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COMMENTARIES

A multidimensional approach to investigations of behaviour: revealing structure in animal communication signals

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Studies of animal behaviour reveal that some species have cognitive skills once believed to be evolutionary adaptations unique to humans (e.g. tool use, cooperative hunting; e.g. Boesch & Boesch 1989; Stanford et al. 1994; Boesch 2001). However, our ability to comprehend and generate spontaneous and novel phrases with underlying semantic and syntactic structure still sets us apart from other animal species. Research suggests that the ability to acquire and use human language is linked to the evolution of specific increased neocortical volume (Barton & Dunbar 1997), which in turn is thought to precipitate a theory of mind, or the cognitive ability to understand that others have beliefs, desires and intentions that are different from one's own (Premack & Woodruff 1978). As primates have evolved, the size and complexity of social groupings have also increased, perhaps requiring a more sophisticated communication system (Dunbar 1993; Hauser 1996). However, exactly how modern human language evolved from our preverbal communication skills is still poorly understood.

It has long been accepted that communication is a process in which animals use their sensory organs to send and receive information about the world (Darwin 1872; Tinbergen 1959; Marler 1965). Humans use a rich repertoire of verbal and nonverbal signals to communicate. Along with the salient auditory signal of vocal speech, we use visual communication signals in the form of manual gestures, body postures, facial expressions and eye gaze, which are important for providing information about individual identity, social hierarchy, emotional states, intentions and receptiveness (Tomasello & Camaioni 1997). Like humans, many animal species produce and respond to information in the surrounding environment with signals comprising combinations of sensory components. These signals are considered to be 'multimodal' or 'multisensory' (Hölldobler 1995; Johnstone 1995, 1996). For instance, in humans, facial expression and visual articulatory movements play a role in vocal perception (McGurk & Macdonald 1976; Smith 1977, 1990; Massaro 1998). Qualitative analyses of communication suggest that signalling is not only a multisensory process, but also a dynamic one that is greatly influenced by contextual factors (King & Shanker 2003).

Evidence from various animal studies has demonstrated the presence of signal structure during communication. These species include the honeybee, *Apis mellifera* (von Frisch 1947, 1967; Seeley 1995; Dornhaus & Chittka 1999), Gunnison's prairie dog, *Cynomys gunnisoni* (Slobodchikoff et al. 1991; Slobodchikoff & Placer 2006), suricates, *Suricata suricatta* (Manser 2001; Manser et al. 2001) and several species of birds, including fowl, *Gallus gallus* (Evans et al. 1993; Evans & Marler 1994; Evans & Evans 1999), ravens, *Corvus corax* (Bugnyar et al. 2001), yellow warblers, *Dendroica petechia* (Gill & Sealy 2004) and black-capped chickadees, *Poecile atricapilla* (Templeton et al. 2005). Semantic or referential structure in animal communication is important because it allows scientists to draw parallels between animal communication and human language (Hauser 1996; Evans 1997; Fitch 2005). Communication research suggests that some nonhuman primates can produce alarm calls with semantic structure (*Chlorocebus aethiops*: Seyfarth et al. 1980a; *Macaca mulatta*: Marler et al. 1992; *Cercopithecus diana*: Zuberbühler et al. 1997; Zuberbühler 2000a). Some species can respond differentially to vocalizations based on the information they provide (*C. aethiops*: Seyfarth et al. 1980b; *Chlorocebus*

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spp.: Cheney & Seyfarth 1981; *Cercopithecus campbelli*: Zuberbühler 2001) and can manipulate call frequency based on their audience (Cheney & Seyfarth 1990; *Presbytis thomasi*: Wich & Sterck 2003).

It would be ethologically valid to hypothesize that the animals with the closest genetic link to humans would express communication skills with some similarities to humans, and that these skills may reveal clues regarding the evolution of modern human language. Nonhuman great apes are often considered a good model to study human behaviour because, like humans, they navigate highly complex social networks using a range of sensory signals and have evolved from a common human/ape ancestor over 6 million years ago. However, the list given above of nonhuman primates with semantic structure in vocal signals does not include our closest genetic relatives. Studies attempting to reveal structure in great ape vocal signals have generally done so with the aim of revealing human language-like structure in the communication signals of nonhuman primates (e.g. Fossey 1972; Marler & Tenaza 1977; Mori 1983; Patterson et al. 1988; Seyfarth et al. 1994; Slocombe & Zuberbühler 2005). Studies have generally revealed a lack of systematic referential signal structure (Mitani & Nishida 1993; Crockford & Boesch 2003) and have produced limited evidence of signal flexibility (the ability to generalize or generate novel sequences) within the vocal mode alone (e.g. Liebermann 1998; Corballis 2002). Although a lack of signal structure in ape communication may seem surprising, there may be a simple explanation having more to do with the partial approach we use to observe and assess communication and less to do with a lack of signal structure in great ape communication. For example, there is a growing body of research supporting evidence of referencing in the visual signals of captive apes, which appears to be involved in more social aspects of communication (Miles 1990; Leavens et al. 2004; Pika & Mitani 2006).

Like those of humans, great apes' communication signals are visual, tactile or auditory in origin (Pika et al. 2005; Liebal et al. 2006; Tomasello & Call 2007). Within the visual and tactile modalities, apes show communicative social skills akin to those of humans for visual facial expression, eye gaze, referential glancing, manual gestures and tactile signals (e.g. huddling, grooming) used for social cohesion (Seay et al. 1962; van Hooff 1972; Suomi 1986; Dunbar 1991; Estes 1991; Preuschoft 1992; Preuschoft & van Hooff 1995; Tanner & Byrne 1996; Tomasello et al. 1997; Schino 2001; reviewed in Emery 2000). Many of these signals are used in social or nonevolutionarily urgent contexts (e.g. grooming, playing) and are akin to the communicative skills thought to be key markers of the cognitive capacity to represent internal thought in humans (see Tomasello & Call 1997 for an alternative view). There is strong evidence to suggest that both vocal and visual communication signals played a role in the evolution of modern human language (Corballis 2002; McComb & Semple 2005). Based on this evidence, one possibility is that a lack of evidence for signal structure in unimodal studies of ape vocal communication is due not to its absence, but rather to an inadequate experimental approach. Unimodal studies are not well suited to tackling questions regarding underlying multicomponent structure and, thus, the communicative consequences of combining signal components in nonhuman great apes and other animal species (including humans) remain poorly understood.

Although multimodal communication has proven to be an important form of signal generation among primate species (e.g. Goldfoot 1982; Rowe & Guilford 1999, 2001; Partan & Marler 1999; Partan 2002) to date, there have been fewer than a handful of modern studies that have attempted to reveal structure in signal production. The existing studies of great ape multimodal communication used various methodologies for data collection and coding (e.g. Altmann 1962, 1965; Partan 2002; Crockford & Boesch 2003; Leavens & Hopkins 2005), most of which completed their analyses of communication with the assessment of two sensory signals (e.g. vocal and manual). These studies have been ground breaking, demonstrating that signal combinations increase specificity levels in particular contexts. They suggest that signal combinations convey context-specific information that would not be available from a single sensory output. These studies have also revealed that apes vary the sensory modality outputs based on the attentional direction of an observer, suggesting that the signaller is capable of discriminating the attentional orientation of their social partners (Hostetter et al. 2001; Liebal et al. 2004). In a recent review of ape communication signals, Partan & Marler 2005 found that most signals were used flexibly, with the majority performed in three or more social contexts and one-third of signals used in combination with other signals. Furthermore, studies have indicated that when a distributed cognition model (DCM) was applied to data sets of animal behaviour (Johnson 2001), the attentional state of the interacting subjects (e.g. eye gaze, body/head position) had a direct effect on the modality used to communicate (Johnson 2001; Johnson & Karin-D'Arcy 2006). The investigations cited above have taken critical steps towards revealing latent structure in great ape communication. However, existing studies have investigated limited and inconsistent sets of sensory channels, highlighting the need for coherent measures across laboratories within a common scientific framework to establish a common scientific language with which to discuss and evaluate animal communication signals.

Methods

One of the goals of presenting a new method is to shift our perception of animal communication from a unimodal process to a distributed network of collaborating modalities, mimicking the distributed processes of disparate brain regions that collaborate for sensory perception. Here, I offer a multidimensional method (MDM) with a primary aim of extracting synchronous and sequential patterns from a distributed database of natural visual, tactile and auditory communication signals. There is no ethological drive to decipher signal meaning or to translate primate behaviour into an analogous human repertoire of events. The MDM is a noninvasive, quantitative approach to the investigation of animal communication. This method considers communication signals within a natural social context through two different visual perspectives using two synchronized digital video recordings. This methodological framework builds upon the work of several previous studies (Adams & Schoel 1982; Hauser et al. 1993; Partan & Marler 1999; Partan 2002; Crockford & Boesch 2003).

There are three key benefits associated with this methodological approach. First, behaviour is captured using two synchronized video cameras to obtain focal animal behaviours within social context from two different focal ranges and two varying visual perspectives social context. Social context refers to factors that are not internal to the focal subject. These factors include variables about the physical environment that may influence communicative signals (e.g. who is present, location of interaction, proximity between animals). While one camera records a focal individual in full frame, a second camera concentrates on a wide angle that encompasses the focal subject and its their social partners and surroundings. The second key innovation of this approach is that video streams are viewed in synchrony and coded offline to establish the direction and timing of physical actions creating an 'action database'. Finally, the flexible nature of the observation and coding techniques makes this a valuable tool for capturing and analysing a large breadth of communication signals across a broad range of animal species, over multiple behavioural levels. The MDM has proven to be a successful tool for recording communication, coding signals and revealing patterns in synchronous signals and sequences of signals (G. S. Forrester & D. A. Leavens, unpublished data; G. S. Forrester, D. A. Leavens, K. A. Bard & N. A. Forrester, unpublished data).

Subject

Although the following method for investigating the structure of communication signals is not restricted to a specific animal species, this study focuses on a single gorilla, *Gorilla gorilla gorilla*, to demonstrate the benefits and practical uses of the methodological technique. Nonhuman great apes provide an excellent model with which to investigate the roots of a highly complex system of dynamic signals as well as to contribute to our understanding of the evolution of modern human language.

The focal subject was Foufou and her social network. At the time of data collection, Foufou was a 13-year-old, high-ranking, adult female western lowland gorilla living in a peer-raised, biological, family group (13; 8 females, 5 males) at Port Lympne Wild Animal Park, Kent, U.K. The family group consisted of one silverback, seven adult females and five juveniles (4 males, 1 female) all fathered by the silverback. The gorillas are considered 'semi free ranging', in that they could move freely about a large indoor/outdoor enclosure composed of four composite parts (inside, caged upper, caged lower and garden). Their enclosure is the world's largest family gorilla house and is modelled on the habitat of wild gorillas. The front of the outside enclosure is glass, and comprises two tiers, both of which are equipped with ropes and nets and other equipment to encourage activity. Inside, there is a play area and 14 bedrooms. The gorillas also have access to a large garden comprising climbing equipment, a small stream and a large pile of boulders. The garden enclosure has viewing windows at ground level and unimpeded visual access via a raised walkway that follows the top of the garden wall.

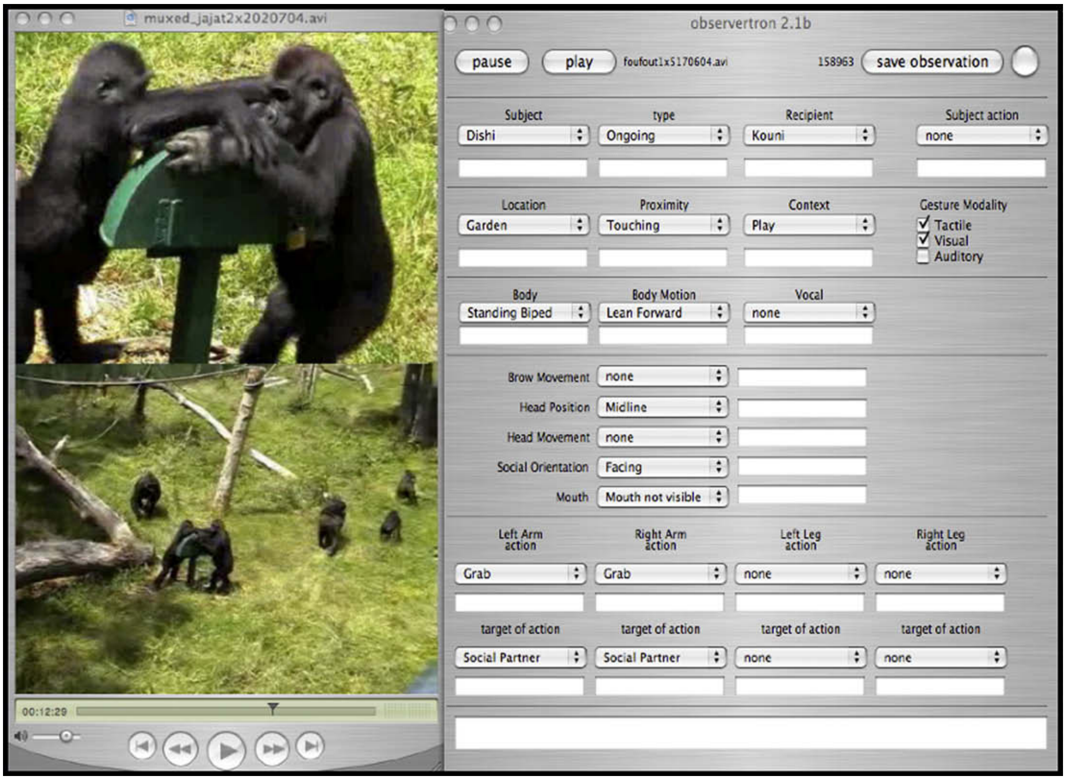
Data collection

Thirteen (15 min duration) focal follows of the subject were recorded, over a three month period (June–August 2004) resulting in approximately 3 h of real-time footage, and equivalent to 6 h of video footage based on two camera-angle captures. Handheld mini-DV camcorders (Panasonic NVGS11B) were used to record the raw footage. The two synchronized digital video cameras were used to gain a unified perspective of the contextual and physical factors influencing behaviour. While one camera focused on the focal individual so that the whole body filled the frame, a second camera concentrated on a wide angle that encompassed both the focal animal and its social partners and surroundings. Video capture was synchronized using a flashbulb at the beginning of each focal follow, followed by an audio account of the date, time and name of the subject. Video cameras were mounted on tripods and followed animal activity using a tilt and swivel lever for direction and zoom to optimize camera view of the focal animal and surroundings. If the animal went out of sight, the cameras kept recording to maintain synchrony while one experimenter followed the animal to assess the validity of moving the cameras to a new location. If the experimenter surmised that data could be collected at the new location, the tripods were moved there to resume filming. The time of data collection for each focal follow was counterbalanced for day and time and notes on weather conditions were taken.

Data streaming

After data collection, raw video footage was streamed from the camera into the Apple OSX IMovie software application via a firewire in preparation for file conversion (AVI) and compression. The resulting pairs of synchronized files were exported at 15 frames/s (each frame = 66.67 ms). These file pairs were then combined, to be viewed simultaneously, using a bespoke software application to produce a single AVI file with the focal animal footage at the top and the wide-angle footage at the bottom of the screen (Joint Software, Brighton, U.K.) (Fig. 1). The synchronized top/down file was then loaded into a bespoke software program, OBSERVATRON, for offline coding and storage of animal behaviour data, which runs on MAC OSX (Joint Software, Brighton, U.K.). This application was developed specifically for the aims of this pilot study; however, OBSERVATRON is currently being developed to include signal variables for a broad range of animal species and will be available for licensed download in the near future.

Within the OBSERVATRON software program each signal is entered as an event record and captures information for each of the physical and contextual factors that comprise behaviour (Fig. 1). For coding purposes, I define



Subject	type	Recipient	Subject action
Dishi	Ongoing	Kouni	none
Location	Proximity	Context	Gesture Modality
Garden	Touching	Play	☑ Tactile ☑ Visual ☐ Auditory
Body	Body Motion	Vocal	
Standing Biped	Lean Forward	none	
Brow Movement	none		
Head Position	Midline		
Head Movement	none		
Social Orientation	Facing		
Mouth	Mouth not visible		
Left Arm action	Right Arm action	Left Leg action	Right Leg action
Grab	Grab	none	none
target of action	target of action	target of action	target of action
Social Partner	Social Partner	none	none

Figure 1. View of the narrow and wide-angle camera perspectives from within the OBSERVATRON software application. While the close-up view (top of screen) captures detailed video footage of the focal individual, the wide angle (bottom of screen) captures information pertaining to the context within which behaviour occurs.

communication broadly, as any act by which an individual gives or receives information about needs, desires, perceptions, knowledge or affective states through intentional or unintentional means, via visual, tactile or auditory signals. This transfer of information can be directed at the self, a social partner, an object or the environment.

Within OBSERVATRON, signals are described as visual, auditory and tactile or as a combination of sensory outputs. For example, a clap can comprise visual, auditory and tactile components creating a multisensory experience. Furthermore, signals can be classed as uni- or multicomponent events. Unicomponent events occur as a single action in time (e.g. limb motion). The single action can be composed of more than one sensory output (e.g. a clap is both visual and auditory), whereas multicomponent events can occur in temporal synchrony (e.g. limb motion + vocalization + head motion), or as a sequence of events, called a 'phrase' (e.g. limb motion → vocalization → head motion). OBSERVATRON was programmed to allow one to play, pause, fast-forward, rewind or advance the video stream frame by frame to code synchronous versus sequential events accurately.

For humans and other animals, it is well proven that the integration of information from multiple sensory channels at the level of neural processing is critical for perception of the external world (Horn 1983; Stein & Meredith 1990; Driver & Grossenbacher 1996; Andersen 1997). The ability to produce and receive synchronous and sequential information from multiple sensory channels tends to lend flexibility to the interactive process by giving animals the ability to amplify or change the significance of a single signal (McGurk & Macdonald 1976; Partan & Marler 1999). To date, the influence of synchronous and sequential multicomponent signals on communication is unknown.

Data coding

Some communicative signals are instantaneous, whereas others invariably have some duration. Signals that build up over time are coded at the peak of activity. For actions that have duration with no obvious peak, actions are coded when a definable action has begun. If more than one motion occurs in close temporal sequence then each individual action is recorded as a single entry in temporal sequence (e.g. drumming). The direction of an action is relative to the position of the body part at the beginning of the signal. If more than one action occurs simultaneously, then all components are coded within a single event record. A position or motion is coded for only when there is activity associated with part of a communicative signal and is always coded for with reference to the focal subject. Each behavioural factor is coded for independently to create a flexible database where one can query for any factors that comprise a sensory signal.

For example, when the focal animal makes an action (head, mouth, right limb, left limb, trunk), not only are the direction and target (e.g. self, object, social partner) of the action noted, but the states of the following variables are also recorded: (1) subject; (2) recipient(s); (3) location (e.g. garden); (4) proximity between interacting animals (e.g. touching, <1 m, 1−3 m, >3 m); (5) time of video frame; (6) modality (e.g. auditory, visual, tactile); (7) body state (e.g. sitting, standing biped); (8) social context (e.g. feeding, playing, parenting); (9) social orientation (facing, averted, peripheral) (Table 1). It is important to record all animals involved in an interaction as studies of primate behaviour show that the frequency of signalling can be affected by who is nearby (Wilson et al. 2001; Mitani et al. 2002). Further information on gender and age can be extracted from the information inherent in the 'subject' category. While for this particular study, vocalizations did not account for a significant number of events, owing to the subtle nature of gorilla calls, audible signals were nevertheless included in the MDM coding scheme, as they are salient communication signals across a wide range of animal species. Table 1 shows the variables held within the OBSERVATRON application for this pilot study. When coding a communication signal, any item from each list can be tagged as part of an event record that describes that signal. If the variable required does not exist, there is an option to choose 'other' or to key in free text. The addition of information regarding the contextual, physical, spatial and temporal elements associated with action signals is what gives behaviour its multidimensional quality. Although coding factors such as 'social context' is only our 'best guess' and is subjectively based on human experience, one would not necessarily require this category distinction for analyses. I explain in the next section how this category could be derived from a combination of other factors.

Table 1. Multidimensional method coding scheme

Variable	Description
Agent	
Subject	Dishi, Djala, Emmy, Foufou, Jaja, Kibi, Kishi, Kouni, M'Passa, Mumba, Tamareilla, Tamki, Yene, keeper, experimenter, public
Interaction with	Dishi, Djala, Emmy, Foufou, Jaja, Kibi, Kishi, Kouni, M'Passa, Mumba, Tamareilla, Tamki, Yene, keeper, experimenter, public
Context	
Social context	Agonistic, elimination, feeding, grooming, locomotion, object use, other, parenting, peering, play, reproduction, rest, social standing
Body position	Bowing, climbing, lying on front, lying on back, other, running, sitting, standing bipedal, standing, quadrupedal, standing tripedal, tumbling, walking
Head position	Midline, left, right, other (all positions are relative to the trunk)
Social orientation	Facing, averted, peripheral
Proximity	Touching, within 1 m, 1−3 m, >3 m
Location	Garden, inside enclosure, outdoor enclosure (upper), outdoor enclosure (lower)
Action	
Modality	Tactile, visual, auditory
Trunk motion	Forward, backward, left, right
Head motion	Up, down, left, right
Mouth motion	Open (with teeth), open (without teeth), closed pursed, bite, kiss, groom, other
Brow motion	Up, down, neutral, other
Vocalization	Call, utterance (e.g. bilabial fricative), other
Limb motion	Right-arm, left-arm, right-leg, left-leg
Limb action	Carry, clap, drum/tap, embrace, grab, hit, hold, horizontal, kick, lower, manipulate, other, poke/prod, pull, push/shove, raise, shake, stretch/reach, throw, touch/stroke, wave
Object	
Target of action	Enclosure, object, other, self, social partner

This list of coded variables was developed to fit within a framework that allows the experimenter to assess any number of factors at multiple levels. This coding scheme also allows one to derive information that is not explicitly coded. For example, one could determine the degree of head motion by referencing the 'Head position' prior to 'Head motion'. A left head motion from a right head position is more dramatic than a left head motion from a midline head position. 'Context' denotes the social environment at the start of the action event. 'Target of action' relates to what each limb motion is acting upon.

Data storage and orientation

Once the event record is coded in the OBSERVATRON application, it is automatically stored in a structured query language (SQL) database along with the file name, time code and frame number of the event. SQL is a computer language designed for the retrieval, manipulation and management of data in a relational database. Storing the signalling data in an SQL database allows one to parse behavioural data in multiple orientations, advancing beyond previous methodological frameworks. The benefits of storing the signalling data in an SQL database allows the MDM to take steps beyond any of its predecessors in that it allows one to parse and analyse behavioural data in multiple directions. Within an SQL database, queries are designed to retrieve data based on specific criteria. Therefore, the database can be queried for any specific criteria and will return the set of event records that contain the requested parameters. From these returned sets of event records, patterns are revealed with respect to those physical and contextual factors that correlate with one another in a significant manner. The results can be easily analysed using simple statistical tests.

Figure 2 gives an example of a query that asks under what social context particular factors occur simultaneously. The requested criteria can be queried for in any direction, and the results reveal not only the physical combinations of motion during signal production, but also the contextual factors that influence them. The MDM does not require a new study or a new level of coding to make as many queries as there are possible combinations of variables. Furthermore, sequences of event records can then be parsed at different levels to probe for signal structure. For the purposes of this study, event records were grouped into signal 'phrases' and 'exchanges' which are defined as a temporal sequence that ceases when there is no signal for more than 10 s. A phrase is when there is a sequence of signals given by a single individual. An exchange is when a single signal or signal phrase is given by an individual and there is a response from a second (or multiple) individual(s) within

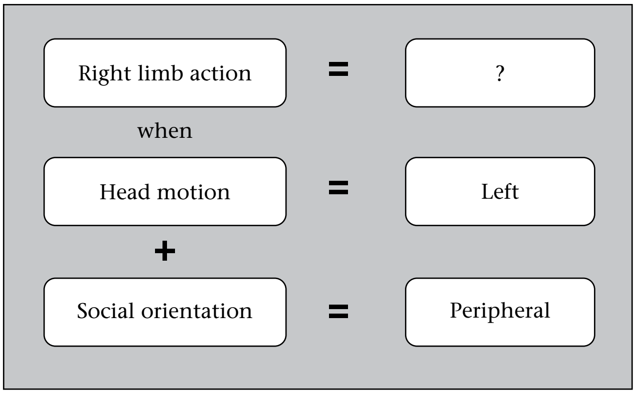


Figure 2. An example of a sample query used to probe the action database. The query asks the database to find event records with instances of synchronous head and right-limb motion, when the focal animal is peripherally oriented to its social partner.

10 s of the completion of the preceding signal. Parsing data in varying orientations can reveal signal patterns that would not be visible under traditional data structures.

The ability to parse data at different behavioural levels makes the MDM differ substantially from other animal communication studies that use a ‘gesture library’. Gesture libraries tend to lump together sequences of actions into a single event and are categorized with regard to the perceived social context (e.g. antagonistic display). In the case of the MDM, sequences of actions that may have been labelled as ‘antagonistic displays’ or ‘tool use’ in a gesture library are no longer lumped and tagged as a single event in the MDM, but rather are coded for the multiple action components and contextual factors that comprise the sequence of events. As a database grows, this method can help establish an ‘action grammar’ from the sequences of primate signals which may bring about a better understanding of why, how and when signals are elicited. Advances in technology and other disciplines (e.g. information theory and back-propagation neural networks) can help to identify patterns within the action grammar of both synchronous and sequential signals.

In Fig. 3, the data-rich sequence is broken down into action components and becomes a sequence of synchronous action components or a ‘phrase’. From this point, we can assess variation by factoring what particular components of the phrase are shared by all aggressive displays, and which portions may be unique to a particular individual. This manner of ‘deriving’ results allows us to take more objective measures of dynamic behaviour. While gesture libraries provide a much more time-efficient process of coding animal behaviour, they can lose much of the detailed behaviours of the animals, leaving an action pattern difficult to define in a sequence of behaviours.

Results

Synchronous signals

Analysing synchronous physical action can help us understand the structure of communication signals, and may provide a better understanding of how animals combine signals to influence signal intensity, efficiency and redundancy of signalling (Partan & Marler 1999). While there are countless ways in which one could analyse synchronous signals, I will give only a few examples to highlight the different levels at which behaviour can be analysed, which are not generally addressed in the conventional animal communication literature. For this pilot study, I assessed the simultaneous physical actions of the head, trunk, right limb, left limb and mouth. Synchronous physical actions is a combination of body segment motions occurring simultaneously. At a maximum, there is the

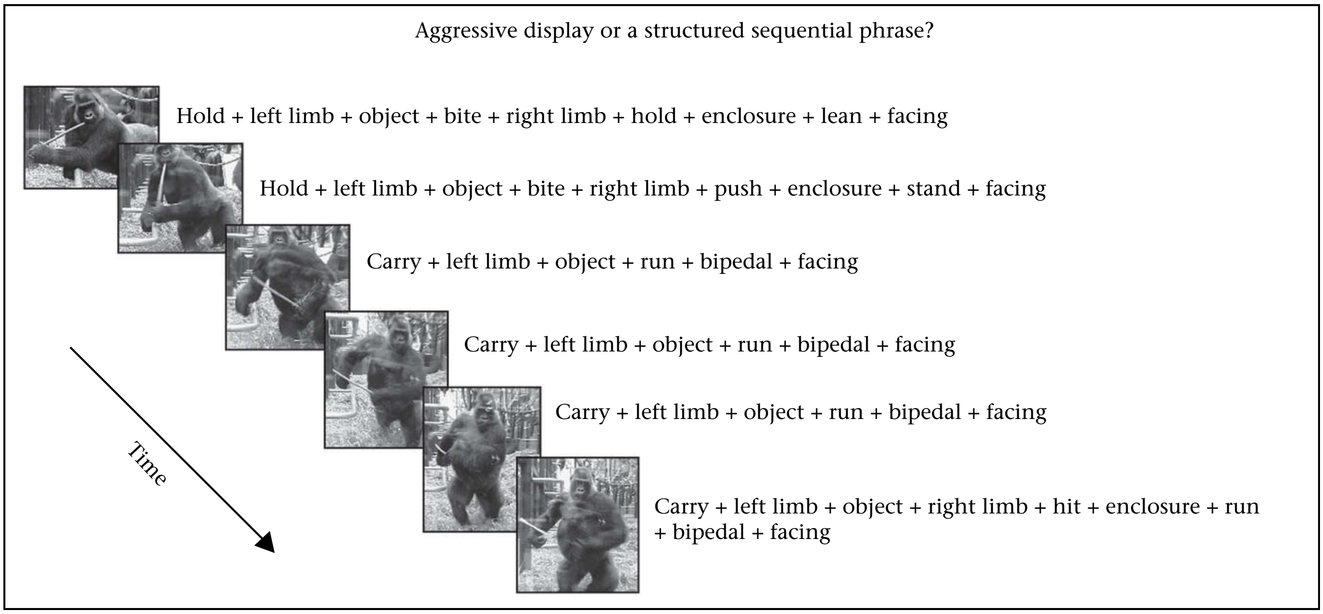


Figure 3. A signal phrase is broken down by event record to highlight the multiple components that comprise this nonarbitrary sequence of signals. This figure illustrates only a portion of the data points collected using the multidimensional method.

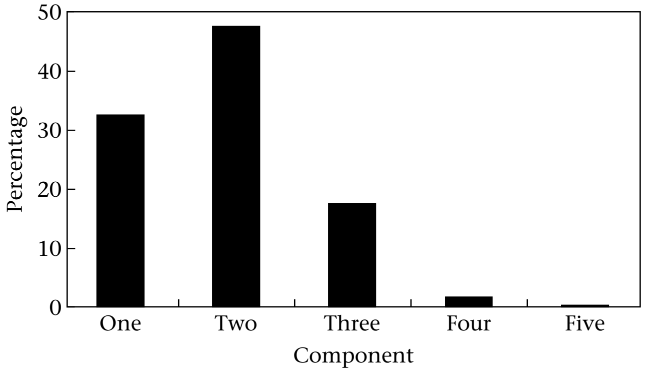


Figure 4. The physical body segments (head, right limb, left limb, trunk, mouth) of the subject were assessed during synchronous motion. The graph shows the frequency of actions involving one, two, three, four or five body segments for the subject.

possibility of synchronizing all five monitored body segments. Figure 4 illustrates the percentages of physical actions that contain the movement of a single body segment versus that of multiple body segments in temporal synchrony.

In Fig. 4, 32.59% of putative communication signals of the pilot subject were a single action (e.g. right limb, left limb motion), while 47.49% were bicomponent, comprising two synchronous actions (e.g. limb motion + head motion) and 17.69% of signals were tricomponent, composed of three synchronous actions. Signals with more than three synchronous body actions accounted for 2.23% of synchronous signals. Further investigation into these data may reveal how synchronizing actions influences signal efficiency and redundancy.

Probing the structure of signals produced through physical action not only reveals information about the strategies of signal deployment, it can also reveal patterns with regard to lateralized motor control (Martin & Niemitz 2003). Lateralized action is of special importance in the study of communication signals because, in humans, the asymmetric use of our limbs is an indirect marker of the location of language areas in the brain. In humans, the left hemisphere of the brain contains specific areas implicated in speech production (specifically, Broadmann's Area 44). One of the by-products of a left-hemisphere bias for language in humans is that we use our right hands significantly more when gesturing (reviewed in Corballis 2002).

In captive great apes (e.g. bonobos, *Pan paniscus*, chimpanzees, *Pan troglodytes*, gorillas, *Gorilla gorilla*, and orangutans, *Pongo pygmaeus*) data on dominant hand use have not been consistent (e.g. chimpanzee: Corp & Byrne 2004; *gorilla* and *orang-utan*: Hopkins et al. 2003; bonobo: Harrison & Nystrom 2008). However, a recent sample of 227 chimpanzees suggested that the development of manual gestures linked to specific tasks were preferentially produced by the right hand (Hopkins & Cantero 2003). Recent neuroanatomical (MRI) images from chimpanzees, bonobos and gorillas revealed that Broadmann's Area 44 is morphologically larger in the left than in the right hemisphere, consistent with the human data (Cantalupo & Hopkins 2001). Cantalupo & Hopkins (2001) posited that during the evolution of modern language, the pairing of these sensory signals, controlled by Broadmann's Area 44, may be responsible for the evolutionary selection of speech in humans.

The MDM has the potential to add valuable data to the study of hominid laterality and its links to the evolution of modern human language. Using the MDM to probe laterality in the focal subject, I conducted an analysis of the pairings of synchronous body actions (right limb, left limb, head, trunk and mouth). These bisynchronous actions produced an interaction between lateralized limb action and body segment action. Figure 5a indicates how each of the body segments can be analysed for synchronous activity with all other body segments.

A chi-square analysis indicated that head and mouth motion had a greater propensity to be paired with synchronous right-arm movement than with left-arm movement. Conversely, the trunk motion had a greater propensity to be paired with left-arm motion than with right-arm motion (see Table 2 for values). These data created a significant interaction of synchronous body segment motion and lateralized limb action ($\chi^2_2 = 12.25$, $P = 0.002$). Figure 5b depicts the bisynchronous motion of the focal subject superimposed upon a gorilla skeleton. The thickness of the lines indicates the degree of frequency of pairings. These data produced a wholly unanticipated pattern of results which would not have been visualized had not multiple and synchronous components been analysed. These data, which support a propensity for gorillas to use the right hand significantly more frequently when making head and mouth motions, may demonstrate a left-hemisphere asymmetry for motor control during acts of communication involving the mouth and the head. If this pattern remains robust throughout the family group, it may form the basis of comparative human and ape investigations of communication tied to the evolution of left-hemisphere language brain regions.

Sequential signals

While synchronous signals give us a snapshot of static-state behaviour within a particular context, it is the sequence of those signals that reveals information about the dynamic and probable nature of behaviour. The data-rich coding approach allows for the data to be examined in different orientations to represent communication in a naturally occurring dynamic process. By viewing data as dynamic sequences we can investigate the architecture of turn taking by splicing signal sequences into 'phrases' and 'exchanges'. For example, I created phrases by grouping the focal subject's signals in temporal sequence before a response was elicited or a time constraint was exceeded. In this manner I determined the range of signals within a phrase. Phrases were further grouped into exchanges, where the phrase from the focal subject was grouped in temporal sequence with the subsequent phrase (often called the response) from the responding animal(s). When analysing exchanges, a sliding scale can be implemented where each response phrase becomes the initiated phrase for the next exchange so that the input–output

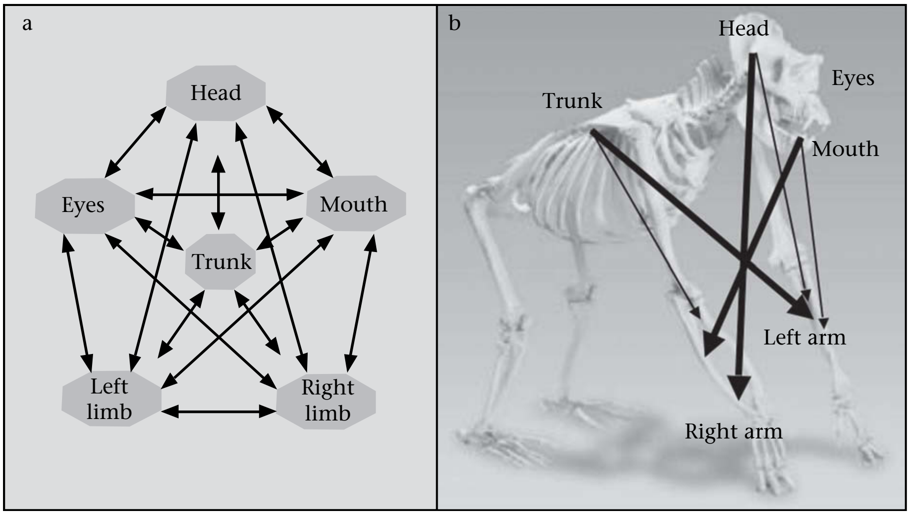


Figure 5. (a) The multidimensional method evaluates all physically synchronous actions of the body in a reciprocal manner. (b) Analysis can reveal coordinated physical action and thus demonstrate differences in lateral motor activity. The heavy arrow indicates a stronger correlation between body segments for the focal subject.

pattern is not biased by a subjective interpretation of when exchanges begin and end. Once signals were organized as phrases and exchanges, I was also able to extract information stored within these dynamic sequences. For example, Fig. 6 shows how parsing data into different sequential groupings can result in significantly different distributions of signal generations.

1182 event records were assessed for the presence of head motions (Fig. 6). When each event record was assessed independently, 43.2% involved a head movement. However, when event records were organized into 647 phrases, 51.3% involved a head movement. When data were organized into 429 exchanges, 70.5% involved a head movement. The distributions of head actions within the different data groupings indicate that the information held within signal sequences is not randomly distributed, and reveal structured information that cannot be found from analysing signals in isolation.

Although the MDM requires a critical mass of data before one can statistically determine a significant communicative pattern of results, these results show how only a few hours of coded behaviour can uncover structured communicative behaviour. Although this study does not go on to analyse sequences of signals, because of the small data set, data in this format lend themselves well to a range of analytical methods (e.g. information theory, neural networks) which have proven to be successful tools for identifying patterns in the communication signals of ants, whales (e.g. Reznikova & Ryabko 1994; Ryabko & Reznikova 1996; Suzuki et al. 2006) and humans (e.g. Elman 1993).

Table 2. Statistics for significant pattern revealed by analysing the synchronous interaction of body motion and limb laterality

	Value	*df*	Asymptotic *P* value*
Pearson chi-square	12.251	2	0.002
Likelihood ratio	12.404	2	0.002
Linear-by-linear	5.202	1	0.023
No. of valid cases	201		

Two tailed.

Discussion

Although we share much of our genetic make-up, cognitive traits and machinery underlying speech perception with nonhuman great apes (Weiss & Newport 2006), to date, there is little evidence that any nonhuman primate surpasses the use of simple semantic rules to extract meaning from communication signals (Zuberbühler et al. 1999; Zuberbühler 2000b) or has the capability to combine signals to create more complex phrases with different meanings (Ghazanfar & Hauser 1999). Without evidence of this nature, it is difficult to contribute to the hypothesis that modern human communication may have evolved from meaningful multisensory sequences expressed through the integration of audible, tactile and visual communication signals (Johnson 2001; Shanker & King 2002). However, there have been few and limited attempts to use

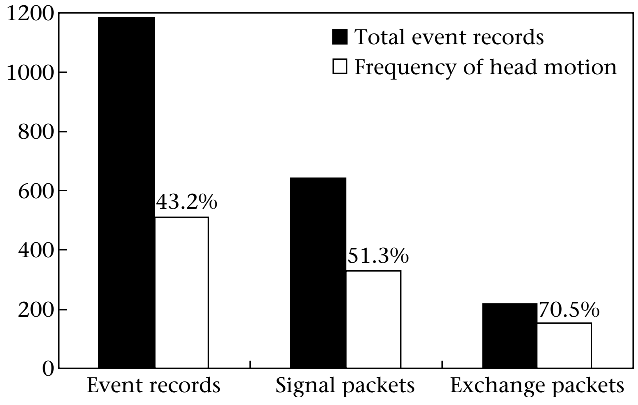


Figure 6. Percentage of head movements from data parsed in different groupings: event records, phrases and exchanges.

a method that can tackle the occurrences of contextually based, multisensory signals in any animal species, including that of humans.

The MDM strives to reveal the structure of information elicited by a focal animal through interactions with conspecifics and the environment. This approach circumvents some of the problems underlying the construction of species' 'libraries' within which to categorize communication signals, by relying on the identification of repeated synchronous and sequential signals given under consistent environmental contexts. While I believe the method described in this manuscript is more objective than previous techniques for assessing communicative behaviour, clearly no human-scored behaviour can eliminate subjectivity. It is my hope, however, that this method offers the potential to decrease subjectivity by merely parsing multicomponent communication signals into discrete units of motion, direction and time within social and physical contexts, and, by doing so, adds a higher level of precision to the study of animal communication signals.

One of the limitations of this type of quantitative method is that it relies on a critical mass of data. It would greatly benefit from collaborative species-specific action databases (including for humans) to which researchers around the globe contribute. Like the human genome project (e.g. Venter et al. 2001), this method is detailed and time consuming; however, a growing collaborative database could increase coding reliability and help elucidate many questions regarding communication structure and strategies, from their evolution to their development and disorders. We understand that a single active gene in the human genome is meaningless in isolation, and it is my hypothesis that this is also the case with animal communication signals.

Extended uses of the MDM

The MDM is flexible in that this method does not require behaviour to be explicit or active. Social information can be transferred in a passive form, through observation (coded using eye gaze), which has implications for learning processes (Harlow et al. 1963; Hinde & Simpson 1975; Maestripieri et al. 2002). It can also be used to capture episodes of learning that may not traditionally be classed as communication. For instance, we know from both behavioural and brain studies that repetition and imitation are important ways in which human and primate infants learn social and mechanical skills (Bateson 1979; Rizzolatti & Arbib 1998) and may have provided an early evolutionary tool for communication during infant development (Bard 1998). These are skills often associated with tool use, and the MDM provides an opportunity to understand the links between tool use and communication. With respect to nonhuman great apes, competent tool use has been observed both in the wild (e.g. Fox et al. 1999; McGrew 2004; Breuer et al. 2005) and in captivity (e.g. Visalberghi et al. 1995; Boysen et al. 1999; Mulcahy et al. 2005). Patterns displayed by wild chimpanzees during tool use have been described in a hierarchical analysis similar to those describing syntactic relationships in language (Byrne & Byrne 1993; Foucart et al. 2005) implying that these sequential skills are not a human-specific adaptation, but rather may be inherited from a common ancestor of humans and extant great apes living over 5 million years ago (Mercader et al. 2007). The MDM allows for the investigation of a broad range of social communicative skills, which are important for our understanding of animal communication.

The flexibility of the MDM makes it easily adaptable for the investigation of other animal species, including human populations. For example, this method could prove to be a valuable tool for investigating the development of communication skills in preverbal children and for creating diagnostic measures for children with language-related impairments. Studies of language development and disorders often rely on the subject's cooperation, and the subject's ability to produce and comprehend language (e.g. autistic diagnosis observational scale, ADOS), making it difficult to assess low-functioning individuals with severe language impairments. The benefit of the MDM is that it allows for the investigation of communication through noninvasive observations of multicomponent signals (e.g. nonverbal vocalizations, facial expression, lateralized motor action, visual gaze) allowing for a comparative framework between different human populations with different language abilities.

Conclusion

MDM demonstrates that when synchronous and sequential signals are analysed in fine detail, considering the physical and contextual factors that influence behaviour, we can take steps towards understanding the architecture of communication signals. The implications of a methodological transformation of studies of primate communication signals are vast. The ability to quantify multicomponent signals and derive patterns from naturalistic behaviour allows for a better understanding of the repertoire of animal communication signals. The theoretical approach and methodological technique discussed in this manuscript are applicable not just to investigations of animal communication signals, but also to any field studying behaviour, including normal and abnormal human populations. This type of methodology could prove to be a valuable tool for the development of a common quantitative framework for analysing communication signals across a broad range of animal species and across multiple laboratories. Moreover, the adoption of a common tool across laboratories would aid in the development of a common scientific language with which to discuss and evaluate animal behaviour. This would be an important step towards placing ourselves and other animal species within a framework for the evolution of modern human language.

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References

Adams, D. B. & Schoel, W. M. 1982. A statistical analysis of the social behavior of the male stumptail macaque (*Macaca arctoides*). *American Journal of Primatology*, **2**, 249–273.

Altmann, S. A. 1962. A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. *Annals of the New York Academy of Science*, **10**, 338–435.

Altmann, S. A. 1965. Sociobiology of rhesus monkeys II. Stochastics of social communication. *Journal of Theoretical Biology*, **8**, 490–522.

Andersen, R. A. 1997. Multimodal integration for the representation of space in the posterior parietal cortex. *Philosophical Transactions of the Royal Society of London, Series B*, **352**, 1421–1428.

Bard, K. A. 1998. Social experiential contributions to imitation and emotion in chimpanzees. In: *Intersubjective Communication and Emotion in Early Ontogeny* (Ed. by S. Braten), pp. 208–227. Cambridge: Cambridge University Press.

Barton, R. A. & Dunbar, R. 1997. Evolution of the social brain. In: *Machiavellian Intelligence II* (Ed. by R. Byrne & A. Whiten), pp. 240–263. Cambridge: Cambridge University Press.

Bateson, M. C. 1979. The epigenesis of conversational interaction: a personal account of research and development. In: *Before Speech: the beginnings of Human Communication* (Ed. by M. Bullowa), pp. 63–77. Cambridge: Cambridge University Press.

Boesch, C. 2001. Cooperative hunting roles among Taï chimpanzees. *Human Nature*, **13**, 27–46.

Boesch, C. & Boesch, H. 1989. Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology*, **78**, 547–573.

Boysen, S. T., Kuhlmeier, K., Halliday, P. & Halliday, Y. M. 1999. Tool use in captive gorillas. In: *The Mentality of Gorillas and Orangutans* (Ed. by S. Parker, R. Mitchell & H. Miles), pp. 179–187. Cambridge: Cambridge University Press.

Breuer, T., Ndoundou-Hockemba, M. & Fishlock, V. 2005. First observation of tool use in wild gorillas. *PLoS Biology*, **3**, e380.

Bugnyar, T., Kijne, M. & Kotrschal, K. 2001. Food calling in ravens: are yells referential signals? *Animal Behaviour*, **61**, 949–958.

Byrne, R. W. & Byrne, J. M. 1993. Complex leaf-gathering skills of mountain gorillas (*Gorilla g. berengei*): variability and standardization. *American Journal of Primatology*, **31**, 241–261.

Cantalupo, C. & Hopkins, W. 2001. Asymmetric Broca's area in great apes: a region of the ape brain is uncannily similar to one linked with speech in humans. *Nature*, **414**, 505.

Cheney, D. L. & Seyfarth, R. M. 1981. Selective forces affecting the predator alarm calls of vervet monkeys. *Behaviour*, **76**, 25–61.

Cheney, D. L. & Seyfarth, R. M. 1990. *How Monkeys See the World: Inside the Mind of Another Species*. Chicago: University of Chicago Press.

Corballis, M. C. 2002. *From Hand to Mouth: The Origins of Language*. Princeton, New Jersey: Princeton University Press.

Corp, N. & Byrne, R. W. 2004. Sex difference in chimpanzee handedness. *American Journal of Physical Anthropology*, **123**, 62–68.

Crockford, C. & Boesch, C. 2003. Context-specific calls in wild chimpanzees, *Pan troglodytes verus*: analysis of barks. *Animal Behaviour*, **66**, 115–125.

Darwin, C. 1872. *The Expression of the Emotions in Man and Animals*. 2nd edn. New York: D. Appleton.

Dornhaus, A. & Chittka, L. 1999. Evolutionary origins of bee dances. *Nature*, **401**, 38.

Driver, J. & Grossenbacher, P. 1996. Multimodal spatial constraints on tactile selective attention. In: *Attention and Performance XVI: Information Integration in Perception and Communication* (Ed. by T. Inui & J. McClelland), pp. 209–236. Cambridge, Massachusetts: MIT Press.

Dunbar, R. I. M. 1991. Functional significance of social grooming in primates. *Folia Primatologica*, **57**, 121–131.

Dunbar, R. I. M. 1993. Coevolution of neocortical size, group size and language in humans. *Behavioral and Brain Sciences*, **16**, 681–735.

Elman, J. L. 1993. Learning and development in neural networks: the importance of starting small. *Cognition*, **48**, 71–99.

Emery, N. J. 2000. The eyes have it: the neuro-ethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews*, **24**, 581–604.

Estes, R. D. 1991. *The Behavior Guide to African Mammals, Including Hoofed Mammals, Carnivores and Primates*. Berkeley, California: University of California Press.

Evans, C. S. 1997. Referential signals. In: *Perspectives in Ethology. Vol. 12* (Ed. by D. Owings, M. D. Beecher & N. S. Thompson), pp. 99–143. New York: Plenum.

Evans, C. S. & Evans, L. 1999. Chicken food calls are functionally referential. *Animal Behaviour*, **58**, 307–319.

Evans, C. S. & Marler, P. 1994. Food-calling and audience effects in male chickens, *Gallus gallus*: their relationships to food availability, courtship and social facilitation. *Animal Behaviour*, **47**, 1159–1170.

Evans, C. S., Evans, L. & Marler, P. 1993. On the meaning of alarm calls: functional reference in an avian vocal system. *Animal Behaviour*, **46**, 23–38.

Fitch, W. T. 2005. The evolution of language: a comparative review. *Biology and Philosophy*, **20**, 193–230.

Fossey, D. 1972. Vocalizations of the mountain gorilla (*Gorilla gorilla beringei*). *Animal Behaviour*, **20**, 36–53.

Foucart, J., Bril, B., Hirata, S., Morimura, N., Houki, C., Ueno, Y. & Matsuzawa, T. 2005. A preliminary analysis of nut-cracking movements in a captive chimpanzee: adaptation to the properties of tools and nuts. In: *Stone Knapping: The Necessary Conditions for a Uniquely Hominin Behaviour* (Ed. by V. Roux & B. Bril), pp. 147–157. Cambridge: McDonald Institute of Archeological Research.

Fox, E. A., Sitompul, A. F. & van Schaik, C. O. 1999. Intelligent tool use in wild Sumatran orangutans. In: *The Mentality of Gorillas and Orangutans* (Ed. by S. T. Parker, R. W. Mitchell & H. L. Miles), pp. 99–116. Cambridge: Cambridge University Press.

von Frisch, K. 1947. The dances of the honey bee. *Bulletin of Animal Behaviour*, **5**, 1–32.

von Frisch, K. 1967. *The Dance Language and Orientation of Bees*. Cambridge, Massachusetts: Harvard University Press.

Ghazanfar, A. A. & Hauser, M. D. 1999. The neuroethology of primate vocal communication: substrates for the evolution of speech. *Trends in Cognitive Science*, **3**, 377–384.

Gill, S. A. & Sealy, S. G. 2004. Functional reference in an alarm signal given during nest defence: seet calls of yellow warblers denote brood-parasitic brown-headed cowbirds. *Behavioral Ecology and Sociobiology*, **56**, 71–80.

Goldfoot, D. A. 1982. Multiple channels of sexual communication. In: *Rhesus Monkeys: Role of Olfactory Cues. Primate Communication*

(Ed. by C. H. Snowdon & M. R. Peterson), pp. 413–428. Cambridge: Cambridge University Press.

Harlow, H. F., Harlow, M. K. & Hansen, E. W. 1963. The maternal affectional system of rhesus monkeys. In: *Maternal Behavior in Animals* (Ed. by R. H. Rheingold), pp. 254–281. New York: J. Wiley.

Harrison, R. M. & Nystrom, P. 2008. Handedness in captive bonobos (*Pan paniscus*). *Folia Primatologica*, **79**, 253–268.

Hauser, M. 1996. *The Evolution of Communication*. Cambridge, Massachusetts: MIT Press.

Hauser, M. D., Evans, C. S. & Marler, P. 1993. The role of articulation in the production of rhesus monkey, *Macaca mulatta*, vocalizations. *Animal Behaviour*, **45**, 423–433.

Hinde, R. A. & Simpson, M. J. A. 1975. Qualities of mother–infant relationships in monkeys. *Ciba Foundation Symposium*, **33**, 39–67.

Hölldobler, B. 1995. The chemistry of social regulation: multi-component signals in ant societies. *Proceedings of the National Academy of Sciences, U.S.A.*, **92**, 19–22.

van Hooff, J. A. R. A. M. 1972. A comparative approach to the phylogeny of laughter and smiling. In: *Non-verbal Communication* (Ed. by R. A. Hinde), pp. 209–242. New York: Oxford University Press.

Hopkins, W. D. & Cantero, M. 2003. The influence of vocalizations on preferential hand use in gestural communication by chimpanzees. *Developmental Science*, **6**, 55–61.

Hopkins, W. D., Stoinski, T. S., Lukas, K. E., Ross, S. R. & Wesley, M. J. 2003. Comparative assessment of handedness for a coordinated bimanual task in chimpanzees (*Pan*), gorillas (*Gorilla*), and orangutans (*Pongo*). *Journal of Comparative Psychology*, **117**, 302–308.

Horn, E. 1983. *Multimodal Convergences in Sensory Systems*. Stuttgart: Gustav Fischer.

Hostetter, A. B., Cantero, M. & Hopkins, W. D. 2001. Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional status of a human (*Homo sapiens*). *Journal of Comparative Psychology*, **115**, 337–343.

Johnson, C. M. 2001. Distributed primate cognition: a review. *Animal Cognition*, **4**, 167–183.

Johnson, C. M. & Karin-D'Arcy, M. R. 2006. Social attention in primates: a methodological review. *Aquatic Mammals*, **32**, 423–442.

Johnstone, R. A. 1995. Honest advertisement of multiple qualities using multiple signals. *Journal of Theoretical Biology*, **177**, 87–94.

Johnstone, R. A. 1996. Multiple displays in animal communication: 'backup signals' and 'multiple messages'. *Philosophical Transactions of the Royal Society of London, Series B*, **352**, 329–338.

King, B. J. & Shanker, S. G. 2003. How can we know the dancer from the dance? The dynamic nature of African great ape social communication. *Anthropological Theory*, **3**, 5–26.

Leavens, D. A. & Hopkins, W. D. 2005. Multimodal concomitants of manual gesture in chimpanzees: effects of food size and distance. *Gesture*, **5**, 73–88.

Leavens, D. A., Hopkins, W. D. & Thomas, R. K. 2004. Referential communication by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **118**, 48–57.

Liebal, K., Pika, S., Call, J. & Tomasello, M. 2004. 'To move or not to move', how apes adjust to the attentional state of others. *Interaction Studies*, **5**, 199–219.

Liebal, K., Pika, S. & Tomasello, M. 2006. The gestural communication of orangutans. In: *The Gestural Communication of Monkeys and Apes* (Ed. by M. Tomasello & J. Call), pp. 1–38. Mahwah, New York: L. Erlbaum.

Liebermann, P. 1998. *Eve Spoke: Human Language and Human Evolution*. New York: W. W. Norton.

McComb, K. & Semple, S. 2005. Co-evolution of vocal communication and sociality in primates. *Biology Letters*, **1**, 381–385.

McGrew, W. C. 2004. *The Cultured Chimpanzee: Reflections on Cultural Primatology*. Cambridge: Cambridge University Press.

McGurk, H. & Macdonald, J. 1976. Hearing lips and seeing voices. *Nature*, **264**, 746–748.

Maestripieri, D., Ross, S. K. & Megna, N. L. 2002. Mother–infant interactions in western lowland gorillas (*Gorilla gorilla gorilla*): spatial relationships, communication and opportunities for social learning. *Journal of Comparative Psychology*, **116**, 219–227.

Manser, M. B. 2001. The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society of London, Series B*, **268**, 2315–2324.

Manser, M. B., Bell, M. B. & Fletcher, L. B. 2001. The information that receivers extract from alarm calls in suricates. *Proceedings of the Royal Society of London, Series B*, **268**, 2485–2491.

Marler, P. 1965. Communication in monkeys and apes. In: *Primate Behavior: Field Studies of Monkeys and Apes* (Ed. by I. DeVore), pp. 544–584. New York: Holt, Rinehart & Winston.

Marler, P. & Tenaza, R. 1977. Signalling behaviour of apes with special reference to vocalization. In: *How Animals Communicate* (Ed. by T. Sebeok), pp. 965–1033. Bloomington: Indiana University Press.

Marler, P., Evans, C. & Hauser, M. D. 1992. Animal signals: motivational, referential, or both? In: *Nonverbal Vocal Communication: Comparative and Developmental Approaches* (Ed. by H. Papousek, U. Jürgens & M. Papousek), pp. 66–86. Cambridge: Cambridge University Press.

Martin, F. & Niemitz, C. 2003. 'Right-trunkers' and 'left-trunkers': side preferences of trunk movements in wild Asian elephants (*Elephas maximus*). *Journal of Comparative Psychology*, **117**, 371–379.

Massaro, D. 1998. *Perceiving Talking Faces. From Speech Perception to a Behavioral Principle*. Cambridge, Massachusetts: MIT Press.

Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R. & Boesch, C. 2007. 4300-year-old chimpanzee sites and the origins of percussive stone technology. *Proceedings of the National Academy of Sciences, U.S.A.*, **104**, 3043–3048.

Miles, H. L. 1990. The cognitive foundations for reference in a signing orangutan. In: *'Language' and Intelligence in Monkeys and Apes: Comparative Developmental Perspectives* (Ed. by S. T. Parker & K. R. Gibson), pp. 511–539. Cambridge: Cambridge University Press.

Mitani, J. C. & Nishida, T. 1993. Contexts and social correlates of long-distance calling by chimpanzees. *Animal Behaviour*, **45**, 735–746.

Mitani, J. C., Watts, O., Pepper, J. & Merriwether, D. A. 2002. Demographic and social constraints on male chimpanzee behaviour. *Animal Behaviour*, **63**, 727–737.

Mori, A. 1983. Comparison of the communicative vocalizations and behaviors of group ranging in eastern gorillas, chimpanzees and pygmy chimpanzees. *Primates*, **24**, 486–500.

Mulcahy, N. J., Call, J. & Dunbar, R. I. M. 2005. Gorillas and orangutans encode relevant problem features in a tool-using task. *Journal of Comparative Psychology*, **119**, 23–32.

Partan, S. R. 2002. Single and multichannel signal composition: facial expressions and vocalizations of rhesus macaques (*Macaca mulatta*). *Behaviour*, **139**, 993–1028.

Partan, S. R. & Marler, P. 1999. Communication goes multimodal. *Science*, **283**, 1272–1273.

Partan, S. & Marler, P. 2005. Issues in the classification of multimodal communication signals. *American Naturalist*, **166**, 231–245.

Patterson, F., Tanner, J. & Mayer, N. 1988. Pragmatic analysis of gorilla utterances: early communicative development in the gorilla Koko. *Journal of Pragmatics*, **12**, 35–55.

Pika, S. & Mitani, J. C. 2006. Referential gestural communication in wild chimpanzees (*Pan troglodytes*). *Current Biology*, **16**, 191–192.

Pika, S., Liebal, K., Call, J. & Tomasello, M. 2005. The gestural communication of apes. *Gesture*, **5**, 41–56.

Premack, D. G. & Woodruff, G. 1978. Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences*, **1**, 515–526.

Preuschoft, S. 1992. Laughter and smile in Barbary macaques (*Macaca sylvanus*). *Ethology*, **91**, 220–236.

Preuschoft, S. & van Hooff, J. A. R. A. M. 1995. Homologizing primate facial displays: a critical review of methods. *Folia Primatologica*, **65**, 121–137.

Reznikova, Z. I. & Ryabko, B. 1994. Experimental study of the ants' communication system with the application of the Information Theory approach. *Memorabilia Zoologica*, **48**, 219–236.

Rizzolatti, G. & Arbib, M. A. 1998. Language within our grasp. *Trends in Neurosciences*, **21**, 188–194.

Rowe, C. & Guilford, T. 1999. Novelty in a multimodal warning signal. *Animal Behaviour*, **57**, 341–346.

Rowe, C. & Guilford, T. 2001. The evolution of multimodal warning signals. *Evolutionary Ecology*, **13**, 655–671.

Ryabko, B. & Reznikova, Z. I. 1996. Using Shannon entropy and Kolmogorov complexity to study the communicative system and cognitive capacities in ants. *Complexity*, **2**, 37–42.

Schino, G. 2001. Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour*, **62**, 265–271.

Seay, B. M., Hansen, E. W. & Harlow, H. E. 1962. Mother–infant separation in monkeys. *Journal of Child Psychology and Psychiatry*, **3**, 123–132.

Seeley, T. D. 1995. *The Wisdom of the Hive: The Social Physiology of Honey Bee Colonies*. Cambridge, Massachusetts: Harvard University Press.

Seyfarth, R. M., Cheney, D. L. & Marler, P. 1980a. Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour*, **28**, 1070–1094.

Seyfarth, R. M., Cheney, D. L. & Marler, P. 1980b. Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science*, **210**, 801–803.

Seyfarth, R., Cheney, D., Harcourt, A. & Stewart, K. 1994. The acoustic features of gorilla double grunts and their relation to behavior. *American Journal of Primatology*, **33**, 31–50.

Shanker, S. G. & King, B. J. 2002. The emergence of a new paradigm in ape language research. *Behavioral and Brain Sciences*, **25**, 605–620.

Slobodchikoff, C. N. & Placer, J. 2006. Acoustic structures in the alarm calls of Gunnison's prairie dogs. *Journal of the Acoustical Society of America*, **119**, 3153–3160.

Slobodchikoff, C. N., Kiriazis, J., Fischer, C. & Creef, E. 1991. Semantic information distinguishing individual predators in the alarm calls of Gunnison's prairie dogs. *Animal Behaviour*, **42**, 713–719.

Slocombe, K. & Zuberbühler, K. 2005. Functionally referential communication in a chimpanzee. *Current Biology*, **15**, 1779–1784.

Smith, W. J. 1977. *The Behavior of Communicating*. Cambridge, Massachusetts: Harvard University Press.

Smith, W. J. 1990. Communication and expectations: a social process and the cognitive operations it depends upon and influences. In: *Interpretation and Explanation in the Study of Animal Behavior. Vol. I: Interpretation, Intentionality and Communication* (Ed. by M. Bekoff & D. Jamieson), pp. 243–253. Boulder, Colorado: Westview Press.

Stanford, C. B., Wallis, J., Mpongo, E. & Goodall, J. 1994. Hunting decisions in wild chimpanzees. *Behaviour*, **131**, 1–20.

Stein, B. E. & Meredith, M. A. 1990. Multisensory integration: neural and behavioral solutions for dealing with stimuli from different sensory modalities. *Annals of the New York Academy of Science*, **608**, 51–65.

Suomi, S. J. 1986. The role of touch in rhesus monkey social development. In: *The Many Facets of Touch: the Foundation of Experience. Its Importance Through Life, With Initial Emphasis for Infants and Young Children* (Ed. by C. C. Brown), pp. 41–50. Skillman, New Jersey: Johnson & Johnson Baby Products.

Suzuki, R., Buck, J. R. & Tyack, P. L. 2006. Information entropy of humpback whale songs. *Journal of the Acoustical Society of America*, **119**, 1849–1866.

Tanner, J. E. & Byrne, R. W. 1996. Representation of action through iconic gesture in a captive lowland gorilla. *Current Anthropology*, **37**, 162–173.

Templeton, C. N., Greene, E. & Davis, K. 2005. Allometry of alarm calls: black-capped chickadees encode information about predator size. *Science*, **308**, 1934–1937.

Tinbergen, N. 1959. Comparative studies of the behaviour of gulls (Laridae): a progress report. *Behaviour*, **15**, 1–70.

Tomasello, M. & Call, J. 1997. *Primate Cognition*. New York: Oxford University Press.

Tomasello, M. & Call, J. 2007. *The Gestural Communication of Monkeys and Apes*. Mahwah, New York: L. Erlbaum.

Tomasello, M. & Camaioni, L. 1997. A comparison of the gestural communication of apes and human infants. *Human Development*, **40**, 7–24.

Tomasello, M., Call, J. & Hare, B. 1997. Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*, **55**, 1063–1069.

Venter, J. C., et al. 2001. The sequence of the human genome. *Science*, **291**, 1304–1351.

Visalberghi, E., Fragaszy, D. M. & Savage-Rumbaugh, S. 1995. Comprehension of causal relations in a tool-using task by chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), orang utans (*Pongo pygmaeus*), and capuchins (*Cebus apella*). *Journal of Comparative Psychology*, **109**, 52–60.

Weiss, D. J. & Newport, E. L. 2006. Mechanisms underlying language acquisition: benefits from a comparative approach. *Infancy*, **9**, 241–257.

Wich, S. A. & Sterck, E. H. M. 2003. Possible audience effect in Thomas langurs (Primates; *Presbytis thomasi*): an experimental study on male loud calls in response to a tiger model. *American Journal of Primatology*, **60**, 155–159.

Wilson, M. L., Hauser, M. D. & Wrangham, R. W. 2001. Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Animal Behaviour*, **61**, 1203–1216.

Zuberbühler, K. 2000a. Referential labelling in Diana monkeys. *Animal Behaviour*, **59**, 917–927.

Zuberbühler, K. 2000b. Interspecific semantic communication in two forest monkeys. *Proceedings of the Royal Society of London, Series B*, **267**, 713–718.

Zuberbühler, K. 2001. Predator-specific alarm calls in Campbell's monkeys, *Cercopithecus campbelli. Behavioral Ecology and Sociobiology*, **50**, 414–422.

Zuberbühler, K., Noë, R. & Seyfarth, R. M. 1997. Diana monkeys long-distance calls: messages for conspecifics and predators. *Animal Behaviour*, **53**, 589–604.

Zuberbühler, K., Cheney, D. L. & Seyfarth, R. M. 1999. Conceptual semantics in a nonhuman primate. *Journal of Comparative Psychology*, **113**, 33–42.