see the signaler to understand the context of use. The fact that they are not used interchangeably allows receivers to extract contextual information from the auditory signal alone, without needing to see the signaler.

This is especially important when signals require a quick reaction. Anecdotal evidence from Taï (Tobias Deschner, personal communication) suggests that the audience already moves away when hearing the leaf-clipping in anticipation of an upcoming display (thereby apparently reducing the risk of confrontation). For knuckle-knocking in Taï, where the signal is used for sexual solicitation by subordinate males as an inconspicuous means of attracting a female's attention

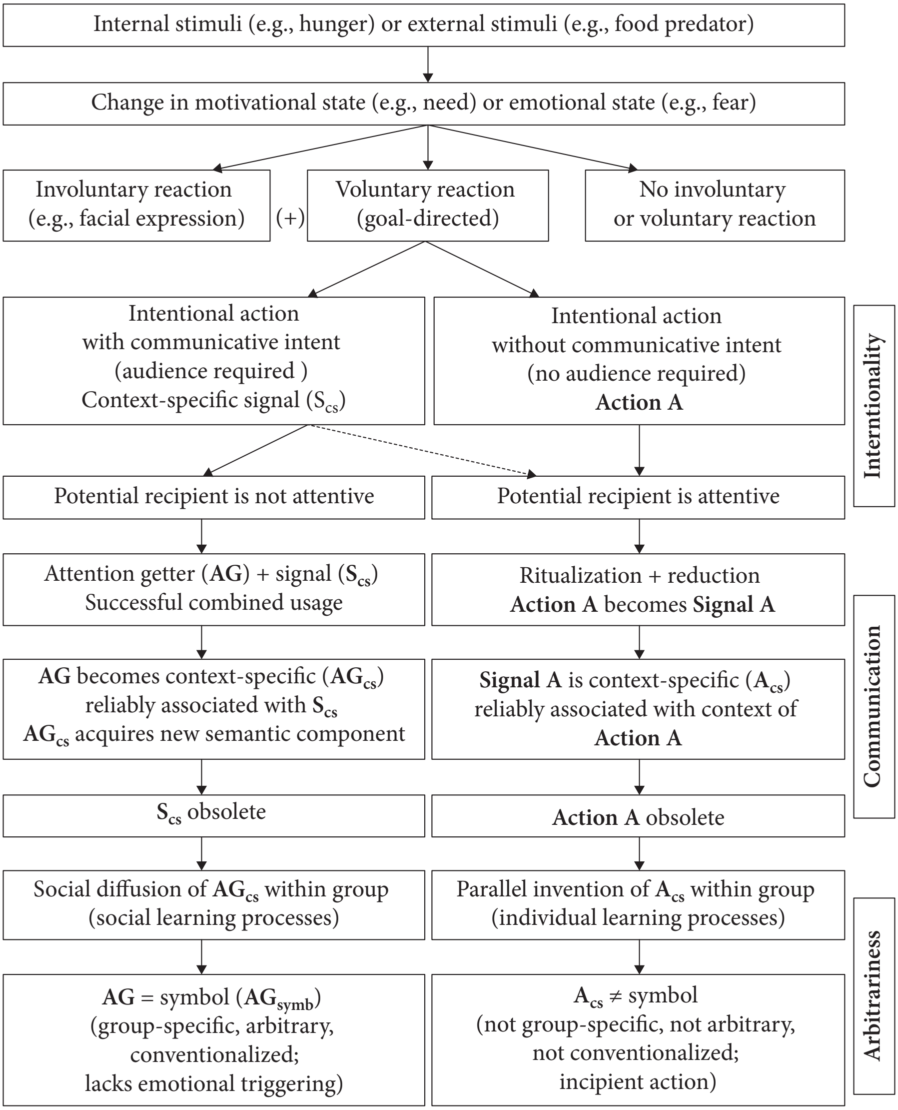

Figure 1. Emergence of a potentially symbolic signal from a general attention getter (left column) and of a non-symbolic incipient action (right column)

without a dominant male noticing, the context needs to be clearly expressed in the signal to get a rapid reaction from females. In a mating system where mating access for males is mainly controlled by dominants, and matings for females are limited by male coercion, there are strong adaptive reasons why signalers and receivers should benefit from conventionalized knuckle-knocking: females gain female choice and subordinate males gain mating opportunities. Thus, when there is a time pressure on signaling, the rapid communication of meaning without a visual component provides an adaptive benefit.

Systematic studies from the wild would be very welcome to achieve clarity on the communicative intentionality on the sender's side. However, given the use of these auditory signals in habitats where visibility is restricted, this might prove difficult. The visual monitoring of the potential recipient (one criterion used in determining intentionality in gestural interactions) might not be possible in many instances. In addition, a clear adjustment of the signal type to the recipient's attentional state (another criterion) would be unnecessary, given the auditory modality of the signal. On the other hand, the criteria of presence of a potential recipient, of goal directedness and of persistence should be measurable.

Moreover, it needs to be clarified whether the leaf-clipping and knuckle-knocking gestures are sufficient by themselves for the audience to deduce the respective meaning, or whether the audience takes into account additional context-specific information, and infers the meaning of the gesture only from the combination of all factors.

The process described in Figure 1 would not inherently be limited to attention getters. In principle, any gesture could undergo a semantic shift, if the resulting arbitrary signal (much like a tool-use technique) provides its users with a material or social payoff, thus becomes attractive to other group members and therefore gets copied (and eventually conventionalized) via social learning. The number of these arbitrary signals could then be enlarged, depending on the anatomical, neural, and cognitive abilities of the individuals involved.

It has been argued that a large part of the intentional gestures used by great apes are derived from actions that have undergone ontogenetic ritualization (these are known as incipient actions, see, e.g., Pika, Liebal, Call, & Tomasello, 2005), while Genty, Breuer, Hobaiter, and Byrne (2009) and Hobaiter and Byrne (2011) explicitly argue against this process. However, Liebal and Call (2012) point out that these studies are not longitudinal and thus lack the possibility of detecting changes within one individual. The forms of these intentional gestures thus resemble a part of an action that got reduced and ritualized (see the right column of Figure 1). The form and the meaning of incipient actions hence are strongly connected and a semantic shift (resulting in arbitrariness) thus becomes unlikely.[5]

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[5] In addition, incipient action gestures originate from individual learning processes rather than from social learning processes. That is, they are created between two individuals rather than being copied (and thus eventually conventionalized) by several individuals of the same population. As they can arise in parallel in several dyads, they might happen to be intelligible between more members of the same group than only strictly within the dyads in which the signal evolved. This intelligibility, however, is the result of parallel emergence and should not be confounded with conventionalization through social learning processes.

Contrary to incipient actions, in auditory gestures (much like in vocalizations) the form (sound shape) and meaning do not have to be closely related. A semantic shift therefore becomes more likely.

Another possible candidate for a semantic shift (and potential symbolic signal use) in an auditory gesture would be the use of buttress-drumming observed in the travel context in the alpha male of a chimpanzee population in Taï National Park (Boesch, 1991a, 1996; Crockford & Boesch, 2003). The so-called 'buttress beat' with hands and/or feet is present in several wild chimpanzee populations (e.g., Whiten et al., 1999, 2001) and is used in the context of display or for long-distance communication on the sender's location. But the gesture apparently underwent a semantic shift in one chimpanzee population in Taï. It seems to have been used by the alpha male to announce resting and/or a change of travel direction. Although being applied by only one individual, the evidence presented by Boesch suggests that the signal's specific usage had been conventionalized within the group as the group members seemed to adjust their travel accordingly. Moreover, the semantic shift provided the possibility of temporal displacement as some of the apparently announced changes in travel direction would not happen before one hour of resting had passed. Interestingly, the alpha male showed this semantically modified signal use only during the presence of numerous adult males, as if to procure group coordination in a large territory with constrained vision. Unfortunately, a similar semantic modification has not been documented in other adult males, in the same or in other populations.

We consider it probable that, in addition to the semantic shifts that have occurred in the gestures of leaf-clipping, knuckle-knocking, and buttress-drumming, there are further similar shifts yet to be found in wild chimpanzees and potentially other great apes, especially in gestures of the auditory modality. Systematic studies are needed to determine their range and usage.

In summary, in wild chimpanzees there seems to exist a mechanism for population-specific semantic shifts in which the meaning of existing communicative signals is modified without changing the signals' form, thus resulting in new vocabulary items. The new signals created thereby might be symbolic due to reference by arbitrary convention. Given the strongly limited production and usage of vocalizations in great apes and other nonhuman primates, the occurrence of the shifts in auditory gestures might constitute a way of bypassing the creation of new arbitrary vocalizations. Thus, we may be witnessing a first step in the evolution of symbolic signals, although these being gestural and not vocal. Maybe there are selective pressures acting, for example in connection with constrained vision habitats, but their effects so far are not strong enough for us to recognize them clearly. However, the number of potential candidates for this process is apparently limited. As argued above, incipient actions may not be as easily be semantically modified as auditory attention getters, because the meaning and form of incipient actions are more closely related. Thus, while these shifts might provide wild great apes with the possibility of expressing displacement (for instance, in the case of buttress-drumming), they do not (so far) constitute a means for considerably enlarging the great apes' repertoire of communicative signals. This enlargement would be necessary to move towards the above mentioned language advantage of open-endedness.

Covertly intentional provision of eavesdroppers with natural meaning

In the following we thus suggest a second means that great apes may be using to communicate a wide array of meanings for effectively informing, helping, and manipulating each other without considerably enlarging their repertoires of intentionally communicative signals. This strategy may not be easily recognizable for human observers. For detecting it, it is essential to perceive the great apes within the context of their natural ecology that over millions of years has shaped their minds and social interactions.

Great apes live in complex material and social environments. In addition to interpreting intentional gestures and vocalizations, they need to rely on other means of gaining information about their conspecifics and their environment in general. A very important, perhaps essential, role in this is played by 'eavesdropping', by which we mean the monitoring and interpretation of conspecifics' behavior to gather information (for example about the location of food or the presence of predators, about directions of travel as well as about social relations) (e.g., Griffin, 1984). Fitch (2005) attributes "highly-sophisticated perceptual and interpretative abilities" and "a complex inferential and interpretative system" to nonhuman primates. This includes the interpretation of movements and body postures as well as the following of eye gaze. It is thus not surprising that captive great apes perform well in experimental studies on gaze following (Call, Agnetta, & Tomasello, 2000; Tomasello, Call, & Hare, 1998; Tomasello, Hare, & Agnetta, 1999; Tomasello, Hare, & Fogleman, 2001). Moreover, findings on captive chimpanzees suggest that they are capable of perspective taking (e.g., Hare, Call, & Tomasello, 2001; Schmelz, Call, & Tomasello, 2011) and understanding others as having goals and intentions as well as knowledge and perceptions of their own (e.g., Call & Tomasello, 2008; Hare, Call, Agnetta, & Tomasello, 2000; Tomasello, Call, & Hare, 2003). Call and Tomasello (2008) thus conclude that chimpanzees have a theory of mind in the sense of understanding that the behavior of conspecifics results from the latter's perception of their environment and the goals that they pursue in it.

Considering (a) the great apes' ability to perceive conspecifics as intentional agents with goals and perceptions, and (b) the fact that they not only monitor others but at the same time are being observed themselves, it seems only a small step to ask how individuals that are being observed by others might go about trying to intentionally influence their observers' behavior (and potentially their mental states).

One possibility would be the use of very subtle intentional gestures and vocalizations that are hard to recognize for the human observer as not even eye contact may be involved. In addition, evidence for attempts of intentional manipulation of conspecifics' knowledge and behavior is provided by cases of passive and active tactical deception in nonhuman primates, that is, the intentionally deceptive inhibition or display of behaviors or communicative signals, for example in the contexts of feeding or mating to increase their food intake or mating success (e.g., Byrne, 1993, 2003, 2010; Byrne & Whiten, 1990, 1992; Slocombe et al., 2010; Slocombe & Zuberbühler, 2007).

We would like to go further than this. We suggest that great apes, in addition to intentional gestures and vocalizations and to deceptive behaviors, intentionally display non-deceptive behaviors with the intent of manipulating their conspecifics' behavior, of helping them or of informing them. In doing so, they would provide their conspecifics with natural meaning (in the sense of Grice, 1957) and thus would be able to express a wide array of (natural) meanings without the need to create new forms (for instance, sound shapes).

Grice (1957) distinguished between *natural meaning*, using the example of "Those spots mean (meant) measles." and *nonnatural meaning*. *Nonnatural meaning* is linked to its respective form non-naturally, that is, arbitrarily (like for instance, symbols in human language or in traffic lights). *Natural meaning*, on the other hand, is not arbitrarily but naturally linked to the respective form and is available in our physical environment. This includes our fellow human beings' behavior. For great apes too, *natural meaning* is provided by their physical environment, which includes their conspecifics. An example for *natural meaning* in great apes would be the sexual swelling in female chimpanzees in estrus. Examples for *nonnatural meaning*, if present at all in great ape communication, may be the signals of leaf-clipping and knuckle-knocking (see Table 1).

Given that overt communicative intent and nonnatural meaning are prevalent in human communicative interaction, studies of animal communication often focus on these in an anthropocentric fashion. We maintain that it is equally important to investigate means of covertly intentional communication, an area which is still covered by the Gricean theoretical framework.

According to Grice, in intentional (nonverbal) communication natural meaning can be provided with overt or covert communicative intent. Grice illustrates this with the following examples (G1 and G2):

- overtly intentional provision of natural meaning

> (G1) Herod presents Salome with the head of St. John the Baptist on a charger.

Herod's communicative intent is made rather overt by the blatant presentation of St. John's head on a charger (instead of simply putting it somewhere for Salome to find it eventually) and is easily recognizable to Salome. This can be compared to intentional (non-arbitrary) gestures by which great apes provide conspecifics with natural meaning: as for example, presenting specific body parts for grooming, or presenting a genital swelling for sexual solicitation. These intentional gestures are marked with overt communicative intent, expressed by the ostensive positioning of the respective body part in the line of sight of the potential recipient (Moore, forthcoming). The recognition of communicative intent, however, is not relevant for successful communication.[6]

- covertly intentional provision of natural meaning

> (G2) Feeling faint, a child lets its mother see how pale it is (hoping that she may draw her own conclusions and help).

Here, the sender's communicative intent is less overt to the potential recipient, or in fact might be completely covert. Still, the communication might be successful in that the mother (knowingly or not) reacts according to the sender's communicative intent. Thus, the recognition of communicative intent clearly is not being relevant for the production of the intended effect in the recipient.

We argue that in the social interactions of great apes there may exist constellations similar to (G2). In order to manipulate their conspecifics' behavior, individuals may intentionally, but without overt communicative intent, display specific behaviors and in this way intentionally provide eavesdropping conspecifics with a potentially wide array of natural meaning as, for example, when a female chimpanzee with a genital swelling walks past a (subordinate) male without overtly presenting the swelling, while still making sure that he notices it.

In the following we suggest behaviors that may be candidates for the covertly intentional provision of natural meaning.

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[6] Scott-Phillips (2015) states that overt communicative intent – in the sense of bringing attention to the intentions that are being expressed – is the key criterion for the presence of nonnatural meaning, and that so far it has not been detected in non-human animal communication. We argue that overt communicative intent does exist in great ape gestural communication. At the same time, the recognition of the communicative intent by the recipient is not necessary for the correct interpretation of these gestures. The presence of overt communicative intent thus would not automatically entail the presence of nonnatural meaning.

Leading. Kummer (1968, 1971) describes the leading behavior of male Hamadryas baboons (*Papio hamadryas*) in the context of morning departure from the night cliff. Individual males suggest a direction of travel by walking several meters away from the troop and sitting down, without overtly marking their behavior as being communicative by looking back or vocalizing (see *body orientation* below) but still providing natural information on the suggested direction of travel. At some point, a dominant male then strides purposefully in one direction, without displaying any overtly communicative signals either, and thus provides natural information on the troop's route of travel.[7] The troop then adopts this direction.

Another example may be provided by chimpanzee males in Mahale (Nishida, 1997) who in the context of courtship try to lead females to specific locations for mating by walking in the respective direction and thus providing the female recipients with natural meaning (direction). The same behavior can be observed in Taï (Boesch, personal observation). Here the male can become aggressive towards the female when she does not follow, which might indicate that the signaling male is not satisfied with the female's behavior.

Body orientation. Further evidence can be found in the great apes' use of intentional body orientation (for instance, whole-body pointing) to direct the attention of conspecifics (or humans) into a specific direction. While some of these might be overtly marked as communicative, for example by accompanying vocalizations (e.g., Menzel, 1971), and thus qualify as intentional gestures with overt communicative intent, there seem to be instances where the communicative intent is covert. Thus, studies of orangutan mother-infant dyads in Tanjung Puting National Park, Central Kalimantan, Indonesia (Cissewski, personal observation) suggested the presence of covertly communicative whole-body pointing in connection with impending travel. An orangutan mother with an offspring that is able to travel on its own will move into the intended direction, but may stop and 'freeze' in the traveling posture without turning around or vocalizing when the infant does not follow. The mother's body posture provides natural meaning on the impending departure and also on the direction of travel. Although no hands or arms are involved nor are gaze alternation or vocalizations, this conforms with Kita's (2003) definition of pointing as a "communicative body movement that projects a vector from a body part. This vector indicates a certain direction, location, or object."

Sharing. Further evidence for the intentional display of behaviors without overt communicative intent to provide conspecifics with natural meaning may be presented by those cases of sharing (that is, the relinquishing of objects like

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[7] In a small number of reported cases, the male's movement was marked by a 'swinging gait' that would qualify as a sign of ostension and thus would express the sender's communicative intent (overtly intentional provision of natural meaning, see example G1).

food and tools to conspecifics) where an individual makes objects accessible to a conspecific by intentionally dropping or leaving them, or by moving them 'inconspicuously' into the potential recipient's direction, e.g., in the case of meat sharing in chimpanzees. (Note that the explicit offering or presenting of these objects would qualify as a gesture, marked with overt communicative intent – see example G1 above.) Although this behavior is not overtly marked as being communicative, it is communicatively directed at (and usually interpreted accordingly by) a conspecific.

Boesch (1991b) observed the sharing of nuts and nut-cracking tools in the Taï chimpanzee community (Côte d'Ivoire). He found that in addition to the widespread (passive) nut sharing and tolerance towards peering (and nut-grabbing) by infants, chimpanzee mothers tried to enhance the acquisition of nut cracking in their offspring by intentionally providing natural meaning (see Table 2). They did so via the following strategies:

(1) *facilitation*, that is, leaving the hammer or a nut for the infant to use, getting a new hammer or nuts for themselves

(2) *stimulation*, that is, leaving the hammer, which the mother usually would carry with her when looking for nuts, next to the anvil with some nuts or even putting a nut on the anvil with the hammer next to it

(3) *active teaching*, that is, demonstrating the correct positioning of the nut on the anvil or an exaggeratedly slow demonstration of getting the right grip of the hammer, while carefully monitoring the infant's eye-gaze

Note that the strategies applied by the chimpanzee mothers correspond to the level of nut-cracking abilities in the offspring, that is, the better the abilities, the less natural meaning is provided. Stimulation thus culminates at the infant's age between 3 and 4 years, facilitation culminates between 5 and 8 years (Boesch, 2012b).

Unfortunately, so far there do not seem to exist systematic studies on the covertly intentional provision of natural meaning in great apes (or other nonhuman primates). As stated above, the human perspective on animal communication is influenced by a strong reliance on language (that is, nonnatural meaning) and on other means of overtly intentional communication. It is therefore understandable that this strategy has not been described yet. However, humans (like many other animals) consciously or subconsciously eavesdrop on an intra- as well as inter-species level. For the latter, consider the keeping of watch dogs whose barking alerts us to possible intruders. And humans intentionally provide conspecifics with natural meaning without overt communicative intent. For example, by making noises like coughing or fiddling with coins by an unattended till to alert a shop assistant of our presence. The communicative intent may not be obvious,

Table 2. Chimpanzee mothers' intentional strategies for enhancing their infants' acquisition of nut-cracking by providing them with natural meaning

natural meaning / intentional strategy	tools/food	set-up	technique
facilitation	✓		
stimulation	✓	✓	
active teaching (rare)	✓	✓	✓

but communication still works. Thus, in spite of the importance of language in our daily interactions, covertly communicative strategies still play a role that should not be underestimated.

Note that we do not intend to suggest that the covertly intentional provision of natural meaning for communicative purposes is used exclusively by humans and other great apes and thus sets them apart cognitively from other animals. Rather, it cannot be excluded that other species (with a sufficiently developed social intelligence) are making use of this strategy as well.

To summarize, the intentional provision of natural meaning without overt communicative intent may allow great apes to communicate a wide array of meanings without creating a language-like system of symbolic communication. The advantage of open-endedness given in language, that is, the unlimited creation of symbols and symbol combinations to express new meanings, may be partly covered by this strategy. There is no evidence so far for its application for expressing temporal or spatial displacement though.

Summary of communicative strategies

The following overview summarizes the intentionally communicative means described above:[8]

(a) covertly intentional display of specific behaviors to provide eavesdropping conspecifics with natural meaning – form and meaning are linked non-arbitrarily

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[8] As the level of intentionality seems to vary in the production and usage of different vocalizations and is still debated, they are not included here.

Example A: A female chimpanzee with a genital swelling walks past a subordinate male without overtly presenting the swelling, while still making sure that he notices it.

(b) overtly intentional use of gestures to provide conspecifics with natural meaning – form and meaning are linked non-arbitrarily
Example B: An individual presents a specific body part for grooming (or a genital swelling or an erect penis as an invitation to sexual intercourse).

(c) overtly intentional use of arbitrary gestures – form and meaning are linked arbitrarily (nonnatural meaning) as a result of population-specific semantic shift
Example C: A Mahale chimpanzee leaf-clips as an invitation to sexual intercourse.

These correspond to the section marked in bold in Table 3 below.

Table 3. Intentional provision of natural and nonnatural meaning in great apes' communicative interactions

natural meaning			**nonnatural meaning**
provided by physical environment (including sentient agents)			provided by sentient agents
unintentional availability of processes, states, and behaviors	*intentional*		*provision of*
	non-arbitrary		arbitrary
	behaviors	gestures	gestures
no communicative intent	covert	overt	overt
	communicative intent		

Discussion and perspectives for future research

We proposed the existence of two strategies that may allow great apes to communicate a wide array of meanings without considerably enlarging their repertoires of overtly communicative signals and thus to cover, to a certain extent, crucial advantages provided by language, namely *displacement* and *open-endedness*.

First, *population-specific semantic shifts* in gestures in the auditory modality in several wild chimpanzee populations may allow for more effective communication under specific social and ecological circumstances, for instance, in the case of need for a rapid response in habitats where visibility is restricted. They thus may provide an adaptive benefit for the sender and the recipient.

It has been stated that in great apes and other nonhuman primates the production and usage of vocalizations is highly constrained (e.g., Fitch, 2005; Hammerschmidt & Fischer, 2008; Seyfarth & Cheney, 2010). In contrast, however, the gestures resulting from population-specific semantic shifts provide the animals with more efficient acoustic signals since they combine precisely defined meanings with a flexible production and usage. They thus constitute a viable alternative to an apparently hard-to-achieve extension (both in size and flexibility) of the vocal repertoire.

In addition, the arbitrary and potentially symbolic nature of the auditory gestures resulting from semantic shifts seems to allow for *displacement* in chimpanzee natural non-vocal communication, as described by Boesch (1991a, see above) for buttress-drumming.[9] This would indicate that the cognitive competencies underlying the expression of displacement with human-provided symbols in captive settings (as discussed, e.g., by Call, 2011; Lyn et al., 2014) are present in wild chimpanzees and thus cannot be interpreted as the result of enculturation. Moreover, the actual expression of displacement in natural great ape communication shows that great apes do not only have concepts of spatially and/or temporally displaced items or events (as described, for instance, by Boesch & Boesch, 1984; Janmaat, Ban, & Boesch, 2013; Mulcahy & Call, 2006; Normand, Ban, & Boesch, 2009; Osvath & Osvath, 2008; Osvath, 2009; Zuberbühler & Janmaat, 2010), but that they also try to communicate them – when motivated to do so.

The symbolic nature of the gestures resulting from semantic shifts still needs to be confirmed. For this, and for analyzing potentially symbolic signals in great ape natural communication in general, it is important to bear in mind that the term 'symbolic', unfortunately, has acquired unhelpful baggage. In particular, like other terms before, for instance, 'culture' and 'tool use', it has been used by some as definitional of human uniqueness. Deacon (1997), for example, restricts linguistic symbolism to human communication only, that is, to complex systems that rely on a multi-level relationship between linguistic symbols. In these systems, the specific meaning of a linguistic symbol is determined by its position relative to other elements in the system. While this may be true, it describes a phenomenon that (at least in its complexity) seems specific to human language, namely the influence that the combination and hierarchical structure of linguistic symbols have on their meaning and resulting reference (but see Crockford & Boesch, 2005; Arnold & Zuberbühler, 2006a, 2006b; Ouattara, Lemasson, & Zuberbühler, 2009a, 2009b; and Zuberbühler, 2002, for evidence of the semantic modification

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[9] For evidence of displacement in great ape vocal communication, see van Schaik, Damerius, and Isler (2013) who discuss possible displacement in wild orangutan males' long calls. Both cases involve the transmission of information on future travel direction.

of communicative signals in call combinations in several non-human primate species). Deacon thus provides us with a (possible) definition of human symbolic communication, but not with a definition of symbolic communication *per se*.

To understand the nature and extent of symbolic signal use in great apes (and potentially other nonhuman animals) we need to abandon an anthropocentric definition of symbolic communication in the sense of language. The evident lack of such a complex system in great apes does not exclude the presence of symbolic signal use.[10] Therefore, when analyzing systematic data on population-specific semantic shifts, it will be necessary to concentrate on the basic characteristics of symbolic reference (e.g., Saussure, 1916/2003) with the signifying form (sound shape) and the signified meaning (concept) of the linguistic symbol being linked arbitrarily by convention through social learning processes within a population. If (even only some of) the gestures resulting from these shifts meet these characteristics, it will be time to accept the presence of symbolic signal use in natural great ape communication.

The data on population-specific semantic shifts in wild chimpanzees available so far are mostly anecdotal in nature. Thus, systematic data collection on the repertoires of auditory gestures[11] as well as on their production, usage and comprehension in different chimpanzee populations is essential to find out where these shifts have occurred, whether the resulting gestures are truly referential (that is, whether they are understood without other contextual clues), whether they are used with communicative intent (thus excluding merely functional reference), and whether they serve to express displacement. A comparative analysis will reveal whether different meanings are expressed by the same form in different populations, or different forms express the same meaning in different populations (as described above for leaf-clipping and knuckle-knocking), thereby not only excluding emotional triggering but also providing further proof for reference by arbitrary convention and thus for symbolic signal use.

Systematic long-term studies would provide insights into the ontogeny of auditory gestures in general and the acquisition of established auditory gestures that result from semantic shifts in particular. Moreover, in the case of ongoing shifts, long-term studies could reveal the mechanisms of transmission involved in the

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[10] Thus, for instance, Wich et al. (2012) report on differences in orangutan calls and their usage in different populations and exclude a role of genetic difference between populations, emphasizing the role of learning. They conclude that these calls qualify as conventionalized 'arbitrary symbols'.

[11] As mentioned above, in auditory gestures form (sound shape) and meaning do not have to be closely related and thus semantic shifts are more likely to occur. In gestures of the visual or tactile modality, to the contrary, the form often in part resembles the original behavior that was reduced and ritualized.

spread and conventionalization of an auditory gesture resulting from such a shift within a population, as well as the selective pressures at work. In which context(s) is the gesture used before and after the shift? How and why is the modified usage copied? Does the usage and comprehension of the modified gesture thus provide an adaptive benefit, and if so, which? Is time pressure of importance, as for instance is hypothesized above for knuckle-knocking in Taï? Does constrained vision play a role? What other social or environmental factors are involved?

Finally, a search for population-specific semantic shifts in the auditory gestures of other great ape species or nonhuman primates in general would reveal whether they are unique to chimpanzees or are a shared phenomenon. Such studies would help to provide insights into the phylogenetic origins of arbitrary gestures and thus of potentially symbolic non-vocal signal use.

As a second strategy of intentional communication we suggested the *covertly intentional provision of natural meaning to eavesdropping conspecifics*. This strategy may allow great apes to communicate a wide array of meanings without considerably enlarging their repertoires of overtly communicative signals and thus to cover in part the language advantage of *open-endedness*. Although this means of communication is not overtly communicative, it may nevertheless provide a powerful tool for influencing conspecifics' behavior.

Research has shown that great apes possess impressive cognitive abilities in the social sphere, including perspective taking and the understanding of others as intentional agents with goals, intentions, perceptions and knowledge of their own (e.g., Call & Tomasello, 2008; Hare, Call, & Tomasello, 2001; Hare, Call, Agnetta, & Tomasello, 2000; Schmelz, Call, & Tomasello, 2011; Tomasello, Call, & Hare, 2003). These inferential abilities seem to result, for instance, in a highly flexible and open-ended comprehension of communicative signals both at an inner-species and inter-species level (for vocalizations, see Seyfarth & Cheney, 2010). However, it also has been stated that nonhuman primates do not seem to be able to communicate a large proportion of their rich mental activity (e.g., Fitch, 2005; Cheney & Seyfarth, 2007).

While this seems to be the case for the means of overtly intentional communication observed so far (that is, gestures and vocalizations), the situation might be different for strategies of covertly intentional communication, especially for providing eavesdropping conspecifics with natural meaning, as described above. Here, the intentional display of behaviors for communicative purposes would be highly flexible and in principle open-ended. This then might explain in part the lack of pressure to develop a more complex system of overt communication.

If the intentionality of these behaviors can be established, this would provide evidence that great apes not only make inferences about other individuals' actions and mental states but also for actively influencing at least their behavior.

Systematic studies regarding the presence of communicative intent underlying these behaviors are needed. As no overtly communicative signals are used, it is hard for a human observer to recognize such behaviors as being displayed intentionally. It therefore might be helpful to apply the intentionality criteria used in studies on gestural communication:

- Is the behavior displayed in the presence of conspecifics?
- Is it adjusted to the potential recipient's attentional state?
- Does the sender visually monitor the potential recipient's reaction?
- Does the sender show persistence?
- Does the sender's behavior stop after the goal is reached?

It is also hard to determine the level of intentionality underlying this communicative means in great apes, especially during observational studies in the wild. Would the apes apply this strategy for triggering specific responses in their conspecifics as learned from previous observation, without taking into account the audience's mental states (first-order intentionality)? Or would they aim at manipulating not only the audience's behavior but also their mental states (second-order intentionality) (Dennett, 1987)?

Given this potential indeterminacy, it is important to be clear about what exactly we are claiming. Namely, we propose that the strategy of covertly intentional provision of natural meaning requires only first-order intentionality to be successful. Our account does not need anything further. Of course, in view of what is known about the presence of mental state attribution in great apes, it will be worth investigating the possibility of second-order intentionality. However, to make progress on this issue we may need the controlled environment of studies in captive settings.

It is impossible to know whether the recipient is always aware of the communicative intent underlying the behavior displayed by the signaler. However, even if the recipient is not aware, this would not influence the communicative success, because, as set out above, the recognition of communicative intent is not relevant for successful communication.

In summary, great apes may possess more strategies to communicate intentionally (and perhaps even symbolically) than has been previously assumed. In the absence of selective pressures that would strongly favor the emergence of a language-like system of communication, these strategies (and potentially others, yet to be discovered) would provide great apes with sufficient means for communicating successfully within their complex material and social ecologies. There is much more to be discovered, through systematic and comparative studies. We hope that our theoretical groundwork will stimulate the research necessary to answer these intriguing and significant questions.

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