15

Implications of mirror neurons for the ontogeny and phylogeny of cultural processes: the examples of tools and language

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15.1 Introduction

In this chapter I explore two qualities of the mirror neuron system that are critical for the evolution of tool use and language, central characteristics of human culture. The two characteristics of the mirror system are: (1) the ability of the system to respond both to one's own act and to the same act performed by another and (2) the system's selective response to intentional or goal-directed action (Fogassi *et al.*, 2005). The ability to respond neurally both to one's own act and to the same act performed by another constitutes the neural foundation of imitation on the behavioral level (Iacoboni *et al.*, 1999) and of repetition on the linguistic and cognitive levels (Ochs (Keenan), 1977). The selective response of the mirror neuron system to goal-directed action constitutes the neural facilitation of goal-directed action on the behavioral level and of intentionality on the cognitive level (Greenfield, 1980). My purpose is then to demonstrate the importance of these neurally grounded behavioral competencies for the evolution and ontogenetic development of two key aspects of human culture, tool use and language. In so doing, my larger goal is to contribute to understanding the neural underpinnings for the ontogeny and phylogeny of human culture.

In order to provide data on phylogeny, I draw upon my own research and that of others to compare chimpanzees (*Pan troglodytes*), bonobos *(Pan paniscus)*, and humans *(Homo sapiens)*. The *Pan* line and the hominid line diverged in evolutionary history approximately 5 million years ago (Stauffer *et al.*, 2001). The two species of *Pan* later separated from each other about 2 million years ago (Zihlman, 1996). By cladistic logic, if we find the same characteristic in all three species, it is very likely to constitute an ancestral trait that was present before the phylogenetic divergence.

Cladistics refers to a taxonomic analysis that emphasizes the evolutionary relationships between different species. A clade – the basic unit of cladistic analysis – is defined as the group of species that all descended from a common ancestor unique to that clade. Cladistic analysis separates ancestral traits, which are inherited from the ancestors of

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the clade, from derived traits, which are possessed by only some of the clade members (Boyd and Silk, 2000). Derived traits arose through natural selection after the divergence of the clade from the common ancestor. Ancestral traits, in contrast, have a genetic foundation in the common ancestor. This genetic foundation drives the development of neural and all other biological systems.

This focus on what was present *before* the divergence of *Pan* and *Homo* is especially relevant to the role of mirror neurons in the evolution of human culture because mirror systems are known to exist in both macaque monkeys (Gallese *et al.*, 1996; Rizzolatti *et al.*, 1996) and humans (Iacoboni *et al.*, 1999) (see Arbib, Chapter 1, this volume for a review). Since Old World monkeys (of which the macaque is one) diverged about 23 million years ago from the hominoid line that became *Homo* and *Pan* (Stauffer *et al.*, 2001) and because the relevant behaviors mirror neurons subserve (reaching and grasping) are possessed by chimpanzees and bonobos, as well as by macaque monkeys and humans, it is likely (and I assume this for purposes of this chapter) that chimpanzees and bonobos also possess mirror neuron systems. There is also a bootstrap element to my evidence: in so far as I find that the behaviors subserved by a mirror system in humans also exist in *Pan*, this provides behavioral evidence suggesting the presence of a mirror system in chimpanzees and bonobos. For ethical and pragmatic reasons, it has not been possible up to now to investigate the presence or absence of a mirror system in *Pan*. One cannot implant electrodes in apes for ethical reasons; one cannot put an ape in a functional magnetic resonance imaging (fMRI) machine for pragmatic reasons – an ape will not lie still in the scanner! However, we may expect better adapted forms of brain mapping to greatly increase knowledge of ape brain function in the coming decades.

Gorillas and orangutans diverged earlier than chimpanzees from the hominoid line; the gorilla more recently at about 6 million years ago, orangutan about 11 million years ago (Stauffer *et al.*, 2001). However, the omission of detailed data on these species in the present chapter is in no way an assertion that they lack tools or the ability to learn a humanly devised communication system. For example, it is known that gorillas spontaneously make tools (Fontaine *et al.*, 1995); and it is equally known that gorillas and orangutans have developed a human protolanguage under the tutelage of human sign-language teachers (Patterson, 1978; Miles, 1990). Hence the capabilities for protolanguage and even tools may have been present in the common ancestor of the whole great ape and hominoid line, a minimum of about 11 million years ago.

Indeed, the most recent evidence from monkeys indicates that, through extended experience in watching human tool behavior, macaque monkeys can develop mirror neurons that respond selectively to observing human beings use tools to act on objects (Ferrari *et al.*, 2005). This implies that a basic cognitive capacity to associate hand and tool is present in the common ancestor of Old World monkeys, apes, and hominoids, a minimum of 23 million years ago (Stauffer *et al.*, 2001). Hence one would expect tool understanding, if not behavior, throughout the great ape line.

In sum, I will use similarities among chimpanzees, bonobos, and humans as clues to what foundations of human language may have been present in our common ancestor

5 million years ago. Such foundations would then have served as the basis from which distinctive traits of human language could have evolved in the following millions of years. While species differences are as important as similarities in determining the evolution of human culture (compare the chapters by Arbib and Stanford, this volume), my focus here is on the similarities. These similarities provide clues as to the capabilities in our common ancestor present 5 million years ago. This focus on the 5-million-year-old foundation of human evolution contrasts with the focus of the Arbib and Stanford chapters on the evolutionary elaboration of human tools and language that occurred in the last 5 million years.

15.1.1 Connection between the evolution of culture and the brain

Although phenotypic variation is the basis for natural selection, there has to be an underlying biological structure in order to have something genetic to select for. Mirror (and other) neurons specialized for different types of cultural learning provide biological structures that could have been selected for in the course of human evolution. Often culture, seen to be a part of the environment, is considered the opposite of biology. However, the notion of neural capacities that make cultural learning possible avoids the either/or dichotomy between biology and environment, biology and culture. Mirror and canonical neurons (the distinction is explained below) provide some key capacities for cultural learning that make an important link between the brain and culture. They provide something biological that could have been selected for as culture evolved.

Mirror neurons

Mirror neurons were originally discovered in monkeys (Gallese *et al.*, 1996; Rizzolatti *et al.*, 1996). Mirror systems were later found in humans (Fadiga *et al.*, 1995; Rizzolatti *et al.*, 1996; Iacoboni *et al.*, 1999). (The term "neuron" is used for the monkey research because the researchers utilize single-cell recording methods. The term "system" is used for the human research, because fMRI and other brain imaging methods used with humans cannot resolve single neurons.) Mirror neurons discharge when a goal-directed action is enacted or observed. In contrast, they do *not* discharge when the same movements are enacted or observed outside the context of the goal. Their activation pattern differs in the context of different goals. An important subset will discharge before the final goal is observed, indicating the perception of intentionality. Finally, mirror neurons do *not* discharge in the presence of a goal-object alone.

Canonical neurons

Like mirror neurons, canonical neurons were originally discovered in monkeys (Gallese *et al.*, 1996). Later, they were found in humans (Garbarini and Adenzato, 2004). They discharge not only when a goal-directed action is enacted (like mirror neurons), but also when a goal-object is observed and may be acted upon. They therefore represent a connection between a goal-object and its associated motor action. However (unlike mirror neurons) they are not active when the subject observes the actions of another.

15.1.2 *Connection between ontogeny and phylogeny?*

Ontogeny does *not* recapitulate phylogeny. However, there are important theoretical and evolutionary connections between ontogeny and phylogeny. First, earlier stages of development are more universal within a species than are later stages of development. Second, earlier stages of development are more similar among phylogenetically related species than are later stages of development. In other words, as phylogenetic divergence progresses, the evolutionarily later developments are more likely to occur later rather than earlier in an ontogenetic sequence. In that way, phylogenetic changes interfere less with subsequent ontogeny. This is because evolutionary change in earlier stages may compromise development in later stages that depend on them. Note that this formulation is contrary to the evolutionary myth that adult chimpanzees resemble human children. The notion is simply that human and chimpanzee babies will be more alike than human and chimpanzee adults. This is a relative statement concerning ontogenetic trends and in no way precludes differences between human and chimpanzee babies from having evolved.

Indeed, one must always remember that *Pan* has undergone evolutionary change in the last 5 million years, just as *Homo* has. We cannot assume either species of *Pan* is closer in form and behavior to the common ancestor than is *Homo sapiens*, although evidence has been presented to support the idea that the bonobo may be closest to the common ancestor of the three species – that is that the bonobo has evolved in the last 5 million years less than humans or chimpanzees (Zihlman, 1996).

Third, as we saw above, similarity of a characteristic among groups of phylogenetically related species indicates that a characteristic was likely to be part of the common ancestor of those species. It therefore follows that early stages of development (ontogeny) provide clues about phylogenetic foundations at the evolutionary point of species divergence. The clues are even stronger if the early stages are shared among a family (or clade) of closely related species. Correlatively, differences in the later stages of development among members of a clade will provide important clues as to species differences in adult capabilities. Again, my theoretical and empirical focus in this chapter is on the nature of the evolutionary foundation that existed 5 million years ago before the divergence of the three species. We are most likely to find clues in the early development in all three species.

These are the reasons why ontogeny can help us understand the phylogeny of cultural processes. In what follows, I examine the development across species of behavioral and cognitive capabilities that correspond to capabilities shown in prior research to be subserved by mirror neurons (and to a much lesser extent, canonical neurons). I then make the case that these capabilities are crucial to the ontogeny and phylogeny of cultural processes.

15.2 Imitation, observation, and cultural learning: ontogeny and phylogeny

In this section, I start with the assumption that observation and imitation are two central mechanisms for cultural learning. I then try to show that both are present from the beginning of life in both *Homo sapiens* and *Pan* (both species, bonobos and chimpanzees). From there, I illustrate the use of these mechanisms in the cultural learning of tool use across species. However, data concerning newborn imitation in humans have a strong traditional opponent in Piaget.

15.2.1 *Piagetian theory, mirror neurons, and newborn imitation in humans*

Piaget's (1962) theory of imitation is basically a visual one. Piaget theorized that action imitation requires seeing both one's own action and the action of the other in order to make the cross-modal correspondence between visual stimulus and motor movement. Yet Meltzoff and Moore (1977) reported that newborns imitate tongue movements, even though the baby cannot see its own tongue (Fig. 15.1). This is cross-modal imitation (the visual model of the tongue being stuck out is responded to motorically in the action response of sticking out one's own tongue).[1] In Piaget's conceptualization, all imitation is cross-modal, linking the sensory to the motor, and therefore had to await what he thought of as a later developmental stage when cross-modal cognitive correspondence would become possible for a baby. It was once thought that cross-modal imitation was a fairly high-level cognitive skill; one needed actively to make cognitive (and presumably neural) connections between visual stimulus and motor response. However, mirror neurons provide a theoretical and neural construct that can explain this seeming contradiction between the young age of a newborn baby and the sophisticated imitation response. Note, for future reference, that I consider the baby's imitation to have an intentional structure, even though it is automatic. Indeed, Miller *et al.* (1960) have made a strong theoretical case for the goal-directed nature of reflexes.

My point here is that imitation is basic, not derived (Favareau, 2002). It is basic because it stems from a neural identity between observing and responding. Learning is not required to imitate (although imitation facilitates learning).

As action sequences become more cortically controlled with increasing age, I theorize that the same basic mechanism can be used to activate imitation of increasingly complex action sequences (Greenfield *et al.*, 1972; Goodson and Greenfield, 1975; Childs and Greenfield, 1980).[2] The reader should also be forewarned that, while neonatal

[1] Some authors reserve the term "cross-modal" for the integration of different *sensory* modalities, but given the importance of corollary discharge and proprioceptive feedback in motor control, the situation here may be seen as falling under this apparently more restrictive definition.

[2] Oztop *et al.* (this volume) take a somewhat different view. While they would not, I assume, deny that the Meltzoff–Moore observations implicate a basic class of mirror neurons in neonatal imitation, they do argue that the mirror neurons for grasping (e.g., that distinguish precision pinches from power grasps) are themselves the result of a developmental process that stretches over the first year (for the human timetable) of the infant's life. They thus distinguish neonatal imitation from what they view

Figure 15.1 A newborn imitates Andrew Meltzoff's tongue protrusion movement. (Photograph courtesy of Andrew Meltzoff.)

imitation undercuts Piaget's notion that imitation cannot take place without seeing one's own response, other parts of Piagetian theory provide important insight into both ontogenetic and phylogenetic aspects of imitation. Thus, I will later have occasion to draw heavily on another aspect of Piaget's theory of imitation, the notion that one imitates (or transforms) a model in line with one's cognitive understanding of the model's actions.

The discovery of mirror neurons suggests that, ontogenetically, imitation does not begin as the relatively high-level cognitive process that Piaget (1962) posited. The explanation of newborn imitation by means of mirror neurons is that observation of adult tongue movement by the newborn triggers the baby's mirror neurons that control his/her own tongue movement. The imitation therefore occurs when observation of the tongue movement excites a series of mirror neurons, which discharge as motor neurons. The discovery of mirror neurons makes the ontogenetic basis of imitation more reflexive and less cognitive than Piaget thought. Clearly at least some mirror neurons are there from birth. But most important, the basic connection between observation and action does not have to be learned through an associative process. The substrate for a cross-modal connection between visual stimulus and action is already present, internal to each mirror neuron of this initial set.

as "real" imitation which requires more cognitive attention to the structure of the imitated action. I accept this distinction, but see the former as the developmental foundation for the latter.

Figure 15.2 In the video frame on the right, a newborn chimpanzee imitates Kim Bard's mouth opening movement shown in an earlier frame on the left. (Photograph courtesy of Kim Bard.)

15.2.2 *Newborn imitation in chimpanzees*

Given that early stages of ontogeny are much more likely to be shared with sibling species than later stages, we might expect that newborn apes would also be able to do facial imitation. And indeed this is the case: chimpanzee newborns are also capable of cross-modal facial imitation (Bard and Russell, 1999). In Fig. 15.2, we see a newborn chimpanzee imitating Kim Bard's mouth-opening gesture.

15.2.3 *The role of imitation in the ontogeny of tool use: intergenerational transmission*

It is not much later in development that observation and imitation begin to be used for tool learning. By 1 year of age, these processes can be used for the transmission of *human* tool culture. To illustrate this point I summarize a videoclip in which NF (age 11 months, 14 days) and his grandmother are out with the stroller and both are involved with cups of water. The clip, which one can think of as video ethnography, is part of a longitudinal corpus designed for cross-species comparative purposes. I will also provide theoretical interpretation of the behavior in terms of the hypothesized operation of mirror and canonical neurons.

(1) NF is in the stroller; his grandmother is next to him with two cups in her hand, an adult cup and an infant's "sippy cup" (a sippy cup is a baby cup with a no-spill top and a built-in straw). NF preferred an adult cup (which he has observed being used by others), over his sippy cup (which he has not observed being used by others). (Here the cups are considered to be goal-objects that can potentially activate canonical neurons, which in turn activate the relevant goal-action.) This preference for the adult cup is hypothesized to reflect a predisposition to imitate, reflecting the operation of canonical neurons. Canonical rather than mirror neurons are invoked here because this is a self-initiated action without any model present to imitate. (See Arbib (Chapter 1, this volume) for an analysis of the many other elements beyond mirror neurons that are necessary for such an action to take place.)

(2) As soon as his grandmother hands NF the empty cup, he responds immediately with a drinking action that he has observed occurring with cups in the past (hypothesized operation of canonical neurons rather than mirror neurons because it is elicited by the goal-object, with no action model to imitate).

(3) NF observes grandmother's drinking action with a similar cup and immediately puts his cup to his lips in a similar drinking action (hypothesized operation of mirror neurons in concert with activity of canonical neurons). (Here there is a model to imitate as well as a goal-object; hence, both mirror and canonical neurons are hypothetically called into play.)

15.2.4 Hypotheses concerning some aspects of the neural and behavioral development of imitation

The immediate translation from observation to action seen in this clip seems to result from lack of cortical inhibition. It has been observed that patients with prefrontal cortical lesions may have problems inhibiting imitative responses (Brass *et al.*, 2005). In (normal) development, prefrontal cortical circuits do not connect with more posterior parts of the brain, such as motor areas, until about age 2 (Greenfield, 1991). Hence, it is logical to hypothesize that a 1-year-old may resemble the patients with cortical lesions in terms of the inability to inhibit imitative responses. Because of the lack of inhibition in the first year or two of human life, the links between observation and manual motor response inherent in the canonical and mirror neurons are more overtly reflected in behavior at this very young age. In the above-described scene with the cups, NF's behavior at 11 months of age suggests the utility of the canonical and motor neuron systems for acquiring skill with cultural tools (e.g., a cup).

15.3 The role of imitation in subsequent development of object-oriented manual activity

With increasing age and development, more complex motor activities can be observed and imitated. For example, we used imitation procedures to elicit a developmental sequence of grammars of action in construction activities from children ranging from 11 months to 7 years of age (Greenfield *et al.*, 1972; Goodson and Greenfield, 1975). By grammar of action, I mean a consistent strategy that is homologous to some element of

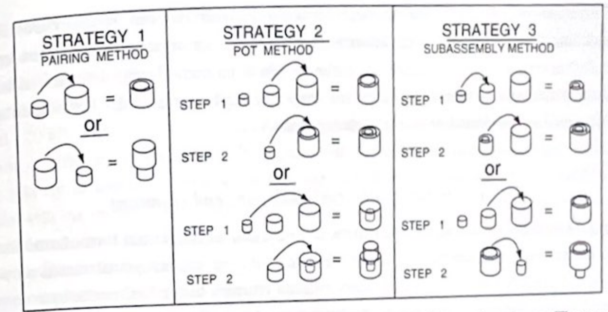

Figure 15.3 Strategy 3 was modeled for children from 11 to 36 months of age. The youngest children "imitated" the model with Strategy 1, the next oldest with Strategy 2, and the oldest with Strategy 3. From Greenfield *et al.* (1972).

linguistic grammar. One of these grammar of action tasks is presented in Fig. 15.3 (Greenfield *et al.*, 1972). In the case of Strategy 1 for example, we can see it as analogous to a linguistic combination of agent (active cup) and object (passive cup) in a simple sentence. Evidence for homology – the involvement of the same neural structures for both the manual and linguistic grammar – will be presented later in the chapter. In addition, Goga and Billard (this volume) present a model of the Greenfield *et al.* (1972) linkage of seriation to language.

For present purposes, note that children of all ages from 11 to 36 months of age were presented with the same model – Strategy 3 below – by an adult experimenter. However, younger children systematically transformed the model in their imitations. The young-est children "imitated" the model with Strategy 1, the pairing method. The next oldest children tended to "imitate" the model with Strategy 2, the pot method. Only some of the oldest children accurately replicated the model, responding with Strategy 3, the subassembly method.

These tasks show that a transition from simple reflexive imitation in the newborn to the imitation of complex action sequences has taken place. However the sequence of stages leading up to the most complex and complete mode of replicating the model also provides evidence for the developmental model of imitation posited by Piaget (1962). That is, at each stage, the child transforms the model by interpreting it through the lens of his or her stage of understanding, i.e., cognitive development. This process also occurs in language acquisition (Slobin and Welsh, 1973).

At the same time, the nesting cup study also provides an example of how observation and imitation might provide scaffolding to bring a child to the next stage of development. This principle has been empirically demonstrated in human language acquisition. In that domain, imitation of a particular linguistic structure is most frequent when the structure in question is neither completely present or completely absent from a child's behavioral repertoire, but instead is in the process of being learned (Bloom *et al.*, 1974). This principle implies that new observational learning must be related to old knowledge; something completely new cannot be imitated. (In a moment I will use this principle to help explain why humanly enculturated apes can copy human tasks better than apes who have little or no familiarity with human tasks.)

15.3.1 The nature of "true" imitation: end vs. means

In contrast to Piaget's theoretical treatment of imitation, an influential formulation in the 1980s posited that true imitation involved accurate or rote replication of means as well as ends; the replication of a model's goals without copying his or her means by rote was demoted to the status of "emulation" in distinction to "true" imitation (Tomasello *et al.*, 1987; Tomasello, 1989). Contrary to this formulation, the development of human imitation is not a question of rote imitation, as we have seen. For each task, it consists of transformations of a model that follow the sequence of understandings and interpretations of a particular task.

Nor is human imitation a question of imitating means rather than ends. In the ontogeny of human imitation, babies often understand and therefore imitate the goal before the means (Bruner, 1974). However, at a later point in development, they will be able successfully to replicate the means as well as the end. In other words, a stage of "emulation" is an intrinsic component of human imitation. As another example, Gergely *et al.* (2002) show that if an adult demonstrates a new way to execute a task to a group of infants aged 14 months, the children will use this action to achieve the same goal only if they consider it to be the most rational alternative. In other words, "emulation" is an important strategy in human imitation. The results of Gergely and colleagues also indicate that imitation of goal-directed action by preverbal infants is a selective, interpretative process, very much in line with the Piagetian framework. In sum, for developmental and pragmatic reasons, one cannot differentiate human and ape imitation according to whether the means is accurately imitated or not; both replication of a goal and transformation of means are important components of human imitation and its role in learning and development.

While not the only learning processes, observation (visual attention on a model) and imitation (attempt to replicate a model's actions) are keys to cultural transmission for humans, and, as such, they first appear early in development. In line with the principle that early stages of ontogeny are most likely to be observed in sibling species, we would expect them in chimpanzees as well. In the next section, we turn to this issue in a species-comparative perspective.

15.3.2 Observation and imitation are keys to cultural transmission for chimpanzees as they are for human beings

Tools are cultural traditions for groups of chimpanzees, as they vary from group to group in ways that cannot be reduced to ecological availability or usefulness (Whiten *et al.*, 1999; see Stanford, this volume). Videotapes made by Christopher Boehm showed that infant and juvenile chimpanzees at Gombe Reserve, Jane Goodall's field station, systematically observed experienced adults use probes (stems or vines) to fish for termites in mounds of dirt. Their gaze often followed the probe from dirt to mouth (Greenfield *et al.*, 2000). The video footage also indicated that imitation can follow observation: an infant or juvenile chimpanzee often grabs the mother's abandoned fishing tool when she gets up to leave; the young chimpanzee will then use the tool to fish for termites, often with no success. The learning process takes years, beginning with playful experimentation with sticks, then moving to observation of models, and finally independent practice (Greenfield *et al.*, 2000). Our future research will elaborate the process of expert–novice apprenticeship in enculturated chimpanzees and bonobos.

I apply the Piagetian perspective on imitation (Piaget, 1962; Greenfield *et al.*, 2000) to non-human primates. As we have seen, this perspective emphasizes the importance of cognitive understanding of the observed model that is to be imitated. Hence, when animals are too young to understand a means–end relationship or lack motor skill to successfully imitate an action, this theoretical perspective implies that an attempted imitation will only partially replicate the model. This developmental principle can explain why it takes chimpanzees so long to learn to crack nuts; they can only imitate what they are developmentally ready to learn both cognitively and physically.

Why do imitative abilities in chimpanzees not lead to rapid diffusion of innovations within a group? Given that 14-month-old babies, in the sensorimotor period of development, rationally evaluate the functional appropriateness of a model's actions for their own situation before imitating it (Gergeley *et al.*, 2002) and given that chimpanzees manifest the same basic stages of human sensorimotor development (Parker and McKinney, 1999), we would expect chimpanzees to be equally selective in their imitations. This selectivity might explain the slow movement of a tool or other cultural innovation within a chimpanzee group.

15.3.3 Observation, imitation, and object combination in monkeys: a comparative and phylogenetic analysis

Experimental study of object combination in four species indicates that the tendency to imitate manipulative strategies for object combination, a cornerstone of tool use, exists in *Cebus* monkeys, a New World monkey, humans, and both species of *Pan* (Johnson *et al.*, 1999). In that study, all four species were shown the model of Strategy 3 (Fig. 15.3) to combine seriated nesting cups. All four species were able to replicate the model when given their own cups, although the monkeys required more training than the other species to do so. (But see Visalberghi and Fragaszy (2002) and Arbib (Chapter 1, this volume) for another interpretation of the monkey data.) In so far as complex sequences were modeled and imitated across all of these species in this experiment, one can see that reflexive imitation at birth grows, in a wide variety of primate species, with increasing age and experience, into skill in intentionally imitating a sequence of acts directed both to a sequence of subgoals and integrated into an overall goal of the sequence itself. Note that for the monkeys and apes in particular, the sequence shown in Fig. 15.3 was a novel one, a type of imitation that is considered particularly important in the human repertoire.

Although all four species learned to use the most complex strategy for nesting the cups, the strategy that was demonstrated at the outset, there were species differences. Monkeys and, to a lesser extent, apes did not construct structures. Instead they would utilize the same strategy to combine the cups in a sequence of moves, but they would then take apart the structure that they had just constructed. Perhaps this is why humans build big complex buildings and other primate species are limited to much simpler technologies and constructions. This ability to make object combination yield complex "permanent" structures is a major achievement of human culture that must have evolved in the last 5000 years, in the period since *Homo* and *Pan* diverged.

Another important difference between chimpanzee and human cultural learning seems to be the cumulative quality of the latter. The cumulative quality of human culture may have to do with increasing memory capacity that is a function of increased brain size that has evolved in *Homo* but not *Pan* in the last 5 million years. It may also have to do with the uniquely human use of symbol systems to transmit or teach cultural skills to the next generation (Greenfield *et al.*, 2000).

Following cladistic logic, the presence of observation and imitation in the transmission of cultural tool traditions in both *Homo* and *Pan* presents the possibility that these processes of cultural learning may go back in evolution to the common ancestor of humans and chimpanzees and perhaps even to our common ancestor with monkeys.

15.3.4 Can apes ape? Mirror neurons resolve a paradox

Apes clearly do ape in the wild: young chimpanzees at Gombe imitate more experienced chimpanzees in learning to termite (Greenfield *et al.*, 2000). However, in the laboratory, only humanly enculturated apes show an ability to imitate the means to a goal in a human tool task, according to Tomasello *et al.* (1993). If we accept for a moment Tomasello and colleagues' emphasis on the accurate replication of means in the analysis of imitation, what conclusion can we draw? Tomasello *et al.* conclude from their data that apes cannot imitate without human enculturation and that imitation is therefore phylogenetically new with humans, rather than part of our primate heritage.

Mirror neurons, however, challenge this interpretation and resolve the paradox between field and laboratory in the following way. Because mirror neurons are part of specific action systems (Buccino *et al.*, 2001), the implication is that an animal or human being would be able to imitate only what he or she was able to do motorically. Imitation proceeds from some understanding of what is being done – whether the understanding comes from the existence of a similar motor response (as in neonatal imitation of mouth movements) or from a cognitive understanding (as in the nesting cup task).[3] Thus enculturated apes have an advantage over wild apes when tested on their ability to imitate a human tool task, since enculturated apes are more likely to have had experience related to this sort of task. Hence, when Tomasello *et al.* (1993) used a human tool task with non-human primates, apes not enculturated by humans were unfamiliar with this sort of task and could not imitate its solution. Humanly enculturated apes, in contrast, were familiar with the genre and could successfully imitate the details of its solution. The hypothesis is that their success was due to familiarity, which led to understanding. Because the non-enculturated apes lacked this familiarity and understanding, they could not imitate the solution to the tool task.

In other words, it is not that apes lack the ability to imitate. Like humans, they can imitate what they can understand. Further evidence on this point comes from careful experimental work (Whiten, 1998). When a human model showed a humanly enculturated chimpanzee in Whiten's study how to open artificial fruit, the chimpanzee at first copied the model's every action, including acts irrelevant to the goal. As the chimpanzees practiced the task and understood its means–end relations better, the irrelevant acts dropped out of the sequence. In other words, chimpanzee imitation, like human imitation, is driven by understanding, not by a motive for rote imitation of a sequence of acts. On the neural level, I believe that future research will show these cross-species behavioral similarities to be driven by similarities on the level of neural functioning, specifically similarities in basic properties of the mirror systems possessed by each species (although evolution may have wrought changes to expand the mirror system to support faster and more flexible imitation in humans: M. A. Arbib, personal communication).

In conclusion, mirror neurons do not provide a *general ability* to imitate in either apes or humans. Instead, mirror neurons provide a set of *specific abilities* to imitate particular actions that are encoded in the motor component of various somatopically organized mirror systems (Buccino *et al.*, 2001) and are therefore understandable on the motor level.

For all of these reasons, I conclude that observation and imitation skills are held in common between humans and apes. These skills are therefore likely to be part of the phylogenetic heritage from our common ancestor and a prerequisite for the evolution of culture. According to my theoretical analysis, these imitation skills are subserved by mirror neurons in both apes and humans.

15.3.5 Mirror neurons, monkey culture, and human culture: what has evolved in the last 5 million years?

Mirror neurons could also contribute to monkey culture (Perry *et al.*, 2003), as they do to human and ape culture. The question then arises as to how mirror neurons can contribute

[3] Oztop, Bradley, and Arbib (this volume) make the point that since we develop new skills, there should be "quasi-mirror neurons" that learn to recognize an action as part of acquiring it. It remains to be seen whether such a mechanism is in fact required or whether the notion that one can use imitation only to learn a skill that is already partly in the repertoire suffices as an explanation for the role of imitation in developing new skills.

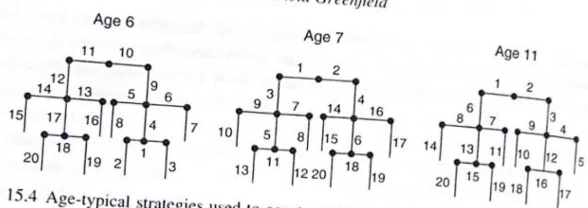

Figure 15.4 Age-typical strategies used to construct a three-level tree structure made of construction straws and presented as a model to copy. The 6-year-old uses a chain strategy beginning at the lowest level in which each successive straw is placed near the one before. The 7-year-old organizes the replication by branches beginning at the highest level. The 11-year-old organizes the replication by levels beginning at the highest level. Each age-typical strategy is considered to be a grammar of action. (From Greenfield and Schneider, 1977.)

to our understanding of the distinctive cumulative quality of human culture, even though monkeys have these neurons, but do not create a cumulative culture. In general, my answer is that mirror neurons are necessary but not sufficient for complex and cumulative cultural learning.

Transmission mechanisms

Only human beings use symbolic means to instruct their young in tool use (Greenfield *et al.*, 2000). This would be an explanation based on the evolution of more powerful transmission systems (Greenfield *et al.*, 2000). The use of symbols to instruct in tool use is a strong candidate for a skill that has evolved in the last 5 million years.

The complexity of human neural programs

In addition, mirror neuron systems are always attached to particular neural programs – e.g., for manual action, mouth action, foot action, emotion – and occur in different, corresponding parts of the brain (Buccino *et al.*, 2001; Carr *et al.*, 2003). In other words they are somatotopic and participate in different circuits.

The neural programs for human action are more complex than those of monkeys. This complexity – for example, the ability to create more hierarchically complex constructions with objects – also would have facilitated the evolution of human culture. Figure 15.4 portrays a complex structure composed of construction straws that was used as a model (already built) and shown to children of different ages with a request to replicate it. No ape or monkey would be able to create a structure of such complexity.

Each age group used a different (and age-typical) strategy to build the model successfully. We conceptualized each strategy as a grammar of action because each involves a different systematic ordering (parallel to a linguistic surface structure) for creating the underlying, hierarchically organized tree-structure (parallel to a linguistic deep structure).

This level of complexity makes human building of permanent structures possible, something that is shared with no other species. Hence, to posit that neural programs subserving more complex action sequences evolved since our split with *Pan* is far from trivial.

15.3.6 A scientific contradiction

Ironically, in the light of the controversy surrounding ape imitation in the domain of tool use, imitative abilities of apes when it comes to language have never been questioned (Terrace *et al.*, 1979). Indeed, Terrace and colleagues used the *presence* of linguistic imitation in a sign-using chimpanzee as evidence that ape learning differs from human learning. In direct contradiction, Tomasello and colleagues use the *absence* of imitation learning in unenculturated apes as evidence that ape learning differs from human learning. The scientific community has shown itself equally ready to accept each assertion, without noticing the contradiction. Why has this happened? My hypothesis is that human beings and science as a human activity are always more willing to accept a conclusion that draws a firm line between human beings and other species. And the use of imitation to draw such a line is what Tomasello and Terrace have in common, despite the fact that the two lines of reasoning are logically incompatible with each other. My enterprise is the opposite: to establish an understanding of the continuities in human evolution.

15.3.7 The role of intentions and goal-directedness in tool use and construction activity

While this section has focused on imitation as an important mechanism in stimulating and guiding tool use and construction activity, it is necessary, before leaving this domain and proceeding to language, to briefly call attention to the other key feature of mirror neuron systems, their goal-directedness and attunement to intentionality. Clearly action models in this domain not only stimulate imitation; they also provide a goal for tool use and construction behavior. Just as clearly, this cultural domain of tool use and construction activity is one in which goals and intentionality are central to domain-relevant behavior. To give a few examples: one intends to turn a screw with a screwdriver. The goal of building is to create a structure such as a house or bridge. Clearly, there is an important match between the goal-directed structure of this cultural domain and the sensitivity of mirror neuron systems to goal directed action, rather than to movement per se.

Up to now, I have tried to establish mirror neurons as the neural substrate for imitation, tool learning, and object combination in both the ontogeny and phylogeny of human culture. In the next section, I show how the structure of the mirror neuron mechanism can be applied to understanding mechanisms of cultural learning in the ontogeny and phylogeny of language.

15.4 Mirror neurons and language: ontogeny and phylogeny

This section is based on an important neuroanatomical link between the mirror neurons discovered for manual action and the neural substrate for language – Broca's area in the left prefrontal cortex of the brain. I begin with a discussion of this link. Next, I discuss implications of the key feature of mirror neurons, their mirroring property – that is, their potential to fire either upon the execution or the observation of an action – for language learning. Finally, I will introduce a second feature of mirror neurons, their sensitivity to goal-directed action rather than to movement per se and draw out its implications for linguistic ontogeny and phylogeny.

15.4.1 Mirror neurons in Broca's area: implications for the ontogeny and phylogeny of language

Broca's area is a key area of the human brain for language. One perspective on Broca's is that it is a programming area for the oral–facial motor area that produces speech or the manual motor area that produces sign (Greenfield, 1991; see also Emmorey, this volume). Rizzolatti and his colleagues (1996) found a mirror system for manual action in the Broca homologue of their monkey subjects' brains. Iacoboni and colleagues (1999) later found mirror neurons for simple manual imitation in the Broca's area of their human participants. There is also evidence that Broca's area (Brodmann area 44) programs (that is, directs) the mirror system responsible for manual action performed on an object (Nishitani and Hari, 2000). (Brodmann areas are a numerical system for identifying different locations on the surface of the human brain.) The location of mirror neurons for manual action in Broca's area has a number of important theoretical implications.

First, this location in Broca's area implies an intimate relation between language and manual action. This theoretical implication has received empirical support in a study of motor evoked potentials; the cortical representation of the hand muscle was excited by purely linguistic tasks, but not by auditory or visual–spatial tasks (Flöel *et al.*, 2003). Indeed, evidence for the intimate neural connections between language and manual action provides evidence for my theory that Broca's area helps program the construction of both language and manual action (Greenfield, 1991). Even in monkeys, mirror and other closely related neurons in the Broca's homologue area discharge at the sound and not merely the sight of an action (Kohler *et al.*, 2002). Understanding the meaning of sound could be considered an evolutionary foundation for language.

Humans with different kinds of cortical damage provide another kind of evidence of a neural link between action and speech. Grossman (1980) gave Broca's and Wernicke's aphasics two versions of the tree-structure model, shown in Fig. 15.5a. Broca's aphasics who are unable to construct hierarchically organized grammatical tree-structures in speech (that is, their speech often consists of a string of isolated words rather than syntactically organized sentences), also had difficulty in constructing a

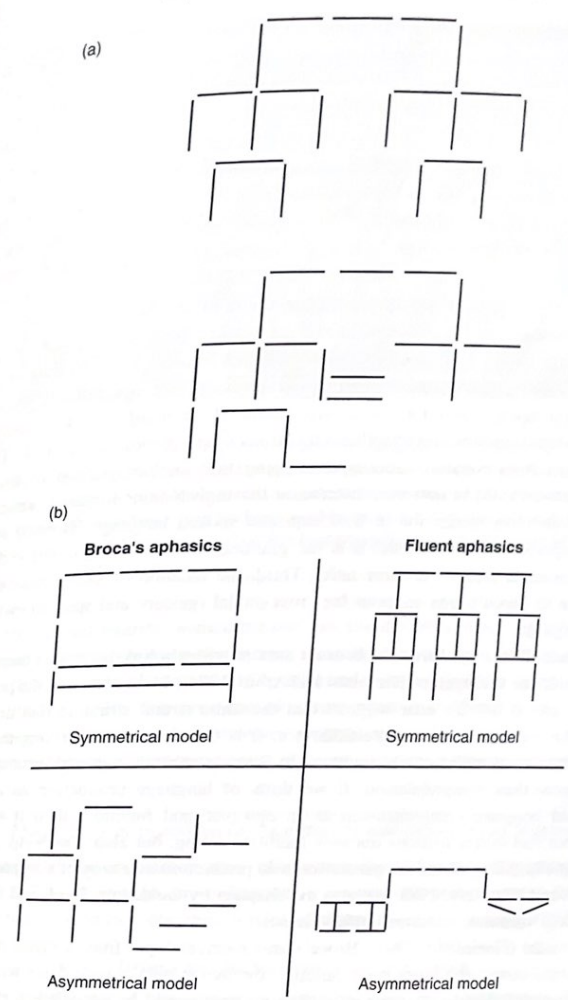

Figure 15.5 (a) Two tree-structures provided as models (constructed with tongue depressors) to Broca's and fluent aphasics (Grossman, 1980). (b) Typical "copies" of the models by Broca's and fluent aphasics. The Broca's aphasics get more detail (number of sticks) but less hierarchical (tree) structure, whereas the fluent aphasics get more hierarchical tree-structure, but less detail. (From Grossman, 1980.)

hierarchically organized multilevel tree-structure with objects, even given a model to copy (Fig. 15.5b) (Grossman, 1980). Their replicas of the model show no conception of the hierarchical structure – there is no sign of levels or branches. In contrast, Wernicke's or fluent aphasics, with Broca's area intact and the capacity to form complex (albeit meaningless) syntactic structures, do not have this same difficulty in building a hierarchically-organized structure with branches and levels (Fig. 15.5b) (Grossman, 1980). More recently, Molnar-Skocas and colleagues (unpublished data) have found that one of Greenfield's manual grammar-of-action tasks utilizes the same neural space as does linguistic grammar. Hence, Broca's area is a key part of two partially overlapping circuits. One combines words into hierarchically organized sentence structures; the other combines objects into hierarchically-organized constructions.[4]

Second, this location is also the site of some important overlapping neural circuitry for spoken and sign language (Emmorey, this volume). My hypothesis is that Broca's area provides programming input to the manual motor cortex for sign articulation, just as it does to orofacial motor cortex for speech articulation (Greenfield, 1991). Emmorey's review (this volume) confirms this hypothesis for Broca's area (Brodmann area 44). There is also evidence from cortical stimulation mapping that another portion of Broca's area (Brodmann area 45) is involved in creating the higher-order linguistic structures necessary for narrative production in both sign and spoken language (Horwitz *et al.*, 2003). My hypothesis would be that it is the grammatical aspect of narrative that is activating Brodmann area 45 in these tasks. Third, the location of mirror neurons for manual action in Broca's area suggests the cross-modal (gesture and speech) evolution of human language.

The presence of mirror neurons in Broca's area provides a link between comprehension and production in language (Rizzolatti and Arbib, 1998). In other words, the presence of such neurons in Broca's area suggests that the same neural structure that produces language also participates in comprehending it. It is therefore not surprising that both production and comprehension are impaired in Broca's aphasia, although production is impaired more than comprehension. If we think of language production as a motor function and language comprehension as an observational function, then it becomes very relevant that mirror neurons not only facilitate acting, but also observing. Furthermore, the motor theory of speech perception sees production as a way of comprehending (Liberman and Mattingly, 1985; see also the chapters by Goldstein, Byrd, and Saltzman and Skipper, Nusbaum, and Small, this volume).

In my model (Greenfield, 1991), Broca's area receives input from a syntactic area in the prefrontal cortex and sends information to the motor strip, which deals with phonological formation. Hence, impairment in Broca's area would be expected to affect both the syntactic and phonological levels. If a neuron can stimulate the same action it responds to observationally, comprehension of that action is implied – because one, in

[4] The partial overlap means that a minority of agrammatic Broca's aphasics can construct hierarchically organized tree structures. See Greenfield (1991, p.537) for details.

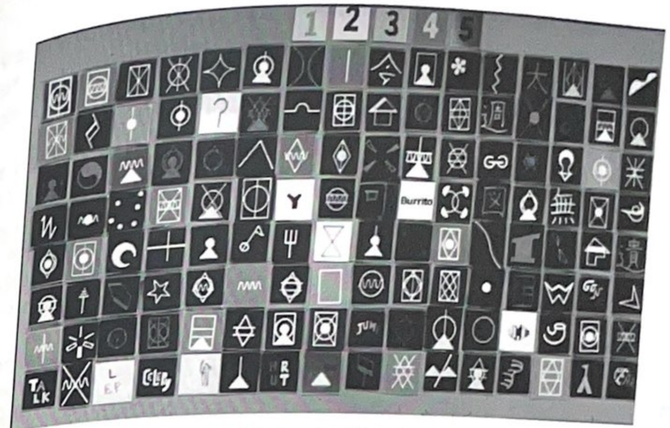

Figure 15.6 Lexigram board. Some of the boards will provide a translation in spoken English when a symbol is touched. In terms of English referents, the numerals on the top row are obvious. In terms of futher examples, the symbols on the next row, from left to right, are translated in English as: sweet potato, tickle, orange, Mary, trailer, peanut, car, raisin, hamburger, Sherman, egg, dig, Kanzi, Austin, fridge, and stand pile. (For the English translations of virtually all the other lexigrams on the board, go to www.iowagreatapes.org/bonobo/ language/pdf/lexo2.pdf.) (Photograph courtesy of Sue Savage-Rumbaugh.)

some sense, "understands" something one can already do. In other words, perhaps there are mirror neurons, yet to be discovered, that respond both upon making and hearing a sound. This possibility has started to be explored with very positive results (Aziz-Zadeh *et al.*, 2004). Finally, the presence of mirror neurons in Broca's area explains the importance of repetition (which involves observation and imitation) as a strategy in the ontogeny and phylogeny of conversational communication. I turn next to repetition.

15.4.2 Role of repetition in the ontogeny and phylogeny of language

Here I draw on an established body of research in child language (particularly Ochs Keenan, 1977), as well as my collaborative research on conversational repetition in bonobos with Sue Savage-Rumbaugh (Greenfield and Savage-Rumbaugh, 1993).

Details and background of the ape studies

The major ape data that I will present on repetition come from two bonobos, Kanzi and Mulika, exposed to a humanly devised language (perhaps better termed, protolanguage) system consisting of arbitrary (non-iconic) visual symbols (Fig. 15.6). They were exposed to the symbols in the course of naturalistic communication, rather than through formal training. Lexigrams are arbitrary visual symbols presented on a keyboard. During the lifetimes of the apes discussed here, many of the keyboards also presented the spoken

English gloss through a speech synthesizer when a particular key was pressed. Most of the lexigram symbols stand for nouns (e.g., banana, dog) or verbs (e.g., chase, bite). The same communication system was used with two chimpanzees, Sherman and Austin. However, their exposure was more in the mode of formal training.

Kanzi was raised at the Language Research Center of Georgia State University by his mother; Mulika did not have a mother present at the center. Kanzi learned to use lexigrams by watching his mother being exposed to the visual symbols. Mulika was exposed to the lexigrams by communicating directly with human caregivers and by watching Kanzi use lexigrams to communicate with the caregivers. Kanzi produced his first lexigram at age 2.6, Mulika at 1.0. At the time of the study, Kanzi was 5 years old, Mulika almost 2.

A 17-month-long investigation of Kanzi's vocabulary acquisition ended when he was 3 years 10 months old. Mulika's vocabulary was studied at a younger age, from before her very first lexigram at 12 months of age; Mulika's 11-month-long investigation of vocabulary acquisition ended when she was 22 months old. Very strict criteria for spontaneous and meaningful usage in everyday life were used to assess lexigram production (Savage-Rumbaugh *et al.*, 1986). At 46 months of age, Kanzi had 44 lexigrams in his spontaneously used, productive vocabulary that met these criteria. At 22 months of age, Mulika had six lexigrams in her spontaneously used productive vocabulary that met these criteria (Savage-Rumbaugh *et al.*, 1986). (Mulika was given the opportunity to use lexigrams at an earlier age than Kanzi, and may have been on track to acquire a larger vocabulary, as Kanzi's productive vocabulary was only seven lexigrams when his spontaneous lexigram use was assessed at 30 months of age. Unfortunately, Mulika's untimely and tragic death made it impossible to assess her later course of development.)

Pragmatic uses of repetition in the ontogeny and phylogeny of language

Ochs Keenan (1977) made the important point that children just starting to speak use linguistic imitation not only to copy but, more frequently, to fulfill many different pragmatic functions in a conversation. These functions include greetings (caregiver "hi," child "hi"), confirmation, and choosing from among alternatives (see Table 15.1). Because the term "imitation" had implications of rote imitation whose only purpose is to copy, Ochs Keenan used the term "repetition." Although not realized at the time, her research was revolutionary because it illuminated imitation/repetition as a phenomenon that was intrinsic to the conversational competence of young human beings. Later, Deborah Tannen (1989) showed how these pragmatic uses of repetition remain part and parcel of the conversational competence of adult human beings.

Ironically (especially in the light of later claims that apes cannot imitate), imitation had been used by the scientific community to minimize and even obliterate the linguistic accomplishments of apes (Terrace *et al.*, 1979). In this historical context, it seemed important to demonstrate that apes use imitation/repetition exactly as human children do. In order to establish this point, I collaborated with Sue Savage-Rumbaugh on a study of conversational repetition in young bonobos (Greenfield and Savage-Rumbaugh, 1991, 1993). I now present cross-species data (Table 15.1) comparing our bonobo data on conversational repetition with the data of Ochs Keenan (1977).

Table 15.1 *Use of repetition in discourse by children and bonobos*

Conversational use[a] of repetition to:	
Confirm/agree	Choose alternative
Human	
Twins, Toby and David, age 2.9, with their nanny Jill	Katie, age 1.2, with caregiver at infant daycare center (Caregiver pretends to pour tea for both of them and they pretend to drink it.)
Jill: *And we're going to have hot dogs.* Toby: *Hot dogs!* (excitedly) Jill: *And soup.* David: *Mmm soup!* (Ochs Keenan, 1977)	Caregiver: *Are you full or do you want some more?* Katie: *More.* (K. Leddick, unpublished data)
Bonobo	
Mulika, age 2, with human Kelly	Kanzi, age 5, with human caregiver/researcher, Rose
Kelly: *GO A-FRAME* (informing Mulika of destination) Mulika: *GO* (vocalizing excitedly) (Greenfield and Savage-Rumbaugh, 1993)	Rose: *You can either PLAY or watch TV* Kanzi: *TV* (Kanzi watches after Rose turns it on)

Note:
[a] For the bonobos, capitals indicate lexigrams (visual symbols) only; for the humans, capitals indicate simultaneous lexigrams and speech. Lower-case indicates speech only.
Source: Greenfield and Savage-Rumbaugh (1993).

In the case of both "confirm/agree" and "choose alternative," the repetition is used selectively to construct a pragmatic function. This table illustrates how both children and bonobos use repetition for two of the same pragmatic or conversational functions: to confirm/agree or to choose from among two alternatives. Note that the other examples in the published papers (Greenfield and Savage-Rumbaugh, 1991, 1993) show that many other pragmatic functions are expressed through repetition by both species, as well as by two chimpanzees, Sherman and Austin, who were also exposed to the lexigram system, but in a more training-like context.

For young children, repetition represents the initial ontogeny of conversational functions. When children first start to talk they have no other way to express conversational functions such as agreement (Greenfield and Smith, 1976). In general children repeat the part that will express the function that they are trying to communicate. For example, when Matthew was 14 months old, his mother said "Do you want to get up?" His selective imitation "up" was a way to express what he wanted to do and his first way of expressing an affirmative (Greenfield and Smith, 1976). Another way of looking at this is that the child repeats the most informative part of the prior utterance, that which is changing or to which there are alternatives.

Because early stages of development are more often similar within a clade or family of species than are later stages, the early appearance of repetition in child language made it likely and reasonable that repetition would be important in ape communication, and this is indeed what we found. In terms of recreating evolutionary history, which took place in the forest and savanna, not the laboratory, it is important to note that imitation/repetition is also crucial in the vocal communication of chimpanzees (third member of the clade) in the wild (for example, exchange of grunts, Goodall, 1986, p.131). Calls in the wild are culture-dependent, in that they are conventionalized in particular groups of animals (Whiten *et al.*, 1999). Because of the lack of data, it is difficult to compare the symbolic qualities of calls and lexigrams.

The evolutionary implication of the parallels between repetition in child and chimpanzee is the following. Because repetition has been found to carry communicative significance in the three species that make up the clade of *Homo sapiens*: chimpanzees, bonobos, and human beings, it is likely that the use of repetition to communicate vocally was present 5 million years ago, before the evolutionary divergence of *Homo* and *Pan* (bonobos and chimpanzees). If this is the case, it could have been one of the foundations for the subsequent evolution of more complex linguistic conversation. This is particularly potent in the light of Jane Goodall's observations of the use of vocal repetition by chimpanzees in the wild communicating at a distance (Goodall, 1986).

In the context of these similarities, Greenfield and Savage-Rumbaugh (1993) also noted two interesting differences between *Homo* and *Pan* in the conversational use of repetition: first, human children sometimes used repetition to stimulate more talk in their conversational partner; the chimpanzees, in contrast, used repetition exclusively to forward the non-verbal action. Second, the 1- and 2-symbol repetitions used by the chimpanzees to fulfill a variety of pragmatic functions were less than half the maximum length found in either the visual symbol combination addressed to them by their adult human caregivers or the oral repetitions of 2-year-old children. As suggested earlier, this species difference probably reflects the evolution of increased brain size and consequent increased memory capacity that has occurred since the phylogenetic divergence of *Homo* and *Pan* 5 million years ago (Greenfield and Savage-Rumbaugh, 1993).

Repetition functions to coordinate intended actions for children and bonobos

Before proceeding to the next section and presenting theory and data concerning intentionality, goal-directed action, mirror neurons, and language, I would like to point to the interpersonal coordination of goals and intentions as a pervasive function for both children and apes of the repetition examples in Table 15.1. For example, in the child example of confirmation/agreement, the conversational use of repetition is used by Toby, David, and their nanny Jill to coordinate intentions concerning the menu of their next meal. In the comparable ape example, Mulika and her human caregiver use repetition to coordinate intentions about what to do next. Similarly, the "choose alternative" examples

for both species are all about coordinating intentions concerning what will happen next. Keep these examples in mind, as I present theoretical concepts and more detailed analysis in the domain of language, goal-directed action, intentionality, and mirror neurons.

15.5 Mirror neurons, goal-directed action, and intentionality: implications for the ontogeny and phylogeny of language

Further implications of the mirror neuron system for the ontogeny and phylogeny of language stem from the fact that both mirror neurons and language, on their different levels, privilege the encoding of goal-directed action. On the neural level, mirror neurons respond to the execution or observation of goal-directed action, not to particular physical movements or to objects in isolation. Goal-directed action, in turn, implies intentionality, which is central to language, a point to which I now turn. The point of this section and the examples that follow is twofold: (1) to show that, just as mirror neurons encode intentional action, so do children spontaneously use language to encode and communicate intentional action at the very dawn of language development; and (2) to show that, just as mirror neurons encode intentional action, so do our closest phylogenetic relatives, chimpanzees and bonobos, when given a humanly devised symbol system and the opportunity for interspecies communication, spontaneously use this system to encode and communicate intentional action. The theoretical hypothesis is that it is the presence of a mirror system in brain areas used to program both language and physical action that makes the encoding of intentional action so basic to the semantics and pragmatics of human language.

15.5.1 Intentionality and language

Let me begin with the words of Jerome Bruner (personal communication, 1979):

> The more deeply I have gone into the psychology of language, the more impressed I have become with the absence in psychology of certain forms of psychological analysis that are needed in the study of language acquisition and language use generally. *One such is the role of intention and the perception of intention in others* (emphasis added). Language use is premised in a massive way upon presuppositions about intentions. . . Yet psychology, or at least positivistic "causal" psychology, ignores the role of intention. . . Such matters are most often treated as epiphenomena.

Whereas Bruner called attention to the importance of intentionality in language, Searle (1980) fleshed out this insight with an analysis of the behavioral and cognitive features of intentions. He identified two key features of intention: directedness and presentation or representation of conditions of satisfaction (i.e., presentation or representation of the goal). He further subdivided intentions into two levels. The first level he called intention-in-action. Intention-in-action involves *presentation* rather than *representation* of conditions of satisfaction. In intention-in-action, conditions of satisfaction are *implicitly* present *during* the intentional action. Prior intent, in contrast, involves a representation of the conditions of satisfaction. In prior intent, a mental model of conditions of satisfaction are *explicitly* present *before* the action begins. As the reader will see, language is a major way of externalizing goal representation.

15.5.2 Intentionality and the ontogeny of language

I begin with the case that the expression of intention-in-action is part of the very beginnings of child language (Greenfield, 1980). Here is an example from an observation of a toddler at the one-word stage. My example occurred during a children's gym class that his mother was teaching and I was observing. This was an unplanned ethnographic example that supplemented systematic formal study (Greenfield and Smith, 1976; Greenfield, 1980).

The child goes toward his mother, whining "shoes, shoes" (he has only socks on). He comes back toward me and gets his blue sandals. I try to help him while standing up, but cannot do it. So I sit down with one shoe, put him on my lap, and put his shoe on. Then I put him down, not saying anything. He walks straight to his other shoe, picks it up, and comes back to me. I put him on my lap and put his other shoe on. He then runs toward his mother still talking, saying "shoe, shoe" in an excited voice. He lifts his foot to show her. When she attends, he points to me. She understands, saying something like "The lady put your shoes on." Both are very excited.

This communication sequence involves social interfacing and coordination of observing and executing goal-directed actions. The sequence includes intention-in-action and the expression of prior intention on the part of the child, my active cooperation to fulfill his intention, and linguistic recognition of fulfilled intention on the part of the mother. Let me show how all of this played out through an analysis of the sequence.

First, the child used his language, a single-word utterance, to communicate *intention* through *explicitly representing* his *goal* ("shoes"); this is the expression of prior intention. I then observed and responded to his *intention* by my own *complementary goal-directed action* (my action of putting on his shoes). This was a goal-directed or intentional act on my part, which of course allowed the boy to fulfill his own intention and reach his goal. The child then used his language to communicate *goal achievement* ("shoe, shoe" in an excited voice). The mechanism of self-repetition, here used to express excitement, could be considered a kind of self-mirroring mechanism. Here he has shown excitement about fulfilling his *intention* and reaching his *goal*. His mother then observes and represents my goal-directed action in a full, adult sentence ("The lady put your shoes on"). This sentence also acknowledges that his intention has been fulfilled, his goal reached.

As the preceding sequence exemplifies, early language is specialized for the representation of intentional action, and early conversation is specialized for the interpersonal coordination of intentional action, as we saw in the earlier examples of conversational repetition. Just as mirror neurons are specialized for goal-directed action, it seems that language is too. The preceding conversational sequence is backed up by the entire corpus of early language studies in many languages (e.g., Bowerman, 1973; Brown, 1973). At the stage of both one-word and two-word "sentences," children encode intentional action. Common semantic functions at the one-word stage are the expression of action on object (for example *ba(ll)*, having just thrown a ball) or action of agent (for example, *up*, trying to get up on a chair) (Greenfield and Smith, 1976). At the two-word stage, again virtually all the semantic relations in child language encode intentional action, such as a relationship between agent and action (for example, *daddy* (agent) *bye-bye* (action) after his father leaves for work) or between object and action (*caca* (baby talk word for "record", the object) *ong* (baby-talk word for "on", the action), while carrying a record to the record player (Greenfield and Smith, 1976). In some instances, like *daddy bye-bye*, the child is describing the intentional action of another, which he has observed. In other cases, such as *caca ong*, the child is expressing his own intention. From the point of view of mirror neurons, the enactment and the interpretation of observed intentionality are equally important.

15.5.3 Intentionality and the phylogeny of language

Participants and background for the ape data

The data in this section come from Kanzi, his half-sister Panbanisha, and Panbanisha's constant companion, the female chimpanzee Panpanzee. All were exposed to English and lexigram communication in a naturalistic rather than a training modality.

The use of symbolic combinations to express intended action and goals by humanly enculturated apes

All three apes developed an open protogrammatical system in which they combined two or three lexigrams together (e.g., touching *playyard* lexigram followed by *Austin* lexigram (when he wanted to visit the chimp Austin in his playyard)) or combined a lexigram with a gesture (e.g., touching *balloon* lexigram followed by gesturing to Liz, who he wants to give him the balloon) to form original utterances that were not rote imitations of humans. These symbolic combinations expressed the same major semantic relations as young children's (Greenfield and Savage-Rumbaugh, 1991; Greenfield and Lyn, in press), relations such as action–object (e.g., touching *keepaway* lexigram followed by *balloon* lexigram, wanting to tease caregiver with a balloon) or agent–action (e.g., touching *carry* lexigram followed by gesture to caregiver, who agrees to carry Kanzi) (Greenfield and Savage-Rumbaugh, 1991). Each of these semantic relations also encodes intended action or an action goal.

While a corpus of combinatorial communications in the wild has not been assembled, it is clear that chimpanzees in the wild can combine gestures to express comparable complex semantic meanings and intended actions (Plooji, 1978). This evolutionary timetable is different from that proposed by Arbib, who places protolanguage after the divergence of *Pan* and *Homo*.

The encoding of intentional action characterizes child language as it dawns in the first year of life. Given that we find the greatest similarity among sibling species at the earliest points in development, it is not surprising that we would find the encoding of intentional action in ape language as well, as the examples indicate. Indeed, specialization for the encoding of intentional action is highly dominant in the spontaneous two-lexigram and lexigram-plus-gesture combinations of both bonobo and chimpanzee (Greenfield and Lyn, in press). Semantic relations that encode goal-directed action (such as agent–action and action–object), both frequent and universal in child language, have similar relative frequency in the spontaneous two-element combinations of two bonobos and a chimpanzee (Greenfield and Lyn, in press). Another example is found in Fig. 15.7. In this example, Kanzi expresses his desired goal by combining a lexigram with a gesture: he first touches the *chase* lexigram, then points to his caregiver, Rose, indicating that he would like Rose to play chase with him. Interestingly, Kanzi's open protogrammatical system also included protosyntax – for example, a creative sequencing "rule" (that is, not modeled by his human caregivers) that gesture generally follows lexigram (Greenfield and Savage-Rumbaugh, 1991).

Intentional action, language, and mirror neurons

Mirror systems clearly privilege intentional or goal-directed action over mere movement, and this holds for monkeys as well as humans. It might be something as simple as lesser brain size that is responsible for the Broca's area analogue in monkeys not entering into a complex symbolic communications system. Be that as it may, the encoding (understanding) of goal-directed action and the enacting of goal-directed action, not to mention the interindividual coordination of goal-directed action are at least as important in the wild as in captivity. This is probably the adaptational reason for the evolution of neural circuitry that both produces goal-directed action and understands it in others. Indeed, observations of chimpanzee communication in the wild have revealed many examples of the use of the vocal system to coordinate action among conspecific members of the group (Goodall, 1986). Observations of chimpanzee families with young children in the wild reveal gestural communication to coordinate action between mother and child (Plooji, 1978). Falk has recently emphasized this type of vocal and gestural coordination between mother and infant apes (Falk, 2004).

Why monkeys have mirror neurons, but do not use symbols to encode intended action

Just as with sequences of actions using objects, the reason for species differences between monkeys, apes, and humans is the following. Mirror properties occur in many kinds of neuron. Presumably they can also occur in the more complex circuits that control action sequences. Hence they are specific to particular kinds of behaviors and behavior sequences. Therefore, if monkeys are lacking certain kinds of neurons or neural circuitry, they will also lack the mirror neurons in those areas. Hence, one would not expect the behaviors to be similar from species to species even though all had mirror neurons in

Figure 15.7 (a) Kanzi touches the lexigram *chase*. (b) Immediately he points to Rose, communicating that he wants her to chase with him. (Photographs courtesy of Sue Savage-Rumbaugh.)

their nervous system. What one would expect to be similar would be the tendency to observe and imitate whatever goal-directed actions were feasible for that species and the tendency to enact and understand those same goal-directed actions.

The use of lexigrams to represent prior intent

This phenomenon has been seen in the enculturated apes, as it is in children. For example, Panpanzee, touched the *dog* lexigram (**agent**) and then touched the *play* lexigram (**action**). She then led her caregiver over to the dog house, where she and the dogs played together (Greenfield and Lyn, in press). In this example, Panpanzee is clearly representing a goal that she intends to attain. Sometimes an ape will combine gesture with lexigram to communicate prior intent. For example, Panpanzee pointed to a tree (**goal**) and then touched the *play* lexigram (**action**). Her caregiver said *yes* and Panpanzee climbed the tree to play. Again, her utterance communicated a goal that she intended to attain through her action. The expression of prior intention is equally central to bonobo communication. For example, Panbanisha touched the *open* lexigram (**action**) and then touched the *dog* lexigram (**goal**). She was asking her caretaker to open the door so they could visit the dogs. Clearly, she has expressed an intended action that she will subsequently try to enact.

In sum, intentional action is as much a focus of the language of *Pan* as it is of *Homo sapiens*. Thus, it is a feature that reaches across a whole family of species. The expression of intentional action is not unique to our own studies of two bonobos and a chimpanzee. Any trait that is found in all branches of an evolutionary tree is a good candidate to be an ancestral trait, that is, a trait found in the common ancestor of all the species in the clade. Although humans have intervened to teach various symbol systems to these animals, in all cases the representation of intended action was a spontaneous use of that symbol system. We tentatively conclude that language has at very least been overlaid on a foundation of intentional action, which it is used to represent (Greenfield and Lyn, in press). Indeed, symbolic communication of and about intended action is particularly valuable for the interindividual coordination of goal-directed action, as in the examples above and in the section on repetition.

15.5.4 Hypothesis concerning the relation between mirror neurons and intentionality in the ontogeny and phylogeny of language

Mirror neurons encode the execution and observation of goal-directed action – such as we saw in a non-verbal action when the boy acted as though his goal was to get his shoes put on *(intention-in-action)* and in the linguistic representation of *prior intent* by child, chimpanzee, and bonobo. An (intentional) agent carrying out action on objects is implicit in children's single-word or telegraphic utterances and more explicit in the adult's longer sentences (as in "The lady put your shoes on"). This latter describes the intentional action of another, based on observation. Indeed, the neural and cognitive linking of observed goal-directed action with enacted goal-directed action is the essence of the mirror system. My hypothesis is that mirror neurons subserve both the expression and interpretation (comprehension) of intentional action in language. Once we take action to the level of symbolic representation we can represent many actions that we cannot carry out ourselves. However, what is important for present purposes is that the comprehension and expression of intentional action is a bedrock of language development and evolution, a foundation from which other functions can develop in both ontogeny and phylogeny. Ontogenetically, language builds gradually on the intentional structure of action, i.e., the structure that is coded by the mirror neurons. That is, mirror neurons may highlight

intentionality, but the particular neurons and neuronal circuits that have mirror properties are responsible for diverse kinds of intentional action, including interspecies diversity in the particular action systems that have evolved.

Early language is used to encode intentional action, but action structures are initially more complex than the language structures available to the child at that time. Hence, in both child language and ape language, more and more of the intentional action can be encoded linguistically as language acquisition advances in both child and ape. Here is an example of such a developmental progression in child language:

Step 1: Representation of intentional action in a **single word utterance** (Greenfield and Smith, 1976)
Matthew (15 : 17)[5]: *crecor* (record) **(prior intent)**
went over to the record player and started pushing the buttons **(intention-in-action)**
Interpretation as an intention by his mother: "I want the record on"

Step 2: Representation of intentional action in a **two-word combination** (Greenfield and Smith, 1976)
Matthew (17 : 18): *caca* (record) *ong* (on) **(prior intent)**
while carrying a record **(instrumental action)** to the record player **(goal location)**
Interpretation as an intention by his mother: "I want the record on"

Similarly, in the ontogeny of ape language, symbolic structure builds gradually over time on the intentional structure of action, i.e., the structure that is coded by the mirror neurons. Thus, Kanzi could use a single symbolic element to communicate intended action such as "chase" at an earlier point in his development than he formed two-element combinations to get across the same message concerning his goal in the situation (for example, *chase* (lexigram) *you* (pointing to Rose) (Fig. 15.7). Similar ontogenetic sequences from single-element to two-element encodings of goal-directed action have been observed in the bonobo Panbanisha, and the chimpanzee Panpanzee.

Phylogenies are simply sequences of ontogenies that are modified over evolutionary time (Parker *et al.*, 2000). Therefore, the common ontogenetic sequence by which linguistic structures come to encode increasingly explicit structures of intentional action across species has potential evolutionary significance. Again, while phylogeny does not recapitulate the ontogeny of one species, common ontogenies across species in the same clade or family imply that the sequence was present, at least potentially or in some form, in the common phylogenetic ancestor.

15.6 Conclusions

Developmental research, cross-species comparison, and mirror neuron studies are converging to provide clues to the neural foundation of cultural learning and transmission in ontogeny and phylogeny. In this chapter, I focus on two central features of human culture, language and tools (Greenfield, 1991). Mirror neurons and canonical neurons provide

[5] The two numbers represent the age in months and days.

neural mechanisms for the centrality of observation and imitation in the ontogeny and phylogeny of the intergenerational transmission of cultural tool systems. The location of mirror neurons in Broca's area provides a neural mechanism for the role of repetition in the ontogeny and phylogeny of conversational discourse, an important component of language evolution. The sensitivity of mirror neurons to goal-directed action also provides a neural mechanism for the role of intentional action in the ontogeny and phylogeny of symbol combinations and their interpretation. Behavioral similarities between apes and humans in these areas suggest that imitation of tool use, repetition as a conversational device, and communication about intentional action constituted a foundation for the evolution of human culture present in the ancestor shared by *Pan* and *Homo* 5 million years ago. Future research at the neurobehavioral level needs to establish empirically these theoretical links between the mirror system and these basic characteristics of the ontogeny and phylogeny of language and tools. A particular need is for the neural investigation of the mirror system in young children and apes of different ages.

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