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## Tool Use

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### Synonyms

Causal understanding; Instrumental object manipulation; Material culture; Object-assisted problem-solving; Physical cognition

### Introduction

Tools and other utilitarian artifacts pervade humans' lives. They have played such a pivotal role in theories of human evolution that tool use has traditionally been considered a behavioral indicator of complex and flexible cognition. While this early promise has long triggered and maintained keen scientific interest for the study of tool use in nonhuman animals, it may also have revived some naïve anthropomorphic and even anthropocentric biases, particularly when studying species that are evolutionarily close to humans. It is noteworthy that not all cases of tool use necessarily imply high levels of cognitive sophistication, and we should not automatically attribute some of our psychological characteristics to other tool-using species, just because tools are part of our human identity. In fact, tool use is a broad functional category of behaviors that includes a wide range of actions directed to various objects, and whose cognitive substrates may differ substantially between species. Among the species-specific factors underlying the expression of tool use, ecological stimuli, social influences, psychological traits (e.g., cognitive processes and motivational determinants), and anatomical features differentially contribute to engaging in the use of objects as tools.

First, definitions of tool use – following a list of relatively consensual criteria – and description of some of its variants are provided. Then, the main ingredients that allow the expression of tool use across taxonomic groups, distinguishing between extrinsic factors (e.g., stimuli from the physical and social environments) and intrinsic factors (e.g., psychological processes and anatomical features), are reviewed. Focusing on the proximate causes of tool use (i.e., mainly mechanisms) may help generate further inquiries about its ultimate consequences (i.e., its adaptive nature). Indeed, the challenges associated with longitudinal designs and correlational tests between tool use and individual fitness benefits make it extremely difficult to unequivocally demonstrate the adaptive value of tool use, as measured by increased survival rate and reproductive success.

Following the "design-feature argument," in which the detailed structure of a given behavior is matched against the requirements of its hypothesized function, one way to circumvent the lack of evidence for the fitness-enhancing value of tool

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use is to conduct an in-depth structural analysis of this behavior. The heuristic power of the behavioral structure-function interface is reflected in the following statement by Pellis and Pellis (1998): "Therefore, behavioral description informs functional inference, which in turn, influences further description" (p. 115). For instance, kinematic and biomechanical analyses of patterns of grip and hand movement capabilities across different primate species are indicative of evolutionary scenarios about stone tool technology in ancestral hominins. By examining the role of ecological factors, social influences, cognitive processes, and motivational determinants in the development, expression, and evolution of tool use, we aim to show that this behavior, characterized by a patchy phylogenetic distribution, is not necessarily synonymous with highly complex intelligence and can be explained outside an anthropocentric framework.

## Defining Tool Use

About 60 years after Jane Goodall's pioneering observations of a wild chimpanzee fashioning and using a stick to extract termites in Gombe, Tanzania, the debate around the appropriate characterization of the term "tool use" is still open. Because the definitions of tool use range from a focus on the *goal* of the action (i.e., the functional consequences of the tool-assisted behavior patterns being performed), to the *means* of the action (i.e., the structural details of these behaviors), to the condition of the *object* employed, there is no universal consensus among researchers about what constitutes tool use and what constitutes (object-assisted) problem-solving. These differences in perspective stem from conceptually and methodologically divergent approaches across academic disciplines (e.g., ethology, psychology, and anthropology), and this situation is often referred to as the "tool use paradox."

Arguably, one of the most widely adopted definitions of tool use was provided by Shumaker et al. (2011). With a focus on the *goal* of the action, tool use is defined 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" (Shumaker et al. 2011, p. 5). With a focus on different functional features of a tool, alternative definitions consider tool use a form of problem-solving that includes the instrumental use of an object (e.g., St Amant and Horton 2008). For example, according to Shumaker et al. (2011), a weighting scale cannot be categorized as a tool because this object does not alter the form, the position, or the condition of another object or the user. However, under St. Amant and Horton's (St Amant and Horton 2008) functional definition, using a weighting scale to detect an object's weight is a way to mediate the flow of information, and as such, it is a form of tool use.

Another criterion for tool use focuses on the condition of the utilized *object.* The same object may be either freely manipulable or attached to a substrate, which potentially affects its action-mediated use. For many authors, a Californian sea otter pounding a stone onto a shellfish to break it open is an example of tool use, whereas a wrasse pounding a shellfish onto a rock to crack it open is not. Clearly, those behavior patterns (i.e., the pounding actions) are structurally similar, but because the rock used by the wrasse is attached to a substrate (i.e., the ocean floor), they are put into separate functional categories by Shumaker et al. (2011). In line with this argument, "true tool-using" avian species (following the definition by Shumaker et al. 2011; e.g., an Egyptian vulture breaking open an egg by dropping a stone on it) have larger residual brain sizes (regressed against body weight) than bird species using attached objects that do not qualify as tools (e.g., a sea gull dropping an egg on a seashore boulder; Lefebvre et al. 2002).

However, some researchers have disagreed about how structurally similar object-assisted actions may be characterized as being functionally so different. By focusing on the biomechanics of tool use, their approach proposes an embodied theory that shifts the focus of study from the object (i.e., the tool) or the goal to the *action* (i.e., "to tool" as a verb; Fragaszy and Mangalam 2018). "Tooling is deliberately producing a mechanical effect upon a target object/surface by first grasping an object, thus transforming the body into the body-plus-object system, and then using the body-plus- object system to manage (at least one) spatial relation(s) between a grasped object and a target object/surface, creating a mechanical interface between the two" (Fragaszy and Mangalam 2018, p. 194). Behaviors that have been historically recognized as tool use, such as a chimpanzee climbing on top of a pile of wooden boxes to reach for a hanging banana, do not qualify as tooling, because the tool has to be grasped (with the hand or the mouth). In a slightly different view, although partly supporting this action-based approach, some researchers argue that this embodied theory of tool use downplays the role of cognitive processes underlying these object-assisted actions. They claim that tool use is not only about manipulating an object to achieve a goal but also about understanding the action-relevant physical properties of this object in the context of achieving this goal (i.e., embodied cognition; Osiurak et al. 2010). In fact, human patients with a left brain-damaged condition that results in an impairment of coordinated movements associated with tool use attempt to perform daily actions using inappropriate tools or display inappropriate actions with everyday tools (e.g., trying to cut a tomato with a comb or rubbing a hammer on a nail instead of pounding). Consistent with our initial objective to dissociate ourselves from the anthropocentric views that have pervaded tool use research in the past decades, we adhere to the action-based approach proposed by Fragaszy and Mangalam (2018), as this may further our understanding of the causal mechanisms underlying the expression of tool use within and across species.

## Different Forms of Tool Use

Even though the behavioral specializations broadly acknowledged as tool use are sporadic in their phylogenetic distribution and relatively rare, it is noteworthy that they are expressed by evolutionarily distant species. However, the systematic comparison of tool use propensities across species often requires the distinction between *stereotyped* and *flexible* tool use. Stereotyped tool use entails limited to no inter-individual variation in the form or frequency of actions directed to similar objects, whereas flexible tool use implies the use of different tools, applied to different contexts, to achieve different goals, with a dissociation of mean-end between action and purpose (Boesch 2013; Hunt et al. 2013).

Stereotyped tool use has been typically associated with invertebrates and fish, because of the relatively low cognitive abilities it requires. However, birds and mammals can also use tools stereotypically (e.g., anting in Passeriformes, a behavior that consists in whipping insects onto one's feathers; stone-throwing behavior in Egyptian vultures to break into eggs). Yet, considering tool use in invertebrates as exclusively stereotyped would be an oversimplification. Octopuses have one of the largest and most complex nervous systems of all invertebrates, and their brain-body weight ratio exceeds that of most fishes and reptiles. They use tools in many ways, from defensive water jets for prey capture to object-sheltering as an anti-predatory strategy, to object-handling serving the purpose of moving away unwanted items, and those examples may be characterized as flexible tool use. Stereotyped tool use is performed by all the members of a given species and sometimes by several species within a given genus, with extremely low levels of behavioral variation in the form and frequency across individuals. For instance, the hunting strategy of pit-building antlions (i.e., throwing sand at their prey once it fell inside a pit to prevent it from escaping) resembles the prey-burying of *Sphecinae* digger wasps, a closely related genus, which compress sediments on top of their nest after putting prey inside to feed their offspring. A possible explanation for this consistency is that stereotyped tool use develops from preexisting behaviors (e.g., flicking sand randomly to maintain the pits in antlions, placing objects to cache the entrance in digger wasps) and are acquired (almost) asocially, and without learning (Hunt et al. 2013). Lastly, stereotyped tool use is generally context-specific (i.e., the same object or action is not employed to attain different goals). For instance, Egyptian vultures do not place stones to hide food from competitors or do not throw them at predators to drive them away.

Instances of flexible tool use have been mostly reported in animal taxa displaying relatively high cognitive abilities, such as corvids and primates. Although flexible tool use may originate from preexisting schemata (e.g., caching behavior in New Caledonian crows closely resembles the developmentally acquired combination of objects that precedes tool use), a considerable amount of time and practice is spent to learn how to successfully use tools, via individual and observational learning, which may partly explain the high degree of inter-individual variation in the expression of flexible tool use (Hunt et al. 2013). In juvenile capuchin monkeys, the full-blown and successful form of stone-assisted nut-cracking behavior emerges after more than 2 years of unsuccessfully percussing nuts and nutshells against substrates, and upon observational learning from proficient nut-cracking individuals (de Resende et al. 2008). Termite-fishing behavior in chimpanzees share similar acquisition patterns, and individuals successfully master this complex tool-aided foraging technique after 5 years of practice (Lonsdorf 2006).

The strong positive correlation found between relative brain size and the ability to use different objects instrumentally, in various contexts, and to reach different goals support the hypothesis that flexible tool use requires advanced cognitive skills (Reader and Laland 2002). Species that can flexibly manipulate different objects to solve functionally similar or different problems tend to outperform closely-related non-tool-using species in cognitive tasks testing for physical cognition, casual reasoning, working memory, and self-control. When comparing pit-assisted hunting behavior in antlions, sponge-assisted rostrum-covering in dolphins, twig-assisted termite-extraction in chimpanzees, stone chopper-assisted meat-processing technique in Oldowan hominins, and spear-making/using technology in prehistoric humans, there was an increase across species in the ability to hold information for later usage (i.e., working memory), expressed by an increase in problem-solution distances (Haidle 2010). When using tools, humans can understand the cause-and-effect relationships between objects (i.e., causal material reasoning); other taxonomic groups capable of performing object-assisted instrumental actions in diverse contexts may be relying on similar cognitive processes.

Intriguingly, some captive members of non-typically tool-using species are able to use objects as tools and possess cognitive skills similar to closely related species with a propensity for tool use in the wild. One way to experimentally test for the mental ability to represent the physical properties of objects (i.e., physical reasoning) is to use the two-trap tube task, a revised version of the tube-trap task. In its original version, the tube-trap task consists in a transparent tube, with food placed in the center and an underside trap into which the food will fall if moved into it. To access the reward, an individual has to maneuver an already inserted stick-tool to extract the food out of the tube while avoiding the trap. The two-trap tube task has an additional nonfunctional trap in which food can pass over a solid base, and the subject has to detect the correct side to avoid the functional trap and retrieve the food reward. When tested on the two-trap tube task, New Caledonian crows (i.e., a typical tool-using in the wild) successfully used a stick-tool to extract the food reward; interestingly, six out of seven captive rooks (i.e., members of the corvid family that do not appear to use tools in the wild) performed similarly (Emery and Clayton 2009). Tool use may be an evolutionary by-product of other adaptive cognitive abilities, rather than an originally adaptative mental trait. What is perhaps even more surprising is that highly proficient tool users in the wild, like chimpanzees, fail popular tests for causal reasoning, like the trap tube task. Chimpanzees learn to avoid the trap after around 80–100 trials, but do not appear to transfer knowledge between different trap problems (Martin-Ordas et al. 2008). Indeed, when the trap is inverted (i.e., the trap tube task is ineffective), chimpanzees keep adopting the previously learned strategy. Similar results have been found in humans, and the effectiveness of the trap tasks for testing for causal understanding has been questioned. In the end, researchers are left with an outstanding question: Is causal reasoning necessary to use objects as tools (and if so, to what extent)? The aforementioned results should also make us cautious when considering the assumption that tool use in humans and non-human animals has a common evolutionary origin and followed similar cognitive pathways of expression.

A necessary ingredient for the expression of flexible tool use is the *propensity* to manipulate objects, which is not only a reflection of anatomical features but emerges from a combination of psychological processes determined by extrinsic and intrinsic factors (Call 2013). Indeed, capuchin monkeys and squirrel monkeys have similar hands, but they markedly differ in their manipulative propensities and their abilities to use tools. Unfortunately, there is no clear consensus on the definition of the term "manipulative propensity," and systematic cross-species comparisons are made difficult by the use of different operational definitions. Manipulative propensity has been measured in terms of *amount* of object manipulation (i.e., frequency or duration), *complexity* of object manipulation (e.g., number of object combinations), or *variety* in the types of object-directed actions. As such, a given species' manipulative propensity may affect its ability to efficiently use tools across different contexts (i.e., flexibly). In the next sections, different extrinsic and intrinsic stimuli influencing the propensity and ability to use objects as tools are reviewed.

## Extrinsic Factors Affecting the Propensity to Manipulate Objects Instrumentally

### Ecological Factors

Food availability is one of the main drives in the propensity to manipulate objects, and thus it is not surprising that most instances of tool use occur within the behavioral domain of foraging activities (Shumaker et al. 2011). According to the "ecological necessity" hypothesis (Fox et al. 1999), tool use may have emerged as a need to exploit novel and hard-to-process food sources due to resource scarcity. Food scarcity may be due to ecological factors (e.g., seasonality), social factors (e.g., dominant individuals having priority of access to main food resources), and intrinsic factors (e.g., higher physiological demand during pregnancy and lactation). The diet of chimpanzees living at Bossou, Guinea, mainly consists of fruit pulp, but during periods of fruit scarcity, these animals rely on oil-palm nuts and pits, which are processed by two types of tool use: stone-aided nut-cracking and pestle-pounding behaviors (Yamakoshi 1998). The rates of tool use increase from 10% to over 30% during fruit scarcity, which indicates that tool-assisted extractive foraging is a necessary behavioural strategy for this population.

According to the "ecological opportunity" hypothesis, individuals should have the opportunity to use tools (e.g., presence of instrumentally-relevant objects or food sources that can be exploited by tool use; Fox et al. 1999). The population of orangutans living at Suaq Balimbing Research Station, in Sumatra, has significantly higher tool-assisted insect foraging rates, compared to other populations of orangutans living at different sites (Fox et al. 2004). The abundance of insects at Suaq Balimbing Research Station is higher compared to other locations, which supports the idea that propitious circumstances may have driven tool invention in this population.

Considering the previous two hypotheses, the need and opportunity to access embedded and rich food sources during seasonal periods of food scarcity in species with omnivorous diets and extractive foraging strategies may have selected for the emergence and refinement of specific object-assisted food-procurement behavior patterns, including tool use (see also: "technological intelligence" hypothesis; Parker and Gibson 1977). In capuchin monkeys, extractive foraging strategies follow seasonal patterns, with the tool-aided exploitation of embedded invertebrates concentrated during periods of food scarcity. However, the "technological intelligence" hypothesis has been challenged mainly because tool use is rare and its phylogenetic distribution is patchy among extractive foraging and generalist primate species (i.e., only a few populations of capuchins, cercopithecines, and great apes routinely use objects as tools in the wild). Similarly, alternative ecological and functional hypotheses only partly explain the occurrence of tool use across evolutionarily related species. Thus, although those hypotheses remain generally valid, ecological factors and the evolution of complex extractive foraging skills alone cannot explain the emergence and spread of tool use behavior in the wild.

### Social Factors

The social influences an individual is exposed to may also drive the expression of the instrumental manipulation of objects as tools. Several food-provisioned groups of Japanese macaques have been reported to customarily engage in a form of culturally maintained, playful, and seemingly functionless stone manipulation often referred to as "stone handling." However, it has been argued that the relatively relaxed dominance style of the captive Takahama group of Japanese macaques housed at the Kyoto University Primate Research Institute might have facilitated the innovation and diffusion of the only (documented) spontaneous and functional use of stone tools in this primate species, possibly derived from the daily practice of stone handling: unaimed stone-throwing behavior mainly expressed during periods of high disturbance and serving the function of amplifying the performer's agonistic display (Leca et al. 2008). Such differential social environments may alter not only the context of expression but also the significance of other tool use variants (Boesch 2003). In chimpanzees, the leaf-clipping behavior pattern is a tool-assisted communication signal that consists for an individual in repeatedly nipping leaf blades with its incisors and lips without eating any part of the leaf. This sound-producing display is culturally mediated and it acquired different social meanings that are population-specific: (1) in Mahale, Tanzania, it is a sociosexual display that serves the function of attracting potential mates; (2) whereas in Bossou, Guinea, it is used to initiate social play interactions; and (3) in Taï, Ivory Coast, it is an important mediator in the context of within-group male-male competition.

According to the "opportunity for social learning" hypothesis, higher levels of within-population social tolerance lead to greater manipulative propensities, because behavioral innovations, like tool use, can spread and be maintained across individuals (van Schaik et al. 2003). Social tolerance allows potential learners to be exposed to the mere presence of skilled group members (i.e., social enhancement), to the presence of tool artifacts previously employed by successful tool users (i.e., stimulus enhancement), and in some cases to demonstrators of the tool-assisted actions (e.g., emulation, imitation, and possibly teaching). The comparative analysis of behavioral data from captive rhesus, long-tailed, and Tonkean macaques showed a significant positive correlation between species-specific levels of social tolerance and the time spent manipulating novel objects, including tool use (Thierry et al. 1994). Similarly, the Goualougo Triangle chimpanzee population, in the Republic of Congo, characterized by a relatively complex tool-use repertoire, including instances of coaction (i.e., when an individual allows another to touch either the hand or part of the tool during use), exhibits levels of social tolerance and spatial proximity that are higher than other populations of chimpanzees (Sanz and Morgan 2013). Relaxed social environments enhance opportunities for behavioral coordination among group members, visual feedback from tool-using conspecifics, and access to the physical traces left at tool-using sites by previous tool users. Such favorable circumstances are conducive to direct and indirect social learning of tool use. In an experimental study aiming to explore the social processes underlying the acquisition of novel object-directed actions in captive capuchin monkeys, seven out of nine subjects preferentially touched the area of the apparatus previously manipulated by their group members (Matthews et al. 2010). Likewise, during an object-choice task, New Caledonian crows preferentially selected the tools previously used by a conspecific demonstrator, compared to other novel objects (Kenward et al. 2006). However, extrinsic factors alone do not suffice to explain the phylogenetic distribution of tool use behavior and a given species' propensity to manipulate objects in either playful or instrumental ways. Intrinsic factors, such as motivational processes, morphological adaptations, and individual history, play a vital role in a subject's proclivity for object manipulation and tool use.

## Intrinsic Factors Affecting the Propensity and the Ability to Manipulate Objects

### Intrinsic Motivation and the Role of Object Play in Tool Use

Broad structural similarities across various object-oriented activities (i.e., exploratory, playful, and instrumental) have been found in an extensive comparison of 74 species of nonhuman primates (Torigoe 1985). More specifically, the overall execution by adult long-tailed macaques of a probably functional activity (i.e., pounding an edible object – a hard-shelled nut – on a hard substrate) and a seemingly nonfunctional one (i.e., pounding a nonedible object – a stone – on a hard substrate) has very similar basic sequential movement components (i.e., upswing, adjustment, and strike; Pellis et al. 2019). Likewise, the fundamental motor building blocks of stone tool-assisted nut-cracking behavior in chimpanzees include actions that are typically observed in explorative and playful object manipulation in this species. Moreover, a number of experimental studies in nonhuman primates and children found positive correlations between the frequency of noninstrumental (either exploratory or playful) object manipulation and measures of success in subsequent problem-solving tasks involving the use of these objects as tools (e.g., shorter latency to succeed for the subjects with previous object-handling experience). For example, the ability to join sticks together to make and use raking tools in order to access out-of-reach food was improved by the prior playful manipulation of sticks in captive chimpanzees (Birch 1945).

The spontaneous manipulation of objects in a nonfunctional way (i.e., play and exploration) may contribute to an individual's propensity to use these objects in functional contexts. In a free- ranging and coastal population of Burmese long-tailed macaques in Thailand that routinely use stone tools to crack open shellfish, developmental data indicate the playful manipulation of lithic material by juvenile monkeys before learning to use stones instrumentally (Tan 2017). In this species, percussive stone-tool use may be facilitated by exploratory and non-instrumental stone- directed actions gradually incorporated into foraging activity. Within the *Macaca* genus, a cluster of macaque species belonging to the *Fascicularis* taxon have a natural propensity to manipulate stones in a playful context; this intrinsic motivation may promote the integration of stones in various behavioral domains, including their functional use in extractive foraging strategies – even though this hypothesis remains to be tested. In an experimental study addressing the role of motivational processes (and previous experience) in tool use performance in great apes, extrinsic motivation (i.e., food reward as an external foraging trigger) had a negative/inhibitory effect on tool-assisted problem-solving success, whereas intrinsic motivation (i.e., the internal neophilic drive to explore a novel, even empty, apparatus) shortened the latency to solve the tool-use task (Ebel and Call 2018). This result is consistent with studies showing that (1) high extrinsic motivation (i.e., higher interest in, and attraction to, a visible food reward during a test) decreases problem-solving performance, and (2) individuals in an atypical hunger state (e.g., due to food deprivation) performed more poorly in a food-rewarded tool task than individuals in a typical hunger state.

Play behavior, including object play, is also intrinsically rewarding, which may contribute to the maintenance of object-directed activities, particularly during the development. First, the frequency of object play is age-dependent: juveniles spend significantly more time playing with objects than adults). Second, the acquisition of flexible tool use is gradual and proceeds through several developmental stages; in long-lived animals, such as primates, it takes years for an individual to master specific and complex tool-use skills (de Resende et al. 2008; Lonsdorf 2006). During such a lengthy acquisition period, object-directed play may serve the function of maintaining high levels of intrinsic motivation (e.g., sustained interest in, and attention to, objects) in unskilled youngsters, before they can be externally rewarded as proficient tool users. Among great apes, who need several years of practice before mastering tool use (Lonsdorf 2006), chimpanzees and humans are the most frequent and versatile tool using species; interestingly, juvenile chimpanzees and children also engage in significantly more object than immature bonobos, which belong to their most closely related species, and a species that is not proficient in tool use (Koops et al. 2015). However, the propensity to manipulate objects is constrained by the physical *ability* to do it, which depends on the individual's anatomy.

## The Role of Anatomical Features in Tool Use Structure

While psychological processes affect the propensity to manipulate objects, anatomical features constrain object-directed actions. Not surprisingly, the most complex and various tool use repertoires are found in primates, and more specifically in humans, followed by great apes, whose hands possess the greatest potential for movement *complexity* and *dexterity* (i.e., grip and grasping postures; Shumaker et al. 2011). Manipulative complexity has been structurally defined in various ways, including manipulation pattern diversity, object-substrate combination, and bimanual asymmetric coordination. In a comparative study across 36 nonhuman primate species, it was measured by the cumulative ranking of occurrence of different categories of object manipulation, based on unimanual/bimanual actions, synchronous/asynchronous use of hands and fingers, and whether the same/different objects were handled (Heldstab et al. 2016). Species displaying more complex types of object manipulation (e.g., tool use) were also able to engage in lower levels of manipulation categories (e.g., grasping and holding). However, hands are not necessary for efficient tool use; morphological characteristics of the beak (e.g., depth, shape) play a major role in the manipulative complexity of tool-using corvids (e.g., New Caledonian crows, Goffin's cockatoos, keas).

Dexterity is the ability to solve a motor task precisely, quickly, and effectively (Bernstein 1996). The same action can be performed more or less dexterously, and an individual with higher manipulative complexity may still act with little dexterity, (e.g., a naïve individual learning a new handling skill). Dexterity requires sensorimotor coordination, which needs to be greater when the action is more complex (i.e., there is a higher number of degrees of freedom to control the moving parts of the body). Dexterity in tool use necessitates a high spatiotemporal organization of the movements performed by the body-plus-tool system (e.g., hand-plus-tool in primates, beak-plus-tool – occasionally coordinated with the foot – in corvids). However, an individual's relationship with a tool does not only result from the propensity and the ability to manipulate this object; it is also affected by the functional properties of this object. Through a variety of object-directed activities, the performer *experiences* the tool.

## The Role of Experiential Learning in the Acquisition of Tool Use

Inter-individual variation in the expression of object-directed activities, including flexible tool use, exists across most taxonomic groups (Kappeler and Kraus 2010), and in the extreme case, tool-use innovations have been documented only in one or few individuals within a species. In capuchin monkeys, individuals vary considerably in their tool use rate and success in experimental tasks, regardless of their age and sex classes (Fragaszy et al. 2004). In chimpanzees, tool-assisted foraging techniques, such as ant-dipping and termite-fishing, are acquired by individuals at different ages, and some individuals never master them (Humle et al. 2009). In the Suidae family, tool use has only been observed in few individuals of a captive population of Visayan warty pigs, and the use of sticks and barks as part of nest-building sequences was mainly expressed by lower-ranking group members including some adult females (Root-Bernstein et al. 2019). Exposure to, and *experiential learning* with, objects play an important role in the emergence of inter-individual variation in tool use.

Tool use acquisition is a continual developmental process in which an individual's understanding of the spatiotemporal relations between objects is mediated by exploratory interactions with the environment, through affordance learning (Lockman 2000). Affordances arise from the relation between a specific individual and a specific environment, with respect to achieving goals (Gibson 1979). For example, a stone affords throwing to an Egyptian vulture, pounding to a sea otter, and knapping to an Oldowan ancestral human. Likewise, object properties may be perceived differently by members of the same species. According to the "affordance learning" hypothesis, the perception of an object's physical properties determines its potential for manipulation, affording the means for goal-oriented behaviors (Lockman 2000). Watching a toddler banging an object on the ground is likely to be interpreted as playful practice for the future functional use of this object as a tool. Most flexible forms of tool use are acquired through long periods of time, during which the learner tinkers with the tool and the possibly functional consequences of its tool-mediated actions. During this critical phase of trial-and-error learning, individuals may perform irrelevant or incorrect actions, express an incomplete or misordered sequence of actions, use inappropriate tools or substrates, and apply their actions towards the wrong goals. Tool use acquisition proceeds through a developmental process of gradual elimination of unsuccessful attempts and honing of successful behavioral strategies.

From the perspective of "affordance learning," it might not be highly relevant to distinguish between an individual attempting to use an object as a tool and an individual engaging in object play. The "affordance learning" hypothesis stems from an ecological approach to the acquisition of tool use (Gibson 1988), which is better explained by a progressive specificity in perceiving and acting on the material world than a sudden insight into the instrumental consequences of object-directed actions. Developmental data indicate that, as children acquire further haptic experience (i.e., tactile feedback about the physical properties of objects), they become more selective in their object exploration. At 6 months (i.e., when functionally directed object manipulation has not emerged yet), infants engage in discriminate exploration when interacting with different objects, by modifying their actions depending on the object properties; for instance, they wave a bell with a clapper more often and more intensely than a bell without a clapper, or they squeeze more a spongy toy than a hard one (Palmer 1989). In the Sonso chimpanzee community in Uganda, where the use of sticks as tools has not been reported, growing individuals show decreasing interest in, and manipulation of, sticks, whereas they preferentially explore other objects that are later used as tools (Lamon et al. 2018). Likewise, during the acquisition of stone tool-assisted nut-cracking behavior, capuchin monkeys gradually learn to select and match the appropriate stones with the appropriate food targets based on the physical properties of these objects (e.g., size, weight, hardness, and resistance) as well as the geographical distance between them (Spagnoletti et al. 2011).

Exposure to, and experience with, objects in a noninstrumental context not only contribute to discovering information about the properties of these objects but also help refine the executive control when handling them in a functional manner, through practice and acquisition of manipulative dexterity (Lockman 2000). By repeatedly performing similar object-directed actions in an exploratory context, individuals acquire the sensorimotor coordination needed to become skilled tool users. As human infants develop, their object-mediated banging actions (i.e., the repetitive striking of a surface through up-down motion of the arm while grasping an object) become less structurally variable, and their movements gradually acquire the biomechanical characteristics of proficient tool-assisted percussive actions (e.g., hammering; Kahrs et al. 2012). Even though juvenile chimpanzees are capable of performing some of the behavioral building blocks of the stone tool-assisted nut-cracking activity, they will not master the complete and successful behavioral sequence until they reach adolescence. In rhesus macaques, repetitive tool-using actions gradually create novel neural projections in the brain areas that process and integrate information about the visual and somatosensory status of the training body-plus-tool system (i.e., visual, frontal, and parietal cortex; Hihara et al. 2006).

## Conclusions

Sophisticated cognitive abilities are not a necessary and sufficient requirement for the expression of all the tool use variants reported in this review. Therefore, an ideal definition of tool use should be devoid of any anthropocentric bias, such as the necessity for the performer to understand how or why a tool works. There is no doubt that tool use independently evolved in several taxonomic groups, as structurally diverse, functionally distinct, and phylogenetically rare behavioral specializations. However, the scarce and patchy distribution of tool use within the animal kingdom cannot be explained by claiming that this behavior is a proxy for intelligence. The expression of tool-mediated actions is the combined result of strategic behavioral responses to various ecological conditions (e.g., necessity, opportunity), sociodemographic variables (e.g., group composition and cohesion, interindividual tolerance), biological traits (e.g., morphological features), and psychological mechanisms (e.g., motivational processes, sensorimotor coordination, experiential learning). Yet, the relative contribution of each of these extrinsic and intrinsic factors to the emergence of tool use in a given species remains to be determined. Arguably, one of the most promising and integrative theoretical approaches to understanding the proximate causes of tool use is the affordance learning hypothesis. More data, beyond the primate taxon, are needed to test it.

## Cross-References

- ▶ Behavioral Flexibility
- ▶ Behavioral Variation
- ▶ Instrumental Learning
- ▶ Motivation
- ▶ Nut-Cracking
- ▶ Play Behavior
- ▶ Stone Tools
- ▶ Technical Intelligence Hypothesis

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