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How can we know the dancer from the dance?

The dynamic nature of African great ape social communication

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Abstract

We argue that dynamic-systems theory (DST) offers researchers a promising alternative to the information-processing framework that has dominated the study of primate social communication. DST rejects a linear view of communication in which a sender transmits a signal to a receiver, who then decodes that signal for its information content. Instead, dynamic-systems theory envisions communication as an intrinsically creative process that unfolds as communicating partners continuously adjust their behaviors to one another. This process of continual adjustment, termed co-regulation, can be identified in the social communication of the African great apes. When researchers study communication in terms of co-regulated social interaction, new insights and research questions emerge that may help anthropologists better understand the nature of the vocal and gestural behaviors of our closest living relatives.

Key Words

African great apes • ape gestures • ape vocalizations • bonobos • chimpanzees • co-regulation • dynamic systems • gorillas • primate social communication

Our goal in this article is to show that understanding African great ape social groups as dynamic systems can add insight and nuance to the ways in which anthropologists assess the social communication of these primates. Dynamic systems are composed of elements that are neither separate nor independent (Bertalanffy, 1968; see Fogel, 1993: 45–8). That is, systems are not composed of autonomous elements, which interact with each other sequentially (or in tandem). As opposed to this atomistic view, dynamic-systems theory argues that one can only break a system down into its constituent parts with the understanding that these elements are internally related to one another. As Kitano puts it, writing about systems biology, a system's 'properties cannot be fully understood merely by drawing diagrams of their interconnections. Although such a diagram represents an important first step, it is analogous to a static roadmap, whereas what we really seek to know are the traffic patterns. . .' (2002: 1662).

That human groups can be understood as dynamic systems is a vital feature of varied approaches within the social sciences. In psychology, for instance, ecological-systems theorists have looked at human development as a dynamic process that occurs within a complex system of embedded relationships that are affected by multiple levels of the environment (see Bronfenbrenner, 1979). In recent years, developmental psychologists have adopted a dynamic-systems approach to study the communication within care-taker–infant pairs, families, or small working groups, with explicit acknowledgment that one person's emotions and behavior may affect the entire system in unpredictable ways (e.g. Fivaz-Depeursinge and Corboz-Warnery, 1999; Fogel, 1993).

The dynamic-systems perspective undergirds some research in social anthropology as well. Its roots stretch back at least to Radcliffe-Browne's (1952) concept of network, though precursors may be seen in the work of Fortes (1949).[1] Best known for a systems framework may be Bateson. When he writes in *Steps to an Ecology of Mind* (1972: 319) that the thinking and acting human 'unit' is 'a *system* whose boundaries do not at all coincide with the boundaries either of the body or of what is popularly called "the self" or "consciousness"', Bateson is describing the embedding of a person within a larger dynamic system. For Bateson, that system is composed not only of other humans, but also of other organisms and nonliving things in the environment, including 'the pathways of sound and light' (1972: 319) along which information travels.

Contemporary dynamic-systems approaches in social anthropology are varied in both topic and methodology. A few examples include Ingold's (2000: 4–5) study of human subsistence, in which he insists that the human body is not complementary to mind and culture but is a 'singular locus of creative growth within a continually unfolding field of relationships'; Lansing's (1999) modeling of cooperative networks among Balinese rice farmers; and Toren's (1999) analysis of Fijian children's emerging understanding of ritual. These works, as we understand them, go beyond the notion of interaction to converge on transformation – the idea that elements in a system, including people, change each other continuously.

Applying a dynamic-systems framework to the behavior of nonhuman primates is still uncommon (but see Hemelrijk, 1996; Johnson, 2001; King, 2002; articles in Kohler and Gummerman, 2000). We argue here that just such an application can aid in understanding the social communication of our closest living relatives, the African great apes (the gorilla, *Gorilla gorilla*; chimpanzee, *Pan troglodytes*; and bonobo, *Pan paniscus*).[2]

GREAT APE SOCIALITY

Our starting point is the inherent sociality of great apes. In our view, even a female orang-utan, foraging alone in the forest, acts as a social creature. This is so because great apes are born into a deeply social world. Right from birth, they shape, and are shaped by, that world, through interactions with their mothers, and in many cases with other relatives and social companions as well.

Humans, of all primates, have the most extended periods of infancy and juvenility.

This extended immaturity is typically explained by the need for social learning in complex environments (see Geary and Flinn, 2001; but see also Janson and van Schaik, 1993). Although some life-history models emphasize features unique to humans (Bogin, 1997; Lancaster and Lancaster, 1983), most employ the notion of a continuum across primates. That is, great apes have extended periods of immaturity compared to lesser apes and most monkeys, and lesser apes and monkeys have extended immaturity compared to prosimians (see Pereira and Fairbanks, 1993).

For our purposes, the main implication of great apes' long period of immaturity is that their communicational abilities may emerge gradually, within a backdrop of ongoing, ever-changing socioaffective interactions. As infants and juveniles mature, they increasingly participate in the social worlds around them by gesturing and vocalizing (as well as through other forms of communication). We see these communicational abilities as emerging from socioaffective relationships. Before we assess the data with this claim in mind, however, we contrast in more detail two approaches to understanding social communication.

CONTRASTING APPROACHES TO SOCIAL COMMUNICATION

For the past 40 years, the standard view has been that communication, whether by human or other animal, 'occurs when one organism (the transmitter) encodes information into a signal which passes to another organism (the receiver) which decodes the signal and is capable of responding appropriately' (Ellis and Beattie, 1986: 3, 4).

The source of this view of communication lies in Claude Shannon's discovery, in 1948, of a revolutionary new way of safeguarding the transmission of electric and electronic signals by converting them into strings of binary digits and building in redundancies so that a listener can understand a broadcast even if certain sounds (e.g. vowels) or pixels are lost during the transmission. Or rather, the source of this view of animal and human communication lies in the *metaphor* that Shannon adopted to describe his method of converting sounds and images into binary strings. For Shannon suggested that this communications technology can be described as a matter of 'encoding' the 'information' that is contained in the 'message' that is being sent.

According to Shannon's information-processing metaphor, there is a 'communication continuum', with simple communication between cells at one end, and communication between machines, mammals, and primates, in stages representing levels of increasing complexity, leading to human communication with language at the other end. The progression from one level to the next was seen as a quantitative, not a qualitative shift. Thus, cells, nerves, computers, monkeys, apes, humans were all said to be communicating in the same general sense and can all be modeled in terms of the basic paradigm:

$$\boxed{\text{State of A}} \xrightarrow[\text{encodes}]{} \underset{\text{signal}}{\text{Nonverbal}} \xrightarrow[\text{decodes}]{} \boxed{\text{State of B}}$$

(Argyle, 1988: 2)

Shannon had based his information-processing metaphor on a model of linguistic communication that was itself based on a telecommunications metaphor. The paradigmatic example of the latter can be found in de Saussure's *Course in General Linguistics*, in which two speakers are depicted as 'encoding' and 'decoding' the information they wish to convey to one another with language (de Saussure, 1916). All Shannon was proposing was that de Saussure's famous 'speech-circuit' diagram (de Saussure, 1916: 27) could be applied to any communications system, albeit with simpler 'codes' than what one finds in language.

Given the interlocking nature of the metaphors at work here, it is all too easy to lose sight of the fact that these are metaphors. De Saussure did not discover that language is really a code that speakers use to communicate their thoughts; rather, he suggested that, for certain theoretical purposes, linguistic interaction could be likened to a telegraph system (Harris, 1980). Similarly, Shannon did not discover that telegraphic communication is really the same process as the one humans use to communicate. When Shannon proposed that telegraphic communication could be likened to the manner in which humans communicate, he was, in fact, presupposing de Saussure's mechanical model of communication. It was the circularity underlying these interconnected metaphors, therefore, that led to the conclusion that the electronic transmission of binary signals could serve as a model for the manner in which all organisms communicate with one another: i.e. that communication simpliciter is a binary encryption process.

Shannon's metaphor presents us with a model of communication that is fundamentally linear and binary. Communication is defined in terms of and confined to the transmission of information. The information conveyed is said to be an internal state that must be encoded and decoded if it is to be communicated. On this paradigm, there can be two or more senders and receivers in a communication system but only one sender at a time can transmit. Thus, the participants in a communication system must be in a discrete state: i.e. either transmitting or receiving, and they must take turns sending and receiving (signaling and responding).

The Shannon metaphor stimulated a great deal of productive research. A metaphor can, however, constrain as well as stimulate research, for example in regard to what kinds of questions get asked, and equally, what kinds of questions don't get asked; what sorts of epistemological or theoretical assumptions are made; and what sorts of methods or data are deemed appropriate and which are dismissed as 'unreliable'. That this should be so is made very clear by considering the dynamic-systems model in contrast to the information-processing model we have been discussing.

In a dynamic system, all of the elements are continuously interacting with and changing in respect to one another, and an aggregate pattern emerges from this process of mutual co-action. Hence communication is seen not as a linear, binary sequence or interaction, but rather as a 'continuous unfolding of individual action that is susceptible to being continuously modified by the continuously changing actions of the partner' (Fogel, 1993: 29). This dynamic process of *co-regulation* involves a 'balancing act by which a smooth social performance is created out of the continuous mutual adjustments of actions between partners. In co-regulated communication, information is created between people in such a way that the information changes as the interaction unfolds' (Fogel, 1993: 19).

The shift from an information-processing to a dynamic-systems paradigm represents an important transformation in our understanding of the nature of communication. Unlike in the information-processing paradigm, as we have seen, in the dynamic-systems paradigm mutual understanding is something that emerges as both partners act. On the dynamic-systems paradigm, in addition to communicating various kinds of information, individuals also communicate their desires and intentions, thoughts and fears, warnings and invitations, and, of course, attitudes and emotions. To reduce all these communicative acts to a single metric is to impose an abstract formalized model on an activity that is fundamentally variegated and dynamic.

Thus, in opposition to the Shannon metaphor, the dynamic-systems paradigm bases the study of great ape communication on the following fundamental themes:

1. Partners are continuously active in communication.
2. The actions of communicating agents are not coordinated by fixed or innate ‘codes’.
3. The actions of communicating agents are fundamentally relational; partners mutually adjust their behaviors to each other in subtle ways that can best be described by the term *co-regulation*.
4. It is often impossible to identify the initiator in a communicative exchange.
5. Communication cannot be reduced to a single modality, nor to the summation of multiple modalities.
6. The communicative significance of a particular gesture, vocalization, facial expression, and so on, is a function of its role within the communicative process and cannot be decontextualized (e.g. a hand movement only counts as a gesture in the context of a communicative exchange).
7. The constraints on communication cannot be quantified: they are a function of biological, psychological, emotional, and social factors.

DYNAMIC SOCIAL COMMUNICATION IN AFRICAN GREAT APES

That social context influences the nature of social communication has long been understood by animal behaviorists (e.g. Altmann, 1967; Smith, 1977). Social context has generally been viewed as a variable that may influence sender–receiver (linear) communicative sequences. Thus, aspects of the social situation may influence various aspects of the communication process, and vice versa. It is fascinating – though given the power of the Shannon linear metaphor, not surprising – how very ingrained and robust this viewpoint has remained across decades of study in primate communication.

Consider the research of Peter Marler. One of the 20th century’s great scholars of bird and primate communication, Marler is responsible for many breakthroughs, including heightened awareness of multimodal signaling and recognition of the distinction between graded and discrete signals (see Hauser, 1996: 53–60). Early on, Marler studied the effect of social context on call meaning. He wrote:

> When it takes place in its proper context, which is the natural environment of the species, the communicative act cannot be isolated from the circumstances in which the signaller and the recipient find themselves at the time they are participating in the exchange. Insofar as the surroundings and concomitant behavior of the signaller are perceptible to the recipient they also may contribute something to the response that it gives to a signal. The events preceding emission of a signal that have contributed to its production may be either external to the animal, or within it, or most likely a combination of both. By the same token, the internal state and external environment of the recipient may affect the nature of its response to a given signal.

> An attempt to unravel all the threads in this complex web of interacting events must necessarily begin. (Marler, 1965: 544)

Marler continues from there; we wish to highlight his theoretical framework, which we find echoed in primatology through subsequent decades of primate-communication research. In the seminal 1982 collection *Primate Communication,* for instance, Waser writes:

> First, the value to a signaler of broadcasting information to recipients, and thus the degree to which selection favors specialized 'information-transfer' abilities, depend on the social system . . . Second, the use to which a recipient can put the information contained in a signal varies strongly with the sex and social status of the recipient and with the nature of the social system. (1982: 118)

Two decades later, as author of one of the best primatology textbooks currently available, Strier employs terms similar to Marler's:

> Communication is a two-way street. There must be at least one actor and one receiver in each interaction, but in primate groups other members may also play active roles. Communication systems can be divided into four interrelated components: signal, motivation, meaning, and function. The *signal* is the form that the act of communication takes . . . *Motivation* refers to the internal state of the actor who is sending the signal . . . *Meaning* refers to the message that is received by the recipients of a signal . . . The function of communication describes its evolutionary advantage. (Strier, 1999: 275)

What unites the work of Marler, Waser, Strier, and countless others in primatology,[3] is their assumption, beautifully in line with Shannon's metaphor, of exchange of signals between senders and receivers for the purpose of transmitting information. The signals originate within the senders, and signal meaning is extracted by the recipient. As we have shown, the dynamic-systems perspective differs in its emphasis on co-regulated social communication. In reviewing recent data on social communication in the African great apes, we offer evidence in support of the view that the most appropriate unit of analysis is not the gesture or vocalization itself, but instead the ongoing, ever-changing socio-affective relationship. We show that co-regulated social communication enables coordination or cohesion of the individuals within great ape dyads or groups.[4]

Spontaneous gesturing of African great apes in captivity

Gesturally-mediated interactions in the great apes may include movements of the entire body, the head and face, and the limbs, including light touches as well as facial expressions; direct locomotory movements or forceful bodily actions are, by contrast, not generally considered to be gestural (Tanner and Byrne, 1999). Research by Tomasello and associates has provided an extensive database for evaluating the ontogeny of gestures in captive chimpanzees. Tomasello's team concludes that young chimpanzees learn gestures by a type of dyadic shaping termed ontogenetic ritualization (OR).

In OR, a movement or bodily action repeated between the same two interactants over time becomes reduced to a gesture. An infant ape may, for instance, first pull on her mother's nipple when it wants to suck. After many such pulls over some weeks, the mother may come to respond before the infant actually contacts the nipple, and eventually the infant may come to convey its interest by touching its mother's arm. In Tomasello's terms, 'a communicatory signal is created by two organisms shaping each other's behavior in repeated instances of a social interaction' (1999: 31).

Reviewing 12 years of their research, Tomasello et al. (1997: 225–6) summarize the ways in which their data support OR (rather than, say, imitation) as the mechanism at work in the ontogeny of gesturing: juvenile chimpanzees use many gestures not used by adults; adults use some gestures not used by juveniles; adult-like gestures replaced some juvenile gestures over time; idiosyncratic gestures occur; and there was 'very low concordance' in the gestures used across generations. This conclusion, however, overlooks the richness of dyadic shaping and its potential for understanding how social communication is created (rather than acquired) during ontogeny. That is, it underestimates the contingent, unpredictable and co-regulated nature of communicative exchanges (see Johnson, 2001).

Consider two representative events recorded by the senior author in her research into the ontogeny of gesture in bonobos at the Language Research Center, Georgia State University:

Event 1. Female Elikya, two months of age, sits with her mother Matata. Her mother hands her over to her older sister Neema sitting nearby. From Elikya's facial pout, it is clear that she is distressed by this transfer. Three times in succession, she extends her arm and hand, palm up, back towards her mother. She is near enough to her mother to touch her, but she gestures instead. After the third gesture, her mother takes Elikya back. As Elikya relaxes against her mother, her sister pats her gently.

Event 2. Elikya, eight months old, moves toward her sister Neema; she may lightly touch Neema's outstretched leg, but it is hard to be certain. Neema lowers her leg, then begins to stomp her feet on a platform as Elikya stands bipedally facing her. Elikya has a playface and raises her arms. Immediately Neema moves to Elikya and hugs her, covering her with her whole body, then quickly moves back and resumes her previous position.

The co-regulated nature of these interactions is clear, for the outcome, in each case, is created jointly by the participants. Elikya experiences situations, well before her first birthday, in which her gestures 'make a difference' socially. These gestures, together with her other movements and vocalizations, help create a shift in the interactions going on around her. Dyadic shaping in this perspective becomes much more than an inferior cousin to imitation; it becomes a powerful route for enhancement of social coordination and cohesion (see King, 2002 for more data on ontogeny of gesture in bonobos and gorillas).

Spontaneous gesturing by captive African great apes may involve the use of iconic gestures in which the gesturer traces an outline of the object or movement to which s/he refers. Captive bonobos use various manual gestures when communicating with each other about copulatory behaviors: position movements, touch plus iconic hand motions, and iconic hand motions alone (Savage-Rumbaugh et al., 1977). A bonobo may indicate that another bonobo should turn around by making a turning motion of the hand at the other's wrist (a 'touch plus iconic hand motion'), or may indicate by moving his own arms that another bonobo should move his arms out from the sides of his body (an 'iconic hand motion' alone). The interpretation of these gestures by the apes did not depend on the true form of the gesture in any reliable way. 'Instead, the body orientation of the initiator and recipient determined the exact topography of the gesture in each instance' (Savage-Rumbaugh et al., 1977: 108). This gestural system is complex because the participants must realize, among other things, 'that the hand is not acting as a hand in the instance of gesturing, but as a symbol for the recipient's body' (Savage-Rumbaugh et al., 1977: 114).

Some captive gorillas gesture iconically. In interacting with a female, Kubie, a male gorilla, used tactile close gestures – tracing or miming on the female's body; head nods produced once the female's visual attention was secured; and audible gestures made in the absence of the female's visual attention (Tanner and Byrne, 1996; 1999). Kubie would, for instance, sometimes tap the female Zura on her body without force, then make an 'armswing under' gesture toward himself, moving his open palm to a final position between his legs to indicate desired sexual activity.

More research on co-regulation and iconicity of gestures would complement the more conventional approach of testing great apes' ability to point referentially using the hand (e.g. Hopkins and Leavens, 1998; Krause and Fouts, 1997; Leavens, et al., 1996). Referential pointing may be accomplished non-manually, as well. Among chimpanzees trained to communicate using a version of American Sign Language, a chin up motion, 'a quick raising of the head with a directional component', was observed wherein 'the direction of the tip (left or right) would indicate direction of the chase, and the active "chin upper" would indicate the chaser' (Fouts and Fouts, 1999: 255).

Spontaneous gesturing by African great apes in the wild

Despite the evident richness of great-ape gesture, little systematic analysis of it has been carried out in the wild (Burling, 1999). Providing evidence of co-regulated gesture in the wild is thus trickier than in captivity, but intriguing hints exist.

Available data on wild gestures show a linkage between spontaneous gesturing and behavioral coordination. Following his first studies of free-ranging chimpanzees in the (then) Belgian Congo, Kortlandt wrote:

> They generally communicated by gesture, or by changes in posture or facial expression. Children asked for food by holding out one hand. If a mother and child were seated side by side and the mother wanted to move on, she had only to look at her offspring for it to jump up on her back. If by chance the child was looking the other way, she merely tapped it lightly on the shoulder or arm. (1962: 131–2)

Kortlandt's 45-minute film (Kortlandt and Trevor, 1964/1986) on Congolese chimpanzees demonstrates a wealth of coordinating social gesture. Twice, a chimp brings a hand up to its shoulder and makes a motion there. Both times, a nearby second chimp immediately walks off together with the gesturer, while the narrator labels the hand movement as 'a gesture for "let's go" '. Several times a chimp stops walking, then lifts a foot with sole turned out (sometimes a hand is lifted as well). In this case, the narrator mentions 'the stop gesture, a warning for those who follow'.

Coordination between apes results, too, when male bonobos gesture as they court females, as was observed at Wamba, Democratic Republic of Congo:

> In the first form, a male attracts the attention of a female who is far enough away that she cannot be touched, faces her, and spreads his thighs. While exposing his erect penis, he sits or moves his squatting body up and down, forward and backward, or side to side. Some males stick out their chest, and some stoop forward while they are displaying. Their hands are extended and moved in any direction according to individual preference, upward, sideways and, most often, forward, as if to beckon the female.
>
> If the female does not respond to this first form of courtship display, the male often changes to a second form of display. He approaches the female, sits or stands bipedally, and extends his hand, lightly touching and then releasing her head, shoulder, back, or knee. His body slowly moves forward and back and side to side. (Kano, 1992: 140)

What is needed now are data detailing the minute-by-minute response of females, to assess the degree to which the male display is co-regulated.

By grouping the gestures of wild bonobos into six patterned types, Ingmanson (1996; 1998; see also Kano, 1992; Kuroda, 1984) has begun to systematize the gestural data from Wamba.[5] Two gestures, peering and direct eye contact, involve the eyes only (a major channel for social communication). During infancy the first gestures to emerge relate to food-begging: infants touch their hands or mouth to the hands or mouth of another bonobo who is holding food or eating. Later, rocking the upper body back-and-forth develops, which is an indicator of desire for social contact. Most interestingly, rocking may be combined with other gestures to indicate the specific nature of the contact desired. Rocking with an arm raised by a male may be a request for submission from another male, whereas adding a genital display to the rocking helps specify that sexual contact is desired (Kuroda, 1984). When combined with a play face, rocking may be a play invitation, and when performed in calm situations, it may invite grooming (Kuroda, 1984). Infants as young as two years will respond appropriately to rocking gestures by others (Kuroda, 1984).

Two other behaviors that involve object use are considered by Ingmanson to be gestures. During play, the apes carry sticks but do not play with them; when one ape drops a stick the play bout ceases until the stick is retrieved. Ingmanson interprets the carrying as an indicator of ongoing play. Branch-dragging, the final gesture, is associated with group movement. Bonobos drag branches to initiate group movement, indicate the direction of movement, signal directional changes once movement is under way, and keep straggling group members together.

At least four of these gestures – those related to food-begging, play, peering and direct eye contact – likely arise during immaturity in intense association with mother and other community members. Indeed, all six bonobo gestures coordinate social interaction (see Vea and Sabater-Pi, 1998, for an example of pointing by a wild male bonobo that also coordinated social interaction).

Chimpanzees, too, gesture frequently in the wild (Goodall, 1968; 1986; Nishida et al., 1999; Plooij, 1978). As with bonobos, food-begging gestures arise early in ontogeny, well before one year. Chimpanzees food-beg by putting the open cupped hand, palm up, near the mouth of another chimpanzee who has food. A large variety of whole-body and arm (including wrist and hand) movements are used in aggressive, submissive, play and sexual contexts. A single gesture may be used in different contexts (Plooij, 1978). A raised arm, for instance, may, communicate desired outcomes in contexts as different as aggression, play, and grooming. Discovering how precisely a chimpanzee youngster constructs, through social interaction, the specific meaning of a raised arm, would come from full descriptive accounts across multiple dyads.

Indeed, when such interactive sequences are published, we see how gestures may coordinate action between individuals. In the following event recorded at Gombe, an infant (FD) chimpanzee interacts with its mother (FF):

> FD was walking on a rock (about 50 cm high) while FF was sitting out of contact but within arm's reach. Then FF stood up slowly, turned her back towards him and approached him while flexing her knees slightly and looking back at him with her lowered back closest to him. FD did not cling immediately and FF waited motionless while looking at him. Finally, he clung and FF walked a few paces to turn around and come back to the same rock to return him on the rock. Over and over she started to travel in this way and when FD did not walk onto the rock himself, she placed him there. Finally, FD clung immediately whenever FF 'signalled' by flexing her knees and looking back.
>
> Next, FF started with the whole procedure again, with FD on the ground. She lowered her back by crouching onto the ground in front of him while looking back at him over her shoulder. Whenever FD seemed not to be looking at FF she would wait and, ultimately, gain his attention by touching him. When touched in this way he always responded by clinging immediately. (Van De Ritj-Plooij and Plooij, 1987: 25; see also Goodall, 1968: 370–71)

That coordination of action results from this event is beyond question. We would go further to suggest that maternal 'signaling' may be an inadequate descriptor term for the complexity of mother–infant actions that unfolds here. The stream of reported behavior does not start with maternal movement but with the infant's precise location, position, and bodily orientation. The infant does not merely respond to, but also sets up, the next maternal move *while* the mother is herself setting up the infant's next move. One chimpanzee's actions are contingent upon its partner's.

Gestures of wild gorillas are not as extensively catalogued or described as those for chimpanzees and bonobos. We have known since Schaller's (1963) day about the communicative value of chest-beating in mountain gorillas. Beating of the ground by gorillas in Congo is associated with the group's beginning to move or altering direction of travel (Mori, 1983 in Tanner and Byrne, 1999). Western lowland gorillas, too, communicate socially through gesture. Fieldworkers Tutin and Parnell (personal communication to Tanner and Byrne, 1999) describe an instance in which a group of gorillas was crossing the savanna between two patches of forest in Gabon. One gorilla, the older of two walking together, moved along with some difficulty. The younger gorilla sometimes walked backwards facing the older one. When the older gorilla stopped, the younger one faced him and waved an arm in front of him. To the observers, this arm gesture appeared to be a way of urging the older gorilla as in a 'come on' gesture.

In sum, when African great apes gesture, whether in the wild or captivity, they do not do so merely to convey some sort of discrete message about their internal state or about the state of the environment. They gesture as one way of bringing about a desired social outcome, and in so doing, adjust, at least sometimes, their behavior in subtle ways as the social partner responds. Future study of African great ape gesture affords rich potential for exploring co-regulation in primate social communication, because gesture-mediated social interactions are clearly visible; can be filmed; and can be analyzed frame-by-frame.

Vocalizations of great apes in the wild

More research has been conducted on vocal communication than gestural communication in African great apes. The vocal work has been carried out selectively, however; vocal production has been studied far more thoroughly than has either the ontogeny of vocal usage or the phenomenon of vocal response (Seyfarth and Cheney, 1997). Of these three processes, vocal production is likely to be least modifiable with experience (Seyfarth and Cheney, 1997; but see Snowdon, 1999). Accordingly, intensified focus on usage and response may lead us to a better understanding of co-regulation (a type of modifiability) in great ape social communication.

Comparative data from three long-term field sites of chimpanzees (Gombe and Mahale in Tanzania, and Kibale in Uganda) allow a more thorough assessment of the chimpanzee's pant-hoot than of any other vocalization made by apes. This is fortunate, because data on the pant-hoot yield a clear example of how co-regulated social communication may result in behavioral coordination among chimpanzees. Both sexes pant-hoot as part of loud long-distance vocal exchanges both within and between groups (Goodall, 1968).

Male chimpanzees (whose pant-hoots have been studied to the near exclusion of females) utter individually distinctive pant-hoots comprising four separate phrases (Marler and Hobbett, 1975). They pant-hoot in responding to other chimpanzee pant-hoots, upon rejoining familiar community members, when meeting unfamiliar conspecifics, while displaying, upon arriving at rich food sources, upon capturing prey, and while recruiting other males as allies from some distance away (Goodall, 1986; Mitani and Nishida, 1993; Mitani et al., 1992). Chimpanzees pant-hoot most often when establishing or maintaining contact with other, distant chimpanzees (Mitani, 1994).

Recently, primatologists have begun to assess variability in two aspects of chimpanzee pant-hoots: the way in which call production varies with social factors,[6] including rank and association with other chimpanzees; and the way in which acoustic structure varies within and between populations. Probably the most productive avenue for understanding pant-hoots would be to study their ontogeny, but this has not yet been done in any detail. We do know, however, that neither male nor female chimpanzees give spontaneous pant-hoots as infants or juveniles, but begin to do so as adolescents (Pusey, 1990). Juveniles of both sexes join in pant-hoot choruses, and males produce 'chorus' pant-hoots more frequently than do females of the same age. Frequency of pant-hooting increases with age in males, and after first estrus in females (Pusey, 1990). Just how subadult pant-hoots are influenced by social interaction during chorusing is unknown.

Among chimpanzees of the Kanyawara community at Kibale, overall vocal production depends on the vocalizer's rank and the composition of the current subgroup or party in which he is traveling. Clark (1993) aggregated eleven call types by Kanyawara chimpanzees into two categories, with pant-hoots included as part of the 'nonsubmissive' rather than 'submissive' division. Across all social contexts, high-ranking adult males were the most vocal of any age/sex class. Further, the presence of adult males increased the call rate of other chimpanzees in the same party: adult females and subadult males, for instance, increased their rate of uttering nonsubmissive calls when with adult males. Clark speculates that advertising party size benefits high-ranking males (some benefits do accrue to comparatively larger subgroups, and the calls may attract mates or allow contact to be maintained with coalition partners). If this is true, then the lower-ranking apes traveling with these males might increase benefits to themselves by calling at higher rates. The possibility that the pant-hoot, disaggregated from other calls, is associated with rank is supported by Mitani and Nishida's (1993) finding that, at Mahale, high-ranking males gave more pant-hoots than low ranking males.

Research at Mahale by Mitani and colleagues shows that not only rates of vocalizing but also the structure of the calls may be altered with social context. When chorusing with other males, male chimpanzees actively alter the structure of their calls (Mitani and Gros-Louis, 1998). Originally, Mitani concluded that males who preferentially associate with each other produce acoustically similar calls (Mitani and Brandt, 1994). After further analysis he realized that a third variable, chorusing behavior, actually accounted for this finding: 'Since males who call together frequently may also frequently associate, call convergence appears to be mediated principally through chorusing per se' (Mitani and Gros-Louis, 1998: 1059).

Significantly, no specific 'chorus call' type of pant-hoot exists and chimpanzees do not match their calls specifically to the pant-hoots of high-ranking chimpanzees. Rather, the call convergence process seems to be analogous to vocal accommodation among humans. Convergence is achieved dyadically, with calls shifting on a moment-to-moment basis: the process is a dynamic one involving adjustments by both partners rather than a linear one in which a chimpanzee matches its vocalizations to another's. In other words, call convergence is an example of co-regulated social communication.

Given the cross-site availability of data on pant-hooting, good inter-population comparisons can be attempted. Pant-hoots by Mahale males differ structurally from those by Gombe males (for precise details of differences in the phrases of the calls, see Mitani et al., 1992). Four possible reasons for such variation have been effectively ruled out: genetic or anatomical differences in the chimpanzees at the two sites; varying behavioral contexts in which calls were given; or temporal variation in the studies themselves (Gombe pant-hoots were recorded years earlier than Mahale ones). Favoring a fifth reason, vocal learning, Mitani et al. (1992: 241) conclude that 'the articulatory movements that are involved [in pant-hooting] may be similar to differences in pronunciation which constitute an additional component of dialectical variation among humans.'

Adding data from the Kanyaware chimpanzee community at Kibale to the data from Gombe and Mahale complicates the picture further (Clark-Arcadi, 1996; Mitani et al., 1999). Kanyawara males pant-hoot differently than do Malahe males (for details see Clark-Arcadi, 1996; Mitani et al., 1999). On the surface, this finding could be taken to support the vocal-learning hypothesis. Yet as Mitani et al. (1999) point out, at about

700 km apart, Kibale and Mahale are likely to be genetically isolated from each other. By comparison, the more proximate sites of Gombe and Mahale have probably only been isolated for a few generations. And only across non-isolated or recently-isolated populations would we expect vocal differences to relate to vocal learning (Mitani et al., 1999).

On this view, comparing pant-hoots from males (and females) in two communities – Kanyawara and the nearby Ngogo, also in Kibale – might be well worth the trouble. Only quite recently have the fascinating demographics at Ngogo come to light: over 100 chimpanzees, including 20 males, congregate there (Mitani and Watts, 1999). The Ngogo community might be an ideal location at which to test hypotheses about the role of pant-hoots in within-group and between-group cohesion, as well as hypotheses about vocal learning and co-regulation of pant-hoots. The point we wish to stress is that, in the current rush to catalogue vocal differences across sites, researchers should not neglect more subtle processes akin to vocal accommodation, or social influences on call development during ontogeny.

Bonobos do not pant-hoot but do utter low hoots and high hoots, each in different contexts. Bonobo high hoots appear broadly similar to the pant-hoot of chimpanzees in that these calls appear to aid social cohesion, specifically the aggregation of dispersed parties. Precise ways in which the hooting calls of bonobos are shaped socially are not yet known. The best information available on high hoots by wild bonobos comes from fieldwork at Lomako in the Democratic Republic of Congo (Hohmann and Fruth, 1994).

At Lomako, high hoots reflect both inter-individual coordination (within dyads in a party) and supra-dyadic communal activity (within parties). When both bonobos in a pair hoot, the calls are uttered ‘in more or less perfect alternation, indicating a remarkable degree of behavioral coordination’ (Hohmann and Fruth, 1994: 779). Whether this behavioral synchrony mirrors the kind of dynamic call convergence found in chimpanzee pant-hooting remains to be seen. A supra-dyadic level is apparent too, as most or all members of a bonobo party tend to produce the high hoots at once. High hoots peak when different parties gather at the same nesting site:

> Gatherings at the nesting site and daily updates of information concerning the locality of other community members may greatly increase potential opportunities for each individual to join other individuals or parties. Consequently, high hoots may be the major device to regulate and to maintain the social network of the community. (Hohmann and Fruth, 1994: 780)

Bonobos, like chimpanzees, produce many vocalizations other than hoots. Field researchers note the ‘nearly incessant vocal activity’ (Bermejo and Omedes, 1999: 355) within bonobo parties, and highlight the importance of the peep and other close calls in short-distance, within-party communication. Yet even confining ourselves to the hoot category, we see that dynamic feedback from calling partners may alter rates and structures of calls. Too few data are available to allow us to assess ontogenetic changes in calling over time, or the role of emotion in this dynamic process. We can, however, reject oft-repeated claims for a stereotyped and invariant nature of chimpanzee vocalizations (Pinker, 1994).

The best-studied call of gorillas is a ‘close call’ uttered at short range rather than a long-distance, loud vocalization. Of all wild mountain gorilla vocalizations, the short-range double grunt is uttered most frequently (Stewart and Harcourt, 1994). Detailed information about wild gorilla close calls derives from studies of mountain gorillas by Harcourt and co-workers (in this section, therefore, ‘gorilla’ refers to mountain gorilla).

Gorilla close calls can be divided into staccato, brief syllabled grunts and longer, non-syllabled calls (Harcourt et al., 1993). They are not uttered within any specific context or associated with any specific behavior, but ‘are commonly given in situations of (a) potential separation, and (b) potential conflict’ (Harcourt et al., 1993: 113). A gorilla may give a close call when a mother leaves her infant, when the end of a rest period nears, when approaching or approached by another gorilla during feeding, and when joined by other apes in close proximity during intensive feeding.

Of all behaviors preceding a close call, most common is a similar call from another gorilla; vocal exchanges are typical. When gorillas are close together and about to change positions, they sometimes exchange close calls at a high rate, resulting in a chorus. ‘Concerted group movement (from resting areas, or nest sites, or between feeding spots) combined elements of both change in spatial position and unusual proximity, and was the most common context associated with vocal choruses’ (Harcourt et al., 1993: 113). Gorillas, then, vocally mediate their social behavior during critical moments for group cohesion, not only through isolated or sequential calls but also through vocal exchanges.

The short-range double grunt consists of two acoustic units, the first shorter than the second. Two acoustically discriminable types exist: ‘spontaneous’ double grunts are given after a period of silence, whereas ‘answers’ are given within five seconds of the same call from another individual (Seyfarth et al., 1994). The former type more often elicited replies than the second, so that two-call sequences were common but three-call sequences were rare. A broad interpretation of the double grunt is that it is ‘an exaggerated announcement of presence, whose function is to attract attention to the caller, and to signal conditional future activity’ (Harcourt and Stewart, 1996: 828). Double grunts may, for example, signal readiness to change activity. They are given more by dominant gorillas, but rather than being a threat – they rarely escalate to really aggressive calls such as cough grunts – they may at times indicate appeasement. Once again, we see an association between vocalizations and behavioral coordination.

We have reviewed only data on vocalizations from wild great apes. Extensive cataloguing of captive great apes’ species-specific vocal repertoires has been carried out, mostly in zoos (e.g. Berdecio and Nash, 1981; De Waal, 1988). Co-regulated communicative sequences may be studied with particular effectiveness in captivity, where apes’ vocalizations and accompanying actions may be recorded and analyzed.

Communication with enculturated African great apes

Enculturated great apes, those raised in enriched environments by human caretakers, provide a different but equally valuable window into co-regulated social communication. More so even than the study of gestures or vocalizations, the field of Ape Language Research (ALR), which focuses on enculturated great apes, has provided a set of hotly-debated data. Here we focus briefly on the work of Savage-Rumbaugh in order to illustrate the potential for interpreting these data from a dynamic-systems perspective (for details, see Shanker and King, in press).

The publication of Terrace's *Nim* in 1979 created a crisis in ALR of such proportions that it seemed unlikely that the field would ever again generate the sort of interest that had greeted the Gardners' work with Washoe (Gardner and Gardner, 1969), Premack's work with Sarah (Premack, 1976), or Rumbaugh's work with Lana (Rumbaugh, 1977). Terrace and other critics of ALR were unanimous in their belief that the behavior of the 'signing apes' could be explained as the result of imitation, trial-and-error learning, instrumental conditioning, unintentional cuing, or over-interpretation by the researchers. But Savage-Rumbaugh's *Ape Language* (1986) marked an important turning point in the fortunes of ALR.

Savage-Rumbaugh made clear that the point of her research with the chimpanzees Sherman and Austin was simply to improve their communicative competence and so come to better understand the skills of early language acquisition. Sherman and Austin were, from the start, sensitive to tone of voice and facial expressions, and frequently gestured to communicate their desires. What they could not do very well, however, was pair lexigrams (colorful, non-iconic symbols) with objects. But after the research shifted to a 'request task' paradigm, in which the experimenter held up a food item that the chimps immediately received if they pressed the right key, they made rapid gains in lexigram–object pairings. Indeed, they began to demonstrate communicative behaviors normally seen in a one-year-old child, using lexigrams spontaneously, in novel situations, to refer to objects, direct Savage-Rumbaugh's attention, and express their intentions (Savage-Rumbaugh, 1986).

In the 1980s Savage-Rumbaugh shifted to working with bonobos, with striking results. Much has been made of her unexpected discovery that, at age two, the male bonobo Kanzi had, without any direct instruction, mastered eight lexigram symbols (see Savage-Rumbaugh et al., 1998). But Savage-Rumbaugh herself places great emphasis on the events leading up to this event. At the age of six months Kanzi 'became mesmerized by the keyboard, staring at the symbols as they flashed onto the projectors at the top of the keyboard' (Savage-Rumbaugh and Lewin, 1994: 129). When he was 14 months old, Kanzi began 'to press keys on the keyboard and then run to the vending machine as though he had grasped the idea that hitting keys produced food' (Savage-Rumbaugh and Lewin, 1994: 130). When he was 18 months old, Kanzi started 'inventing simple iconic gestures, the first of which indicated the direction of travel in which he wished to be carried' (Savage-Rumbaugh and Lewin, 1994: 134). He 'added emphasis to his gesture by forcefully turning [Savage-Rumbaugh's] head in the direction he wished to go [and] at other times . . . he would lean his whole body in the desired direction of travel so that there was no mistaking his intent' (Savage-Rumbaugh and Lewin, 1994). He often vocalized while gesturing, with emotional affect. Around the age of two, Kanzi began deliberately to select the 'chase' symbol, then look around to see if Savage-Rumbaugh had noticed and would indeed chase him.

It is important to stress that the lexigram board was not designed to test or to instruct: it was designed to facilitate interactions by providing Kanzi with an artificial communication tool (and a cumbersome one at that). As a result, Kanzi's 'communications soon began to revolve around his daily activities' (Savage-Rumbaugh and Lewin, 1994: 139). Kanzi's language development was thus a prolonged process that occurred because he 'was aware that we employed the keyboard as a means of communication and apparently felt keenly motivated to do so as well' (Savage-Rumbaugh and Lewin, 1994).

The focus of this research is, of course, on Kanzi's production and comprehension skills, which have been assessed as comparable, respectively, to those of a one-and-a-half-year old and two-and-a-half-year old child (Deacon, 1997). But by studying how Kanzi performs in isolated conditions (e.g. on match-to-sample tasks or novel sentence tests) we run the risk of misconstruing, not just the extent of his capacities, but more importantly, the key factors involved in the development of these capacities. From the dynamic-systems perspective, what really needs to be studied is Kanzi's communicative behavior in natural, interactional activities. On this framework, the most significant questions raised by this research concern how Kanzi's attentional capacities, his use of lexigrams, and his comprehension of spoken English, all developed as a result of being nurtured in language-enriched interactions with his caregivers.

CONCLUSIONS

In a previous section, we presented seven ways in which the dynamic-systems perspective of social communication differs from that of the linear information-processing framework. These points all, in one way or another, converge on the idea that social communication of great apes emerges via co-regulated action between social partners, and cannot be simply reduced to a process of fixed, linear message-sending and message-decoding. The 'goodness of fit' between our theoretical expectation of co-regulated social communication and the available data from African great apes varies, as would be expected when assessing research derived primarily from the information-processing framework. Among the strongest examples of co-regulated social communication may be gesture-mediated interactions (iconic and otherwise) in captive gorillas and bonobos; call convergence in pant-hooting among individual wild chimpanzees; and the bonobo Kanzi's development of linguistic skills in the context of language-enriched interaction with his caregivers.

Research into co-regulated social communication by great apes would be facilitated by the adoption of methods sensitive enough to record comprehensively the continuous mutual adjustments of the social partners. Great ape social communication, like all primate social communication, is multimodal; the abilities we have focused upon here are not in reality separable from other forms of visual, tactile and chemical communication. Facial expressions, which we defined as a type of gesture but did not discuss extensively, may be particularly important in assessing co-regulation and behavioral coordination (see e.g. Parr et al., 1998; Tanner and Byrne, 1993).

Although we expect that all primates are capable of co-regulated social communication in some form, we think it reasonable to hypothesize that the great apes (including the orangutan), compared to lesser apes or monkeys, display the most highly elaborated skills of mutual adjustment and flexible, fine-tuned response to the social partner. Great apes appear to use social gesture in more cognitively complex, highly social ways than do lesser apes and monkeys (Burling, 1999; Maestripieri, 1999). Great apes seem more capable than other nonhuman primates of imitation, perspective-taking, and teaching, all skills dependent on the ability to monitor and 'read' the social partner's actions and intentions, and to assess what the social partner can (or cannot) see, or does (or does not) know (e.g. Boesch and Boesch-Achermann, 2000; Byrne, 1995; Hare et al., 2000; Parker, 1996). The dynamic-systems perspective applied to social communication patterns of great apes will yield rich information of value to anthropologists in modeling the evolution of both communication and cognition in primates.

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Notes

1 We thank Vinson Sutlive for pointing out these early links within social anthropology.

2 We omit the orangutan only because of limited space.

3 Included is a work by the senior author, *The Information Continuum* (1994)

4 By coordination and cohesion, we do not mean to imply an absence of conflict or deception; we see conflict not as ‘negative’ but as part of larger social forces that exist in social, group-living organisms (De Waal, 1996).

5 In the DST view, a shift would be welcome, in this example and elsewhere, from focusing on gestures as discrete units that may be extracted from the behavioral flow and then classified, to studying the co-regulated social interaction of which gesture is one part.

6 As we describe this work, note the power of the traditional framework in which social variables are seen to impinge upon communication.

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