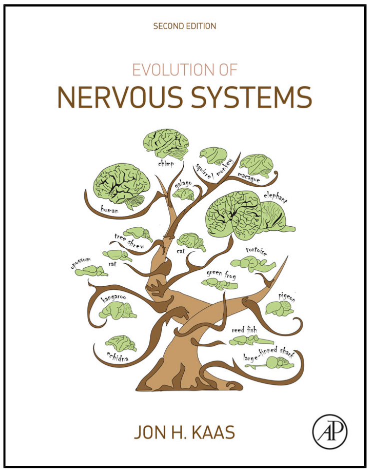

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3.17 Tool Use in Nonhuman Primates: Natural History, Ontogenetic Development and Social Supports for Learning

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Abstract

Humans have used tools since the dawn of our species. A few other species of primates in South America, Africa, and Asia also use tools, primarily to obtain foods that cannot be obtained by other techniques. Using a tool challenges movement coordination and planning. Although nonhuman primates neither teach others nor learn via imitation to use tools, their ways of using tools are traditions. Young individuals learn to use tools through sustained practice, which is supported directly and indirectly by social partners.

3.17.1 Introduction

Tool use is central to our identity as humans; it is associated with human intelligence, dexterity, behavioral adaptability, and cultural variation. Accordingly, the appearance and elaboration of tool use in human evolution has been the focus of much theorizing and research. In this chapter, we confine our discussion to hand tools—objects used to produce a mechanical effect on a surface, medium, or other object. One way to understand the origins of human characteristics is to compare humans and nonhuman primates. These comparisons allow us to determine those characteristics that are uniquely human and those that are evidently shared in some fashion with other primate taxa. In the case of tool use, comparative inquiry immediately leads to a conundrum: Tool use is taxonomically widespread in the animal kingdom, including invertebrate groups, but not widely observed in nonhuman primates (Shumaker et al., 2011; Sanz et al., 2013). Where it is present in nonhuman primates, several key differences are apparent between humans and other primates. For example, in those wild populations where tool use is commonly observed, it is not known to be essential for survival, as it is for all humans. Second, all forms of tool use seen in nonhuman primates are structurally simple, compared to common forms of tool use in humans. For example, nonhuman primates use one object at a time; humans often use two or more objects concurrently (for example, two chopsticks, or knife and fork).

There are points of similarity in tool use between humans and in other primates, however. First, tool use is thought to be maintained as a tradition (ie, acquired in part through social learning (Fragaszy and Perry, 2003) in all groups of primates in which it is common. Second, it is often associated with gaining resources (most often, food) that are otherwise inaccessible or costly to access (eg, cashews by bearded capuchin monkeys (Visalberghi et al., 2016); Neesia fruit by orangutans (Van Schaik and Knott, 2001); and driver ants by chimpanzees (Humle and Matsuzawa, 2002), indicating continuity in ecological function. Third, the three taxa in which routine tool use is most widely geographically distributed across wild populations (macaques, *Macaca*; chimpanzees, *Pan*; and tufted capuchins, *Sapajus*) are recognized as ecologically highly adaptable (that is, they live in a wide range of habitats, and have diets that vary across habitats, with accompanying variability in activity patterns and group size). The association of tool use with high ecological adaptability provides another point of continuity with humans. Finally, nonhuman primates manipulate tools with their hands, as do humans. Thus there is continuity of actions used to grasp and maneuver objects, and accordingly, potential continuity of anatomical structures and coordinative processes.

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The reasons for the uneven appearance of tool use across species, and the uneven diversity of tool technologies across populations of the same species, are not fully understood. The variations across taxa are assumed to reflect species-typical perceptuomotor attributes and local (including social) circumstances. Variations within taxa are assumed to reflect individual experience in conjunction with locally variable environmental conditions, just as do variations in other natural behaviors, such as locomotion and foraging. Some hypotheses regarding the appearance of tool use have been presented. First, the relative profitability of foraging for embedded foods (obtainable only by using a tool) compared to other foods has been proposed as an environmental prompt for the appearance of tool use (Rutz and St Clair, 2012). Second, opportunities to discover the utility of using a tool, or to develop variable techniques of using a tool, may be greater when foraging on the ground than when foraging in trees (Visalberghi et al., 2005; Meulman et al., 2013). Third, aspects of the social system are thought to affect the likelihood that socially biased learning will support learning to use a tool (Sanz and Morgan, 2013). Altogether, a mix of individual, social, contextual, and ecological conditions contribute to the appearance and maintenance of technical traditions, including tool use (Fragaszy et al., 2013a). These are not mutually exclusive hypotheses.

Our goal in this chapter is to consider tool use in primates as a spontaneous, naturally occurring behavior that presents varied forms within and across taxa. We begin by presenting a definition of tool use that follows from the premise that using a (hand) tool involves moving an object in space to relate it to a substrate or another object. Working from this definition, we explain how tool use depends upon a particular form of perceptuomotor coordination. We then review the best-studied forms of tool use in wild primates, describing perceptuomotor features, and ontogeny and social supports for learning. We close by pointing to some potential directions for future work in evolutionary neuroscience bearing on the relations among the nervous system, tool use, and traditions.

3.17.2 What is Tool Use?

3.17.2.1 Definition of Tool Use in Terms of Goals

In the comparative literature, tool use is defined conventionally by the inferred goal of the action with an object, such as "termite fishing" or "nut cracking," coupled with restrictions on the status of the object. For example, Shumaker et al. (2011: p. 10) define tool use as "the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool." This operational definition permits classification of an action as tool use, but it does not support predictions about the relative difficulty of using particular objects as tools to reach particular goals, nor about relations among anatomy, physiology, current context, or experience of the tool user and its behavior with a given object, for example. Thinking about tool use prospectively requires a theoretical orientation. We view the lack of theoretical frameworks providing the basis for predictions about tool use as a severe limitation of the field at this time, and we hope with this chapter to prompt others to join us in thinking about this problem.

3.17.2.2 Definition of Tool Use in Terms of Movement

We adopt a definition drawn from movement science: Tool use occurs when an individual moves an external object to produce a force upon another external object or surface, when such movement involves managing altered degrees of freedom (DoF) of movement of its own body (Mangalam and Fragaszy, 2016). This definition includes an inferred goal ("to produce force"), but the remainder of the definition derives from biomechanics, rather than from consideration of the state or properties of the external object. Biomechanics describes movements in vertebrates in terms of the coordination and control of a system of kinematic links. Each link constitutes one or more DoF. In the language of biomechanics, a (hand) tool transforms a body-only system into a body-plus-tool system by adding one or more DoF associated with the tool, which may result in redistribution of the existing DoF of the body. For example, to use a hammer held in the hand, a person alters the normal distribution of muscular flexion and extension of the forelimb to accommodate the torque and inertial tensor of the hammer. Thus, using a tool entails adjusting the movements of the body to accommodate the new set of DoF, as well as the altered spatial relation between the hand and the intended target (which is now contacted by the head of the hammer, some distance from the hand).

3.17.2.3 Developing Tool Use

As the example of using a handled hammer suggests, a definition of tool use grounded in principles of movement allows us to recognize that using a tool harnesses features of our perceptuomotor system that are used in diverse situations. Thus, there is continuity in the function of this system across tool-using and other activities. Learning to use a tool requires developing particular perceptuomotor skills, and members of each species will develop these skills from their species-typical repertoire of movements and perceptual abilities.

Development of tool use by young individuals is paced by perceptuomotor constraints on the performance of the movements needed for effective use of a tool in a given situation (for example, for hammering by human children, accurate aiming when striking develops from the second year of life (Fragaszy et al., 2016a)). It is also paced by the quantity, timing, and nature of practice—multiple spaced opportunities for practice in variable situations support the development of skill. Social context plays a role as well. Social partners impact a young individual's opportunities for practice through provision of materials and settings for practice, and impact the young individual's interest in practice through their own activity. The totality of social supports for learning can be conceived as a constructed niche, wherein the activity of conspecifics shapes the environment of development of young individuals (Sirianni and Visalberghi, 2013; Laland et al., 2015). Where social supports contribute substantively to young individuals' skill development, we speak of traditions (Fragaszy and Perry, 2003). Known cases of tool use by populations of wild primates are characterized as traditions. In the next section, we provide examples of two better-studied cases of tool-use traditions in wild nonhuman primates, mentioning the most evident perceptuomotor attributes, the developmental timeline, and the nature of social supports for learning for each case where such data are available. We close the section with an example of a relatively simpler form of tool use, to highlight that the challenge of using a tool, as in performing any skilled movement, depends jointly on the demands of the task, the properties of the immediate setting, and the perceptuomotor characteristics of the actor.

3.17.3 Examples of Tool Use by Primates in Natural Settings

3.17.3.1 Using a Stick to Extend Reach

Using a stick (or other long, thin, relatively rigid object) to extend reach is one of the most common forms of tool use observed in nonhuman primates. Using a stick enables the individual to contact something that cannot be grasped directly, or to contact something that might be harmful to the body if touched directly. Chimpanzees, orangutans, and capuchin monkeys in natural settings have been seen using sticks or other plant material (stems, etc.) to "fish" for termites, probe for honey, flush or disable prey, and remove seeds from fruit, and other similar uses (Van Schaik and Knott, 2001; Falótico and Ottoni, 2014; Sanz et al., 2009a,b, 2004; Sanz and Morgan, 2009; Souto et al., 2011; Pruetz and Bertollani, 2007). We describe fishing for termites in chimpanzees as the earliest and best-documented example of this family of actions.

3.17.3.1.1 Termite Fishing by Chimpanzees

Termite fishing by chimpanzees (*Pan troglodytes*) was the first tool-use behavior by wild primates to be described systematically (Goodall, 1964). Goodall (1964) described chimpanzees inserting a piece of grass into an epigeal (aboveground) termite nest, or mound, and eating the termites that clung to the grass when it was withdrawn from the nest. Chimpanzees in many regions across Africa fish for termites in a similar manner (eg, Sanz et al., 2004). In some places chimpanzees use a set of two different tools: one to get into the nest (stout sticks to puncture the ground above an underground nest, or perforating twigs for above ground nests) and a second, more delicate probe for extracting the termites (Sanz et al., 2004). Chimpanzees in central Africa fray one end of the tool to create a brush-tip, which may increase the number of termites that can cling to the probe (Sanz et al., 2004). Chimpanzees carry to the nest site probing tools that were collected and prepared elsewhere. Puncturing sticks are often left at the site and later reused (Sanz et al., 2004; **Fig. 1**).

3.17.3.1.1.1 Movement Features of Termite Fishing

In kinematic terms, using a probing tool to collect termites requires placing one end of a relatively rigid probe into a small opening in the termite nest (an exit tunnel created by the termites, in the case of epigeal nests, or the opening created by a puncturing stick, in the case of underground nests). The probe is then moved into the nest to some depth and sometimes moved delicately within the

Figure 1 An adult female chimpanzee in Gombe National Park, Tanzania, removing termites from a probing tool as her offspring watches her and touches her tool and the termites on it. Chimpanzees across Africa capture termites by probing into their nests with stems or sticks. Young chimpanzees at Gombe master termite fishing between 5 and 6 years of age (Lonsdorf, 2005). Photo courtesy of Joshua Leonard.

tunnel, using small movements of the wrist. Using the probe adds one additional DoF to the body system (the DoF between the hand and the point of the probe) and an altered spatial relation between the hand and the termite nest. We do not yet have detailed characterizations of the control of the probe's entry and retraction from the termite nest, although it is evident that individuals vary in how they manage the task, and that with practice chimpanzees become skilled at these movements. The probes may be held with precision or power grips, and a variety of grips are used (Lesnik et al., 2015).

3.17.3.1.1.2 Developmental Timeline for Termite Fishing

Lonsdorf (2005) described the development of termite fishing in young chimpanzees. All young chimpanzees were seen manipulating a probe used by another by 18 months, but they did not insert a probe into the termite nest until 2.5 years of age at the earliest. Some individuals did not succeed at extracting termites before 5.5 years of age. In the years between the time their interest was first piqued by others' actions at termite mounds, and when they could fish for termites themselves, the young chimpanzees engaged in a variety of inefficient behaviors at the mound, such as poking and sniffing at the mound, and actions with the probe, such as swiping at the mound, and pressing the probe to the mound. Even after they began to insert a probe into the termite nest, they had to refine their technique—to learn how deeply to insert the probe, how to move it, how long to leave it in the nest, how quickly to retract it—before they captured termites efficiently. This process may take more than a year (Lonsdorf, 2005).

3.17.3.1.1.3 Social Context for Termite Fishing

Typically a single individual or small parties of chimpanzees fish at a termite mound. Young chimpanzees initially watch their mothers use probes to catch termites, and then begin at around 2 years of age to inspect the mound and handle the mother's probe tools (see **Fig. 1**). The mother is tolerant of her offspring's attention but does not actively guide the youngster's actions (Lonsdorf, 2005). We do not yet have strong evidence that chimpanzees learn particular techniques for using the probe or preferences for probes with particular properties from working with others' tools or watching others.

3.17.3.2 Using a Percussor to Apply Force

We have more detailed information about wild primates using hammers than about wild primates using sticks to extend reach as in termite-fishing. In part this reflects the wider distribution of percussion across species, and in part it reflects strong interest on the part of anthropologists in percussive tool use, because of the prominence of percussive tools in the archaeological record of our own lineage (Roux and Bril, 2005; Haslam et al., 2009). Some wild populations of chimpanzees, tufted capuchins, and long-tailed macaques use a wood or stone percussor to smash or crack nuts, seeds, other tough plant materials, or shellfish and crabs against a stone or wood anvil. In all these species, the items cracked and the tools and techniques used to crack them vary considerably across regions, in accord with the body mass of the individuals wielding the percussors, the resistance of the food items to be cracked, and the availability of materials for percussors and anvils, and in the case of macaques cracking oysters, the position of the oyster on the rock (on the underside of a rock, for example) (Fragaszy et al., 2004; Whiten et al., 2001; Morgan and Abwe, 2006; Tan et al., 2015; Visalberghi et al., 2015; Canale et al., 2009). We will describe percussive tool use in each of these genera in turn.

3.17.3.2.1 Nut Cracking by Chimpanzees

Most of our knowledge about nut cracking in chimpanzees comes from two sites. In Bossou, Guinea, where loose stones are abundant, the chimpanzees use two movable stones as hammer and anvil. The hammerstones are most commonly granite, and the anvils are usually bigger than the hammers (average weight of 2.1 vs 0.7 kg) (Sakura and Matsuzawa, 1991). In the Taï forest, Ivory Coast, the chimpanzees use anvils embedded in the ground or crack directly on a tree, and often use wood as a hammer (Boesch and Boesch, 1984; Boesch and Boesch-Achermann, 2000). In Taï, chimpanzees select objects to use as hammers in accord with the resistance of the nut they intend to crack—stones (ranging in mass from <1 to 24 kg) for more resistant nuts; wood pieces (up to 4 kg) for less resistant nuts (Boesch and Boesch, 1982; Sirianni et al., 2015). Typically the chimpanzee, in a seated position, places one nut on the anvil surface, sometimes holding it there with one hand, and uses one hand to strike with the stone. For softer nuts, a single strike is sufficient. As in termite fishing, females engage in nut cracking at a higher frequency and with greater efficiency compared to males (Boesch and Boesch, 1981). In kinematic terms, using a hammer to crack a nut requires placing the nut on an anvil surface, and then striking with adequate force and orientation with a hammer. The hammer is held in a power grip, in one hand if it is small enough (as is usually the case). As for termite fishing, using a stone to strike a nut adds one degree of freedom to the body system. However, the details of execution differ as dramatically between the two tasks as practicing calligraphy versus playing tennis. Using a probe to fish for termites requires delicate movement within a confined space, whereas using a hammer depends on vigorous, rapid movement in an unconfined space.

3.17.3.2.1.1 Development of Nut Cracking by Young Chimpanzees

Infant chimpanzees in Bossou, Guinea, handled African oil-palm nuts (*Elaeis guineensis*) and stones in the first year of life (Inoue-Nakamura and Matsuzawa, 1997). By 1.5 years they began to strike a surface (the ground) with a nut or stone, and they did this more frequently as they got older. Inefficient actions—such as raking the nuts or rolling them—disappeared by 3.5 years of age (Inoue-Nakamura and Matsuzawa, 1997). Boesch and Boesch (Boesch and Boesch-Achermann, 2000) presented a similar picture of the development of nut cracking by infant chimpanzees in the Taï forest, Ivory Coast. Infants showed an interest in nuts and tools, but no chimpanzee younger than 4 years old was seen trying to crack Coula nuts, and only individuals aged 5 year and older cracked these nuts, that are more resistant to cracking than oil-palm nuts.

The challenges in this task for young chimpanzees include positioning objects appropriately and striking with force and accuracy. Young chimpanzees initially move objects against surfaces gently, rolling or pressing them, rather than percussing them forcefully (Takeshita et al., 2005). They may strike the nut directly on an anvil, or with a stone while the nut is on the ground, among other ineffective combinations of placement and action (Inoue-Nakamura and Matsuzawa, 1997; Biro et al., 2006). We do not yet know the timeline for young chimpanzees to learn to control the force or precision of their strikes with hammers of varying mass, or to select appropriate materials.

3.17.3.2.1.2 Social Context of Nut Cracking by Chimpanzees

Young chimpanzees aged up to 5 years spend most of their time near their mother. During this time the mother is highly tolerant toward her offspring, letting them sit next to her as she cracks nuts, touching the stones and her hands, and even taking kernels of cracked nuts. In this way, the mother provides her offspring with "an excellent setting in which learning aided by observation can take place" (Biro et al., 2006: p. 496). Matsuzawa et al. (2001) propose that juvenile chimpanzees have to figure out the details of successful nut cracking by themselves, but they do that in an environment that facilitates this learning. Similar to what was seen in termite fishing, young chimpanzees selected recently used stones as hammers over 40% of the time, compared to 20% of the time in the adults (Fragaszy et al., 2013a). We do not know how observing another nut cracking impacts the probability with which the young chimpanzee acts with nuts or stones or approaches an anvil.

3.17.3.2.2 Nut Cracking and Seed-Cracking by Capuchin Monkeys

Wild tufted capuchin monkeys living in savannah and semiarid habitats (*Sapajus libidinosus*, *S. xanthosternos*, and *S. flavius*) use stone hammers to crack nuts and seeds on anvils of stone or wood (Fragaszy et al., 2004; Canale et al., 2009; Ferreira et al., 2009). At one site, Fazenda Boa Vista, the monkeys crack several species of palm nuts across the year (Spagnoletti et al., 2011). Palm nuts are never a staple component of the diet, as they appear to be for chimpanzees in the Taï forest when they are in season (Boesch and Boesch-Achermann, 2000), but rather appear to be a highly preferred treat, exploited opportunistically when they are encountered. The monkeys use hammerstones that weigh on average about 1 kg, which is a considerable proportion of adult body mass (adult males average 3.6 kg; adult females 2.1 kg) (Fragaszy et al., 2016b). Adults typically crack a nut open in 10 or more strikes, with wide variability in accord with the mass and skill of the monkey, the mass of the hammerstone, and the species and size of the nut (Spagnoletti et al., 2011; Fragaszy et al., 2010a). After collecting a nut from a palm tree, monkeys carry the nut to an anvil (a fallen log, crotch of a tree or large tree limb, or most often, a stone outcropping or boulder, typically with shallow pits on its surface from previous use as an anvil (Visalberghi et al., 2007)). Anvils are abundant throughout their home range (Visalberghi et al., 2007). If there is no hammerstone at the anvil, the monkeys transport one from nearby, walking bipedally erect with the stone, using a bent-hip, bent-knee walking gait (Duarte et al., 2012; Hanna et al., 2015). Once they have placed the nut in a pit on the anvil, standing bipedally, they lift the hammerstone to about shoulder height, then strike it vertically onto the nut (Liu et al., 2009; **Fig. 2**).

The monkeys prospectively manage several features of the task. First, they select hammerstones of appropriate size and material (Visalberghi et al., 2009). Monkeys generally prefer heavier hammerstones up to their limit to handle them (Fragaszy et al., 2010b). They take distance to the anvil and mass of the stone into account when choosing among hammerstones of different masses in field experiments (Visalberghi et al., 2009; Massaro et al., 2012). Second, monkeys position the nut with its more symmetrical edges facing the lateral sides of the pit, so that it does not wobble when released (Fragaszy et al., 2013b). Finally, when cracking softer nuts, they modulate the force of their strikes in accord with the state of the nut after each strike, cracking with less force once the shell has begun to crack, for example (Mangalam and Fragaszy, 2015).

Cracking a palm nut of any species requires considerable force. The force of a strike depends on velocity at impact and the mass of the hammer. For a hammer of a given mass, the individual can modulate the force of the strike by altering the velocity, which can be accomplished by raising the hammer to a different height, or by adding work on the downward strike. Capuchins modulate the force of their strikes primarily by adjusting the amount of work they add to the stone in the downward strike (Mangalam and Fragaszy, 2016, 2015; Liu et al., 2016).

3.17.3.2.2.1 Development of Nut Cracking by Capuchin Monkeys

Young capuchins start hitting a nut on a surface at about the same time that they first pick up nuts, within the first year of life, but they do not crack nuts for several more years (Eshchar et al., 2016; Resende et al., 2008). Actions combining nuts with stones appear in the second year of life, around the time of weaning. In the years after weaning, the repertoire of actions with nuts expands and then contracts, as inefficient behaviors drop out (Resende et al., 2014). Successful cracking first occurs at around an age of 3 or 4 years, first with pieces of partially cracked nuts collected from adults' cracking activities (Eshchar et al., 2016; Resende et al., 2008, 2014) but for several more years young monkeys are not as proficient as older animals at cracking more resistant nuts. This long period of skill development matches a long period of physical development—body mass increases very slowly from just over 1 kg at weaning (18 months) to adult body mass at an age of 9 or 10 years (Fragaszy et al., 2016b).

Figure 2 An adult male bearded capuchin in the process of cracking a section of a palm nut. He opened the whole nut a moment ago and is now opening the sections produced in that first event. To crack the nut, he placed it on a stone anvil (a sandstone outcrop). The hammerstone weighs about 1.5 kg; the monkey 4.4 kg. A monkey carried this stone to the anvil from the surrounding area some time in the past, and this monkey will leave it at the anvil, together with shells and other debris from his cracking activity, when he finishes cracking this nut. It will be several years before the juvenile onlooker can crack nuts on his own, but in the meanwhile, he will explore the anvil site and handle the nut shells and hammer stone when the anvil is not occupied. Photo courtesy of Barth Wright.

3.17.3.2.2.2 Social Context of Nut Cracking by Capuchin Monkeys

Typically there is one hammerstone at an anvil, and thus only one monkey can crack nuts at a given anvil at one time. Immature monkeys' interactions with nuts and hammerstones are influenced by the activities of other in the group, as well as the presence of cracking artifacts (Eshchar et al., 2016, see **Fig. 2**). In one study, the rate of manipulation of nuts by the immature monkeys quadrupled when others in the group cracked and ate nuts, and immature monkeys were 10 times more likely to handle nuts when they themselves were near the anvils—where many discarded nut shells were present, as well as a hammerstone in most cases. Moreover, immature monkeys were three times more likely to be near an anvil when others were cracking (Eshchar et al., 2016). Observing adults cracking and eating nuts motivated immature monkeys to handle nuts (social facilitation) and drew them to the anvils (local enhancement), which provide appropriate practice sites. In this way, the behavior of adults provided the opportunity for the juveniles to manipulate nuts and stones in different ways, especially on the anvils, and motivated them to continue with this manipulation even in the absence of immediate tangible reward. Through this type of practice, which extends over years, capuchin monkeys eventually master nut cracking, and the nut cracking tradition is maintained across generations (Fragaszy et al., 2013a; Coelho et al., 2015).

3.17.3.2.3 Cracking Mollusks by Long-Tailed Macaques

Long-tailed macaques (*Macaca fascicularis*) are relative newcomers to the club of wild tool–using primates: the first systematic study of tool use in this species was published in 2007 (Malaivijitnond et al., 2007). Several populations on the coast of Thailand and Burma use hammerstones and anvils to process loose bivalves, gastropods, and crustaceans (**Fig. 3**). These items are collected in the intertidal zone and brought to an exposed rock, where the monkeys break them with a hammerstone using a method termed "pound hammering." The macaques also chip at sessile oysters using a method termed "axe-hammering" (Gumert and Malaivijitnond, 2012). The shape of the tool, the rate of striking, and the way the monkeys grip the stone are different for these two methods of tool use (Gumert et al., 2009). Tan et al. (2015) identified 17 different action patterns used by run the macaques for different food items, distinguishable by a unique combination of materials and behavioral elements. From use-wear on the stone, one can classify what kind of action it was used for, and thus what kind of food item the stone was used to process (Haslam et al., 2013; **Fig. 3**).

3.17.3.2.3.1 Developmental Studies and Social Context of Cracking Mollusks

Like capuchin monkeys, long-tailed macaques live in cohesive social groups. The monkeys forage as a group along the shore, where small stones and boulders are abundant. We know that young macaques, like young capuchins and young chimpanzees, master using percussive tools over the course of a few years. Studies on the development of percussive tool use by long-tailed macaques are in progress.

Figure 3 A female Burmese macaque (*Macaca fascicularis auriensis*) foraging along the shore at low tide in Myeik Archipelago, Tanintharyi Region, Myanmar. She is using a sharp-edged stone to chip an oyster attached to a rock, a technique called "axe-hammering" (Gumert et al., 2009). Macaques feed on oysters found in diverse locations on the rocks, adapting their body postures and the angle of their striking actions as needed. Photo courtesy of Michael Gumert.

3.17.3.3 A Simpler Form of Tool Use

Of the many examples of tool use described for chimpanzees, orangutans, capuchins, and long-tailed macaques, some are relatively simple in their requirements for positioning the body or managing force relations between tool and target substrate. Leaf-sponging is one such example. Individuals in many chimpanzee populations use leaves to sponge up water from cavities in tree boles or large limbs, or from surface water (van Lawick-Goodall, 1968; Quiatt and Kiwede, 1994; Sugiyama, 1995). The chimpanzees crumple or fold leaves in their mouths to create a crude "sponge," which they dip into water in cavities and then put in their mouths and suck (Tonooka, 2001). In Bossou, Guinea, young chimpanzees began to use leaf sponges at around an age of 2 years, just before they began using sticks to fish for termites. At first they only used sponges that were discarded by adults. When they were about 3.5 years old they began manufacturing their own sponges (Biro et al., 2006).

Using a sponge is a relatively less challenging form of tool use than using a probe or using a hammer, as the whole hand places the sponge directly in the water. There is no requirement for accurate placement of the sponge once it touches the water. The young chimpanzee learns that the sponge is wet when it picks up a used sponge. While holding a used sponge, a simple exploratory reach into the cavity or body of surface water where an adult was sponging is enough for the young chimpanzee to discover the utility of the action. The materials composing the sponge (leaves) are usually close to where the sponge will be used, and their collection and transport are not physically challenging. Thus it is not surprising that this behavior appears early in life, and modifications of sponging are readily learned (Hobaiter et al., 2014). Comparing sponging with known forms of percussive tool use highlights that tool use can vary in difficulty in accord with several dimensions of the task.

3.17.4 Socially Biased Learning in Nonhuman Primates, With Special Reference to Learning to Use a Tool

When learning is facilitated by observing or interacting with a conspecific, or encountering another's products, we speak of social learning (Heyes, 1994) or socially biased learning (Fragaszy and Visalberghi, 2004; Galef, 1995). Socially biased learning is common throughout the animal kingdom and is found in all classes of animals (Galef, 1996; Galef and Laland, 2005; Leadbeater and Chittka, 2007; Wilkinson et al., 2010). When a behavior is acquired at least in part through social influence and is transmitted from generation to generation, it is a tradition (Fragaszy and Perry, 2003). Species in which socially biased learning is a prominent part of daily life may find the behavior of conspecifics particularly interesting or memorable. In some of these species, familiar conspecifics play a particularly important role in what young individuals learn with and from others, and that is generally the case in primates, which have richly structured social relationships.

Several processes are widely discussed in the animal behavior literature as supporting socially biased learning. The most general are social facilitation and local enhancement. Social facilitation occurs when observing a demonstrator performing an action, or a set of actions, increases the probability that the individual observing the demonstrator will engage in the same activity (Heyes, 1994; Galef, 1996; Visalberghi and Addessi, 2000). Local enhancement occurs when exposure to an individual's activity, or to the products of this activity, draws the observer's attention toward the location and/or a specific object in this location involved in the activity (Heyes, 1994; Hoppitt and Laland, 2008). The observer then is likely to explore the object or the location, even if it does not perform the same activity as the "demonstrator." Local enhancement can be conceived as coordination in space and social facilitation as coordination of activity in time (Coussi-Korbel and Fragaszy, 1995). These processes support group cohesion and behavioral synchrony, as, for example, in traveling and foraging, as well as learning.

The process of vicarious reinforcement (associating a particular activity in a specific place with a positive outcome from watching another (Bandura, 1977)) contributes to learning in these situations. Through vicarious reinforcement, for example, animal *a* watching animal *b* feeding in a certain place associates that place with feeding, which is positively reinforcing, even though animal *a* did not eat in that place. Vicarious reinforcement may be related to vicarious emotion, discussed in the human neuroscience literature as "empathic emotions" or "emotional contagion" (Hatfield et al., 1994; Paulus et al., 2013).

Since 1990s, researchers studying how nonhuman primates in captivity learn to solve instrumental problems (such as opening a puzzle box) have been particularly concerned with distinguishing between two forms of social learning: imitation and emulation, because imitation was proposed by some researchers as being essential for cumulative cultural evolution as evident in humans (Wasielewski, 2014). Imitation is broadly defined as "copying the form of an action" (Whiten et al., 2009: p. 2418) and in some cases, more narrowly, as copying the exact actions of an agent (see Chapter 3.26, The Cultural Capacity of Human and Nonhuman Primates: Social Learning, Innovation, and Cumulative Cultural Evolution). Emulation is defined as copying the end state of an action—in this process, the learner acts to achieve the same outcomes but uses different behaviors (Hoppitt and Laland, 2008; Whiten et al., 2009). These two processes are alternative means to achieving the same end result as a demonstrator.

Imitation functions in humans as a means of play and social signaling, as well as leading to learning. Humans imitate readily from a very young age to solve a novel problem, such as taking apart an object (Meltzoff, 1996). However, nonhuman animals do not usually learn by imitation, in captivity or in nature (Tomasello, 1994, 1996; Boyd and Richerson, 2005). Instead, nonhuman animals solve novel manipulative problems that they see others solve through their own discovery activity, producing emulation (Tomasello, 1994, 1996; Nagell et al., 1993). Recent advances in how we conceptualize imitation may alter this generally negative assessment of imitation as a means of learning in nonhuman animals (Huber et al., 2009). Marmosets, for example, can learn how to open a box to retrieve food from watching a video of an unfamiliar conspecific opening the same box (Gunhold et al., 2014). At this time, however, the conservative starting point for considering how social influence aids a nonhuman primate to learn how to solve an instrumental problem is that social facilitation and local enhancement are likely the most powerful influences.

Social influence can also occur through interactions with the artifacts left by others, outside of the time when others are using them. Artifacts provide opportunities to explore sites and to handle materials made attractive by others' activity. Enduring artifacts associated with technical activities (such as open shells, broken branches, and holes dug in the ground, in the case of nonhuman primates) extend the time depth of social influence, and permit practice in a less competitive context than while adults are handling the relevant materials or occupying the relevant place (Fragaszy et al., 2013a). As mentioned above, artifacts appear to support young individuals learning to use percussive tools in capuchins and chimpanzees. In both species, hammerstones are left near anvil sites, and young individuals handle these items frequently over long periods. Young chimpanzees also rely on probing tools manufactured by others for a long period before they begin to manufacture their own tools (Fragaszy et al., 2013a). However, some kinds of tool use do not result in recoverable artifacts, such as using a stick to flush prey (typically, lizards) from crevices in a cliff face, as capuchin monkeys are known to do in some areas (Falótico and Ottoni, 2014). In this situation, the monkey using the probe is not near others while searching for prey, and it drops the stick to catch the fleeing prey. We do not yet know how monkeys learn to use probes to flush prey.

The construct of social facilitation is expanded in an important sense here to incorporate behavioral facilitation associated with artifacts, at a time distant from when the artifact was produced. Definitions of social facilitation and related terms (eg, coaction, social enhancement, stimulus enhancement (Galef, 1988)) are couched in terms of increased probability of a behavior concurrent with or immediately following perception of its performance by another. Facilitation induced by enduring physical artifacts can be long distant in time from the actions and individuals producing the artifact.

3.17.5 Traditions of Tool Use in Nonhuman Primates

Most cases of tool use in nonhuman primates endure over time, are shared among members of group, and are known or assumed to be acquired in part via socially biased learning. They are behavioral traditions. They are also variously termed cultural traits, cultural behaviors, or simply cultures (Laland and Hoppitt, 2003). Some evolutionary biologists propose that traditions of behavior, and the artifacts they may generate, produce a constructed niche that functions as a "second inheritance system" that extends and interacts with the genetic inheritance system (Laland et al., 2015; Jablonka and Lamb, 2014). The social and physical setting in which young individuals acquire traditions is part of a constructed niche. This conception of constructive processes in development and evolution and inclusive mechanisms of inheritance underlies the developing "extended evolutionary synthesis" (Laland et al., 2015). According to this modified view of evolution, developmental processes participate in shaping "the direction and rate of evolution, the origin of character variation, and organism–environment complementarity" (Laland et al., 2015: p. 1). Understanding the evolution of the nervous system from this broadened evolutionary perspective is a challenge for evolutionary neuroscience.

The power of a tradition to canalize behavior in a new situation is illustrated by Gruber et al.'s (2009) finding that chimpanzees (*Pan troglodytes schweinfurthii*) from two neighboring communities that have different traditions of tool use (sticks for collecting honey in one community, but not in the other; sponging for water in both) approached a novel problem differently. The novel problem provided to the chimpanzees was to extract honey from holes drilled into horizontal logs. Chimpanzees in the community that use sticks to collect honey from wild bees' nests generalized this behavior to extract the honey from logs using sticks. In contrast, chimpanzees in the other community that sponge but do not use sticks as tools, tried to use their fingers to collect the honey and some individuals used leaf sponges. Bearded capuchin monkeys living about 350 km apart in Brazil did the same: monkeys in the population that routinely uses sticks as probing tools to collect honey and to flush lizards from rock crevices readily began to probe with a stick in a box containing molasses, whereas monkeys in the population that uses stones as hammers, but does not use sticks to probe, did not discover that they could get the molasses using a stick (Cardoso, 2014).

It is not surprising that prior experience influenced individuals' approach to a new problem. The key relevance to our discussion is that individual experience in each community reflected that community's shared traditional approach to the general problem of collecting a liquid. In essence, a shared tradition for solving one problem shaped a shared approach to a new problem. Thus over time behavioral patterns can diversify across groups along different trajectories, in line with each groups' traditions.

3.17.6 Open Questions Posed by Tool Use in Primates for Understanding the Evolution of the Nervous System

We close with some thoughts on what the varieties of tool use evident in contemporary nonhuman primates suggest about the evolution of the nervous system in our order. This is largely unexplored intellectual territory, as we do not as yet have a clear understanding of the functional organization of the brain with respect to coordinating movements relating one object to a surface or another object, which is of course a fundamental requirement for using a (hand) tool. Historically, evolutionary and comparative investigations of the relations of movement and the nervous system in primates have focused on posture, locomotion, the integration of vision with movement, and reaching and grasping (eg, Karl and Whishaw, 2013). Tool use involves the integrated functioning of movement at all these levels, plus social dynamics. When it is a tradition, which is normally the case, tool use reflects socially biased learning, and we are at an early stage in understanding neural correlates of socially biased learning. In essence, we are trying to understand the integrative functioning of the nervous system in dynamic intercourse with the physical and social world, over the course of the life span and in variable environments—a tall challenge (Charvet and Finlay, 2012).

With this broad goal in mind, we suggest two promising directions for evolutionary neuroscience studies to take in the near future. The first concerns coordination of movements of the body when the individual is managing an altered set of DoF, associated with managing the relation between a tool and the object or substrate it contacts (Mangalam and Fragaszy, 2016). Apparently nonhuman primates can manage one additional DoF associated with handling a tool. This holds whether the tool is held in one or both hands, or in the mouth, as orangutans sometimes do when using a short stick to pry out seeds from Neesia fruit (Van Schaik and Knott, 2001). Humans, in contrast, often use tools that add more than one degree of freedom to manage concurrently (for example, two chopsticks held in one hand, or knife and fork in two hands). Nonhuman primates' limitation to managing one additional DoF of movement is equally evident when the task involves placement, rather than using an object as a tool (La Cour et al., 2014; Fragaszy et al., 2011, 2015). Nonhuman primates align features of the object they are holding to features of the surface they contact with less precision than do humans, using just one feature, and apparently relying primarily on haptic perception rather than vision. In contrast, even young children can precisely align two or three features of an object to a matching cutout and translate and rotate objects to achieve alignment (Fragaszy et al., 2015; Jung et al., 2015; Street et al., 2011; Smith et al., 2014). These findings imply profound differences in the integration of vision and action in humans compared to nonhuman primates.

A second promising direction concerns the integration of socio-emotional features with instrumental learning—the social side of socially biased learning. Vicarious reinforcement via "empathic emotions" or emotional contagion (Hatfield et al., 1994; Paulus et al., 2013) may be supported by mirroring processes in which an individual adopts similar postures and expressions as another is currently expressing. Mirroring processes have been studied in nonhuman primates in relation to the movement of the hand in 3D space (Rizzolatti and Sinigaglia, 2007). Mirroring processes have also been implicated in imitation of facial expressions in infant macaques (Ferrari et al., 2006) and linked theoretically to human language and social cognition more generally (Iacoboni, 2008; Rizzolatti and Craighero, 2004; Gallese, 2014). This area seems promising for comparative and evolutionary study. Birds, cetaceans, and a host of other members of the animal kingdom, as well as primates, have much to teach us about the varieties of neural organization that support rich traditions for communication, technical skills, use of space, and other domains (Rutz and St Clair, 2012; Whitehead and Rendell, 2015; Bugnyar, 2015).

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