
36 Primate Vocal and Gestural Communication

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One way to investigate animal cognition is to investigate acts of social communication. In the broadest definition of the term, many acts of communication do not involve complex cognitive processes, since they are simply involuntary behavioral reactions or emotional displays in social situations. However, especially in the case of primates, there are many acts of communication that clearly involve complex cognitive processes, since they are undoubtedly “flexible behavioral adaptations in which individual organisms make informed choices based on mental representations” (Tomasello and Call 1997, p. 12). Here we review—very schematically—what is currently known about the cognitive processes involved in primate communication. Based on the above definition, we focus on two key aspects: (1) the flexibility with which individuals use their communicative signals and (2) the mental representations that might underlie this use of signals. We review first the findings for vocal communication, which mostly involve monkeys, and then those for gestural communication, which mostly involve apes.

Vocal Communication

Primates vocalize to one another most often in the context of evolutionarily urgent events such as avoiding predators, defending against aggressors, traveling as a group, and discovering food. For the most part, all of the individuals of a given species use the same vocal signals, and no new vocal signals are invented by individuals. However, there is some flexibility in the precise manner in which a given call is produced. For example, rhesus monkeys can be trained to alter the duration of their “coo” calls (Sutton et al. 1973); newly paired pygmy marmosets tend to converge on a common structure in their “trill” calls (Snowdon and Elowson 1999); and subordinate cotton-top tamarins change the way they

produce food “chirps” as soon as they become dominant (Roush and Snowdon 1999).

Ontogenetically, there is evidence that in natural populations learning plays at least some role in determining the exact acoustic structure of vocalizations. For example, the coo calls of rhesus monkeys are acoustically more similar within than between matriline (Hauser 1992), and a number of species display population-specific “dialects” in some vocal signals (e.g., saddle-backed tamarins, Hodun et al. 1981; chimpanzees, Mitani et al. 1992, and others). Experimental studies suggest, however, that such flexibility is limited. For example, in a cross-fostering experiment, Owren et al. (1992) found only limited modifications in the calls of two cross-fostered macaque species. The modifications that were found occurred in only a few limited contexts and involved only a subtle shift in some vocalization patterns and an increase in the frequency of use of calls already in the animals’ repertoires. It is also relevant that squirrel monkeys produce most call types from soon after birth, even if they are reared in isolation (see Snowdon et al. 1997 for a review), and that hybrid gibbons (*Hylobates lar* and *H. pileatus*) produce songs with an acoustic structure morphologically intermediate between those of the two parent species (e.g., Geissmann 1984).

As with call morphology, call usage seems to have only limited flexibility, with learning playing a highly limited role. Thus in most cases calls are used in adultlike contexts from early in infancy, but then there is a learning phase in which more adultlike usage is fine tuned (Seyfarth and Cheney 1997). For example, infant vervet monkeys often make mistakes by giving an eagle alarm call in response to various moving things in the sky (Seyfarth and Cheney 1986), and they produce intergroup calls whenever they are distressed. Only later do they confine these to adultlike contexts (Hauser 1989). And young pigtail

macaques are less precise when using agonistic screams than are adults (Gouzoules and Gouzoules 1989). Flexibility of use persists to some degree in adults. For example, in cotton-top tamarins, social and reproductive status can affect call usage (Roush and Snowdon 2000), and Japanese macaques show population-level differences in their use of food and contact calls (Green 1975; Sakura 1989).

An especially important type of flexibility concerns audience effects, in which an individual uses its vocal signals differently, depending on the social-communicative situation. Audience effects are especially important because they suggest that individuals are strategically modifying their use of a signal based on their current assessment of how it might affect potential recipients. For example, red-bellied tamarins produce food calls when they discover food, but the call rates depend on whether other group mates are present (Caine et al. 1995); male chimpanzees pant-hoot more frequently in traveling contexts when their alliance partners are nearby (Mitani and Nishida 1993); and vervet monkey females adjust the rate of alarm calls according to whether their own offspring are present, while males call more in the presence of females than males (Cheney and Seyfarth 1985). On the other hand, macaque females who were shown a predator, either in the presence of their offspring or alone, did not attempt to alert ignorant offspring more than knowledgeable ones, suggesting that audience effects may not be the result of callers assessing the knowledge of recipients (Cheney and Seyfarth 1990). Overall, there clearly are audience effects for some primate vocal signals, but the degree and consistency of the effects are modest and the underlying cognitive processes are not well understood.

Undoubtedly, primates display most flexibility in the way they perceive and understand vocal signals. The classic case for context-sensitive semanticity is vervet monkey alarm calls in which individuals respond to acoustically distinct calls with particular types of antipredator responses,

even in the absence of the predator (Seyfarth et al. 1980). [See Zuberbühler et al. (1997) and Zuberbühler (2000c) for comparable research with Diana monkeys and Campbell's monkeys, respectively; see Macedonia (1990) for research with prosimians.] The other classic case is rhesus monkey recruitment screams, which encode various aspects of the agonistic encounter, especially the relative rank of the attacker and the severity of the attack (Gouzoules et al. 1984). In this case responders base their reaction (e.g., aiding the attacked individual or not) on their understanding of who the aggressor is and what kind of aggression is occurring. Convincing evidence that recipients are indeed responding to the meaning (reference) of such calls, and not to such things as their emotional intensity or the like, comes from habituation experiments in which individuals habituated to some call show dishabituation only when the meaning (referent) of the call is changed (e.g., Cheney and Seyfarth 1988; Zuberbühler et al. 1999; Zuberbühler 2000c). It is interesting that there are no convincing observations of such "referential signals" in any ape species, the closest possibility being chimpanzees' differential use of food grunts for different amounts of food (Hauser and Wrangham 1987; Hauser et al. 1993).

As recipients, primates thus exhibit a fairly sophisticated understanding of the meanings associated with various calls, which possibly involves mental representations of the referential situation. Even more impressive, some species seem to be able to take into account the possible causes of an alarm call, rather than responding to the alarm calls directly (Zuberbühler 2000a,b). Thus, savannah baboons respond differentially to a played-back submissive grunt, depending on their understanding of who the caller is and whom she is giving the submissive grunt to (Cheney et al. 1995). Finally, the learning skills used in call comprehension show almost unlimited flexibility, since a number of primate species can learn to use effectively the calls of various other sympatric species, both primate and nonprimate. Thus,

Diana monkeys understand the meaning and underlying cause of other primate species' alarm calls (Zuberbühler 2000c), guinea fowl alarm calls (Zuberbühler 2000a), and different kinds of chimpanzee screams (Zuberbühler 2000b; see Hauser 1988, for similar findings with vervet monkeys).

In sum, although primate vocalizations seem to be under significant genetic control in their morphology and usage, there is also evidence that the callers have some limited flexibility. In particular, social factors may affect the structure of certain calls, and audience effects may influence the way calls are used in some circumstances. Current evidence suggests that primates possess the most flexibility in call comprehension. Many primate species comprehend vocal signals as indications of specific external events; this includes the calls of other species, which obviously must be individually learned. Moreover, the recipients take into account various kinds of causal relations in making the appropriate responses.

Gestural Communication

Primates communicate using manual and bodily gestures mainly in social contexts such as play, grooming, nursing, and during sexual and agonistic encounters. These are in general less evolutionarily urgent functions than those signaled by vocal communication. Unlike the case of vocal signals, however, there is good evidence that individuals of some primate species, especially apes, may invent new gestural signals as needed. Goodall (1986) and Tomasello et al. (1985), for example, report much variability in the gestures used by individual chimpanzees, including a number of idiosyncratic gestures used by single individuals only that could not have been either genetically determined or socially learned. Tanner and Byrne (1993, 1996) also report much individual variability in the gestures used by gorillas. The only systematic studies of monkeys'

gestural communication give no information about individual differences, but it does not seem likely that individuals invent gestures on their own (Maestriperi 1998).

Chimpanzees (and probably gorillas) learn their gestural signals via a process of ontogenetic ritualization (Tomasello 1996) in which two organisms shape one another's behavior in repeated instances of a social interaction. The general form of this type of learning is as follows: (1) Individual *A* performs behavior *X*. (2) Individual *B* reacts consistently with behavior *Y*. (3) Subsequently *B* anticipates *A*'s performance of *X*, on the basis of its initial step, by performing *Y*. (4) Subsequently *A* anticipates *B*'s anticipation and produces the initial step in a ritualized form (waiting for a response) *in order to* elicit *Y*. The main point is that a behavior that was not at first a communicative signal becomes one by virtue of the anticipations of the interactants over time. There is no evidence that chimpanzees, or any other ape species, acquire gestural signals by imitative learning (Tomasello and Call 1997). In the case of monkeys, de Waal and Johanowicz (1993) looked at the reconciliation gestures of juvenile rhesus and stump-tail macaques who were co-housed for a period of 5 months and found that the nature of the gestures and displays for reconciliation remained unchanged for both species (even though some other behaviors did change).

With regard to flexibility of use, Tomasello et al. (1994, 1997) found that many chimpanzee gestures were used in multiple contexts, sometimes across widely divergent behavioral domains (an average of 2.5 gestures per individual were used for more than one function). Also, sometimes different gestures were used interchangeably in the same context toward the same end—and individuals sometimes performed these in rapid succession in the same context (e.g., initiating play first with a “poke-at” followed by an “arm raise”). By all accounts, the gestural signals of monkey species do not show this same

degree of flexibility, but rather their gestural signals are as tightly tied to particular communicative situations as their vocal signals. However, in some instances both monkeys and apes have been observed to use some gestures in a way that suggests tactical deception, which—regardless of the appropriateness of this appellation—at least indicates that the human observer saw a gesture used outside its ordinary context (Whiten and Byrne 1988).

In terms of audience effects, Tomasello et al. (1994, 1997) found that chimpanzee juveniles give a visual signal to solicit play (e.g., “arm raise”) only when the recipient is already oriented appropriately, but they use their most insistent attention-getter, a physical “poke-at,” most often when the recipient is socially engaged with others. Tanner and Byrne (1993) reported that a female gorilla repeatedly used her hands to hide her play face from a potential partner, indicating some flexible control of the otherwise involuntary grimace, as well as a possible understanding of the role of visual attention in gestural communication (see also de Waal 1986, for a similar observation for chimpanzees). In an experimental setting, Call and Tomasello (1994) found that at least some orangutans also were sensitive to the gaze direction of their communicative partner. Kummer (1968) reported that before they set off foraging, male hamadryas baboons engage in “notifying behavior” in which they approach another individual and look directly into their face, presumably to make sure that the other is looking before the trek begins. Overall, audience effects are very clear in the case of ape gestures, and there may be such effects for monkey gestures as well.

Since the gestures of apes are produced so flexibly, flexible skills of gesture comprehension are required as well. Virtually no ape gestures are referential in the sense that they indicate an external entity (e.g., there is no pointing in the human fashion); they mostly concern the dyadic interactions among group mates. It is interesting for the process of comprehension that Tanner

and Byrne (1996) have reported on a number of gorilla gestures that seem to be iconic. That is, an adult male gorilla often seemed to indicate to a female playmate iconically, by using his arms or whole body, the direction in which he wanted her to move, the location he wanted her to go to, or the action he wanted her to perform (see also Savage-Rumbaugh et al. 1977, for bonobos). However, these might simply be normal ritualized gestures, with the iconicity being only in the eyes of the human; in fact, a role for iconicity in gorillas’ and other apes’ comprehension of gestures has not yet been demonstrated (Tomasello and Call 1997).

In sum, primate gestural communication shows more flexibility than primate vocal communication, perhaps because it concerns less evolutionarily urgent activities than those indicated most often with vocalizations. Apes create new gestures routinely and in general use many of their gestures quite flexibly; more research is needed with monkeys. Audience effects and flexibility of comprehension are routine with ape gestural communication, and again more research is needed with monkeys. However, neither ape nor monkey gestures seem to be used referentially, as are some monkey vocal signals.

Conclusion

By most definitions, cognition involves mental representation. Nonhuman primates mentally represent their worlds in many different ways, including in the domains of space, objects, categories, quantities, social relationships, and others (Tomasello and Call 1997). Primate communication also involves mental representation in some cases, most clearly in the representational vocalizations used by some monkey species. A major question in this respect is whether apes also use some representational signals, either vocal or gestural, in some as-yet to be discovered domain.

But the prototype of a cognitive process also involves the flexible use of these mental repre-

sentations. Much primate communication, perhaps especially the gestural communication of apes, involves very flexible behavioral strategies. Ape gestures have flexible connections between signal and function, a clear sensitivity to audience, and at least some combinatorial possibilities, all of which rely on the flexible way in which gestural signals are ontogenetically ritualized. The most urgent question in this respect is whether some monkey species also use their gestural signals in highly flexible ways in some as-yet to be discovered behavioral domain.

Finally, there is also the question of how to characterize the communicative activities of human-raised apes who learn something resembling human language (e.g., Greenfield and Savage-Rumbaugh 1990; Savage-Rumbaugh et al. 1993). A review of this research is beyond the scope of this essay, but it is clear that there are a plethora of interesting but unanswered questions about these unique individuals.

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