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TOOL USE IN ANIMALS

COGNITION AND ECOLOGY

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Tool Use in Animals

Cognition and Ecology

The last decade has witnessed remarkable discoveries and advances in our understanding of the tool-using behavior of animals. Wild populations of capuchin monkeys have been observed to crack open nuts with stone tools, similar to the skills of chimpanzees and humans. Corvids have been observed to use and make tools that rival in complexity the behaviors exhibited by the great apes. Excavations of the nut-cracking sites of chimpanzees have been dated to around 4000–5000 years ago. *Tool Use in Animals* collates these and many more contributions by leading scholars in psychology, biology and anthropology, along with supplementary online materials (available at www.cambridge.org/9781107011199), into a comprehensive assessment of the cognitive abilities and environmental forces shaping these behaviors in taxa as distantly related as primates and corvids.

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Part I

Cognition of tool use

1 Three ingredients for becoming a creative tool user

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The bird approaches the transparent vertically oriented tube and looks down its opening with apparent interest. Then it looks at the tube from the side and walks around the tube to look down into the opening with one scrutinizing eye once more. There is a worm located at the bottom of the tube, beyond the bird's reach. After a few seconds, the bird steps away from the tube, picks up a stick with its beak and inserts it down the tube's opening. Once inside, it grabs the tool again and applies downward pressure on it so that the tool dislodges the platform that is keeping the worm inside the bottom of the tube. The worm drops free from the bottom of the tube to be picked up by the bird, which quickly flies away.

Observations like this pose a double challenge to researchers in the field of comparative cognition. The first challenge is to explain why some species can come up with innovative solutions while others facing the same situation do not do so. For instance, pigeons presented with the same task as crows and left to their own devices may be incapable of producing the same solution, even after hours of exposure to the same problem. One possible explanation for this outcome is that this crow species, unlike the pigeons, may have a strong predisposition to using tools since this has offered it an adaptive advantage. In fact, the crow is in all likelihood a New Caledonian crow (*Corvus moneduloides*), well known for their propensity and dexterity at making and using tools to extract embedded food from substrates. The fascinating thing is that the above description is not about a New Caledonian crow, but a distantly related cousin, the rook (*Corvus frugilegus*). Rooks, unlike New Caledonian crows, do not usually use tools in this way, but they can do so in the laboratory, as Bird and Emery (2009) discovered. This revelation poses a second challenge to comparative researchers: How are rooks solving this problem? What cognitive mechanisms are responsible for the observed behavior and what experiences are necessary for this clever solution to emerge? Since all species are endowed with associative learning mechanisms, a key question to be explained is where interspecific differences come from. Nowhere is this challenge so acute as in the area of tool use in animals.

The main goal of this chapter is to discuss three ingredients that are sufficient, perhaps even necessary, to become a creative (i.e., flexible) tool user, defined as using multiple tools (not necessarily in combination) to solve multiple problems, particularly when tool-using solutions can be classified as innovations (see Reader & Laland, 2002). Possessing those ingredients may allow certain species that seemingly do not possess a propensity to use

tools in their natural habitats to become proficient tool users under certain circumstances. But before we get to the three ingredients I will briefly explore the relation between tool use and intelligence, and contrast two pathways by which even non-tool-using creatures can become proficient tool users. Then I will turn my attention to whether tool use can be considered a cognitive specialization, and will devote much of the rest of the chapter to exploring the cognitive mechanisms underlying flexible tool use. Surprisingly, there has been relatively little progress in the last 50 years in elucidating the processes that may underlie problem solving in general (and tool use in particular) in non-human animals. For those to whom my assertion may sound exaggerated, let me clarify that I am not referring to learning but to reasoning. I hope it will become clear in the rest of the chapter that these are two different processes that can play a role in problem solving. The comparative literature could have benefited from insights from cognitive psychology in this area, but such transfer of ideas has not taken place, at least not as much as it occurred many years ago. Therefore, one second overarching goal of this chapter is to bring closer data and concepts developed in cognitive psychology that can find some application in comparative psychology.

Is tool use an indicator of intelligence?

Tool use, defined as using an object to alter the position or form of another object or individual, has traditionally been regarded as an indicator of intelligence and complex cognition (e.g., Köhler, 1925; Thorpe, 1963; Parker & Gibson, 1979). In fact, before it was discovered that wild chimpanzees manufacture and use tools with regularity, some scholars considered tool using and tool making as a human Rubicon (e.g., Oakley, 1976) – something that separated humans from non-human animals. Even today, species that use tools seem to enjoy a special status, and new discoveries on tool-using behavior quickly grab the attention not only of academics but also of the mass media and the general public. From the point of view of animal intelligence, this fascination for tool use is perhaps a bit surprising given that other skills such as spatial navigation, which may involve equally impressive cognitive sophistication, do not enjoy such a prominent status.

One contributing factor to the special status of tool use is its narrow distribution in the animal kingdom. Although there are many species that use tools occasionally, and many more that with appropriate training can use tools, spontaneous and customary tool use is relatively rare among animals. Rarity, however, is not a synonym of intelligence, as there are many rare traits (e.g., electrocommunication) that are not assumed to entail advanced intelligence. Another contributing factor is that humans also use tools; in fact, it is safe to say that we are a species obsessed with tools and artifacts. By analogy, we may be prone to attributing some of our human cognitive qualities to those species that display a behavior that is strongly tied to our own species identity. Moreover, tool use has played such a pivotal role in theories of human evolution that seeing another species use tools automatically grabs our attention as it may provide clues about the evolution of technology.

Although the two previous arguments may have some appeal and explanatory power, they do not provide a strong case for tool use as an indication of intelligence. Other authors, however, have provided arguments grounded on the psychological processes involved in

tool use to support the idea that using tools is cognitively demanding (e.g., Piaget, 1952; Parker & Gibson, 1979). At a very basic level, using an object to affect a second object involves more elements, and consequently requires more coordination, than acting on the second object directly. It is easy to underestimate how cognitively demanding this kind of coordination can be. However, some studies have shown that simply changing the number of tools available and their position can substantially affect subjects' performance on trap tasks (e.g., Girdt *et al.*, 2008; Seed *et al.*, 2009). However, this still does not seem a good reason to single out tool use, given that other behaviors like spatial navigation also involve coordinating between the subject, multiple external entities and their relations.

Other authors have focused their attention on the suddenness with which some solutions appear in order to discuss their cognitive significance. Similarly, solutions that represent a significant departure from previous attempts would also fall into this category. There is indeed something enthralling about observing an individual facing a reward that is located outside of reach and after several unsuccessful attempts to get it, turn around and pick up a tool and use it to retrieve the reward. Even if we had witnessed the same animal finding another solution by changing their spatial orientation or position, the tool-use example would still convey a stronger sense of cognitive sophistication. However, it is important to emphasize that not all cases of tool use necessarily imply the cognitive sophistication described above. In fact, tool use is a very broad functional category that includes very different examples whose cognitive substrate may differ substantially between and within species.

Some animals use a single tool for a single purpose in a particular context. Modifying slightly the problem shows that those cases of tool use are best described as inflexible specializations. For instance, archer fish (*Toxotidae*) can use water to down insects located above the water level. However, archer fish, as far as we know, do not use this skill in any other context. In contrast, other animals are capable of using multiple tools for multiple purposes in multiple contexts. Unlike the case of tool specialists previously alluded to, here alterations of the problem space invariably produce changes in the behavior that help the individual to adapt to the new problem space. In some cases the problem space is even moved outside of their natural ecological niche and yet subjects still can solve the problem. For instance, orangutans (*Pongo abelii*) can use water to raise the level of a peanut floating at the bottom of a tube so that they can grab it (Mendes *et al.*, 2007). The rooks mentioned at the beginning of the chapter using tools to get food that is located outside of their reach (Bird & Emery, 2009) would also fall into this category. Thus, whereas some examples of tool use are best characterized as behavioral specializations, other examples appear to be behavioral innovations – a term that Reader and Laland (2001: 788) defined as “the ability to respond to novel circumstances or stresses with new behaviour patterns.”

It is this type of tool use that we have characterized as behavioral innovations that may be more properly labeled as intelligent because it possesses two key features: adaptability and creativity. Individuals are not only able to use old solutions to solve novel problems but also can generate new solutions for old problems when the original solutions no longer work, or even produce new solutions for novel problems. In some cases such solutions do not simply entail using a tool, but also manufacturing the tool or using a sequence of

several tools to achieve a particular goal (e.g., Mulcahy *et al.*, 2005; Wimpenny *et al.*, 2009; Taylor *et al.*, 2010). In some cases, individuals can anticipate problems with the tools and they can select novel tools before having obtained feedback on how effective they are, just based on their features (e.g., Marín Manrique *et al.*, 2010, in press; Marín Manrique & Call, 2011). Finally, some species such as the great apes can use a tool for multiple purposes, and one purpose can be served by multiple tools.

Traditionally, primates – the great apes and capuchin monkeys (*Cebus apella*) in particular – were the best examples of creative tool users. In the last decade, however, birds – more specifically corvids – have emerged as serious contenders for the title of most creative non-human tool user on earth. New Caledonian crows in particular, which use tools to extract embedded food, manufacture hook-shaped tools with various materials (Hunt, 1996; Weir *et al.*, 2002). They can also use tools in sequence, such as using a short tool to get a longer one that can be used to get the food (Wimpenny *et al.*, 2009; Taylor *et al.*, 2010). Recently they have also been reported to use tools not just to obtain food but also to investigate their environment (Wimpenny *et al.*, 2011). We devote the remainder of this chapter to exploring the cognition underpinning flexible tool use.

Two routes for becoming a tool user

Despite its restricted appearance in the animal kingdom, with proper training numerous species that do not usually use tools can become proficient tool users. Some can even learn to use tools in sequence and distinguish the features of good and bad tools. How they manage this achievement is a different matter. Following Maier and Schneirla (1935) we can distinguish two main ways in which a species can solve a problem: learning and reasoning. Learning entails combining contiguous experiences. For instance, an individual who initially showed no preference for pulling from two parallel strings develops a preference for pulling the string that is closest to the food to which it is tied. Here the subject develops a preference for selecting those responses that are reinforced and discarding those responses that are not reinforced or negatively reinforced. Thus, reinforcement is the glue that binds stimuli and responses together. Although this is a very powerful mechanism for acquiring new responses, it also has a serious limitation. There has to be spatio-temporal contiguity between stimuli, responses and reinforcement for these elements to effectively bind together.

The other way to become a tool user is reasoning, which Maier and Schneirla (1935) broadly defined as combining separate experiences. For instance, a subject is given the opportunity to explore one part of a maze on one day and on a separate day she is allowed to explore the rest of the maze. Later on, the subject is tested on whether she can find the most efficient route to go from point A to point B, which entails navigating the entire maze, not just a part of it. Here we can distinguish between acquiring information in the absence of reinforcement but in the context of exploration and combining the information to find a solution. Obviously, information that has also been acquired by reinforcement can later be combined with information acquired through exploration. This means that learning and reasoning are not necessarily mutually exclusive. In fact, both learning and reasoning can

contribute to problem solving, of which tool use is a particular example. Katona's (1940; see also Wertheimer, 1959) distinction between reproductive and productive thinking is relevant here. Reproductive thinking entails applying familiar procedures to solve problems that have been encountered before, or slight variations on those problems. In contrast, productive thinking entails inventing new procedures for solving a problem, either familiar or unfamiliar.

Learning and reasoning have things in common and things that distinguish them. Both mechanisms have in common that experience plays a crucial role for solving problems. Individuals engaged in trial-and-error learning do not engage in every possible attempt. Often their attempts are canalized and they are likely to first try things that have worked in the past in similar situations. Similarly, reasoning does not work in a vacuum of experience. Indeed, experience is necessary for reasoning to occur. According to Wertheimer (1959) the crucial question in problem solving is not whether past experience plays a role or not, but what kind of experience is implicated in generating solutions, blind connections or structural grasp. Thus, the distinction between both mechanisms (or between reproductive and productive thinking) is not on whether one is based on experience and the other one is not, but on what type of information is acquired and how it is managed to produce a solution to the task. This distinction is important, but it has often been neglected by comparative psychologists.

One crucial distinction between learning and reasoning lies in the amount of separation that may exist between two experiences and yet be able to combine them to produce a novel solution to a problem. At the most basic level, separation is strictly determined by spatio-temporal parameters. The closer events occur in time and space, the more likely they are to become associated. For instance, for instrumental learning to occur, responses and reinforcement have to occur in close temporal proximity, whereas this is not a necessary condition for reasoning. At a more abstract level, separation between experiences may be determined by their "symbolic" distance. Learning can cope reasonably well with deviations from stimuli dimensions, such as color or sound frequency. For instance, pigeons trained to peck on a blue disc show some stimulus generalization to blue-green discs. However, in some cases the new stimuli do not share perceptual features with familiar ones, but share instead functional features. For instance, although a hole on a platform and a barrier on a platform both impede the displacement of an object from point A to point B on the surface of the platform, they have different perceptual features. It is less clear that stimulus generalization, originally developed to account for coping with variations within stimuli dimensions, is also responsible for categorizing the hole and the barrier as equivalent from a functional point of view. Wertheimer (1959) argued that focusing on physical features could enable the transfer to highly similar features, whereas focusing on structural features could enable transfer to a greater variety of problems that differ in terms of physical features but share structural features. In both cases connections are established by similarity, but the nature of this similarity is either physical or structural. In the case of the barrier and the hole mentioned before, seemingly disparate stimuli (a barrier and a hole) are related because both impede the progression of the food on the table. In this sense, their symbolic distance (or functional distance) is smaller than the perceptual distance that exists between a hole and a barrier. Note that to

be able to reduce the distance, and therefore facilitate the combination of separate experiences, the mind has developed a new type of representation that enables the system to classify both a gap and a wall as obstacles toward a goal. Being able to conceive objects and events at different representational levels is therefore one important way to facilitate connectivity, thus greatly enhancing the ability of a system to put together disparate pieces of information.

Are learning and reasoning the same process?

Over the years there have been several attempts to reduce these two processes into one (e.g., Maltzman, 1955; Epstein *et al.*, 1984; Weisberg, 1986). However, by conflating both mechanisms there is the danger of losing sight of one of the most important aspects of reasoning: relating disparate pieces of information. After all, if all there is to problem solving is trial and error and learning via reinforcement, automatic chaining and/or resurgence (see Epstein, 1987), one still has to explain why rooks can solve the tool-using task and pigeons presumably cannot. Some authors have argued that a pigeon (*Columba livia*) can solve problems just like chimpanzees (*Pan troglodytes*) by using the same learning mechanisms indicated above. For instance, Epstein and colleagues showed that pigeons were able to solve problems with multiple steps comparable to those in which chimpanzees stacked boxes under a banana hanging from the ceiling, beyond their reach. In the final solution the performance of the pigeon is truly impressive. Faced with a target that is located too high and out of reach, the pigeon diligently pushes the box under the target, hops onto it and triumphantly pecks at the target.

Despite the apparent similarity between the pigeon and the chimpanzee performance, the cognitive processes involved in the solution could be quite different. Simply put, automatic chaining is not equivalent to reasoning as is intended to be used here (see also Ellen & Pate, 1986). One crucial distinction is that chimpanzees, unlike pigeons, were not shaped to respond to each task separately before they were presented with both tasks in combination. As Epstein and colleagues convincingly showed, a pigeon that had been shaped to respond to two tasks separately could combine them to produce a solution based on chaining one response after the other in the absence of trial and error. However, one crucial aspect that was missing from the pigeon's behavior was spontaneity. It is true that the pigeons had never faced the target located at a higher position, and therefore the pigeon showed flexibility when it was able to adapt and solve this new challenge. But the key question is whether pigeons would have spontaneously produced those chains of responses without the benefit of having been reinforced for each task separately. The answer to this question seems to be negative, since pigeons failed to solve the task when one of the components was not trained (Epstein, 1987).

Chimpanzees spontaneously stack boxes in the context of play, which provides them with crucial experience that later they will be able to use for problem solving (Birch, 1945). The role of experience in problem solving has often been misunderstood and used as evidence that learning rather than insightful problem solving was responsible for the observed solutions. However, gestalt psychologists were quite clear in the crucial

role that experience played in problem solving, both in terms of facilitating and hindering potential solutions (e.g., Duncker, 1945; Köhler, 1967). Accordingly, solutions cannot be reduced to automatic chaining simply because experience is an integral part of problem solving. Chimpanzees do require experience to produce insightful solutions, but note that such experiences are not identical to those later required to solve a task. Additionally, those experiences that will later be used to solve a task were often acquired in the context of exploratory play. Acquiring and using this information is quite different from training the pigeon to move the box under the target. All the experiences that the pigeons received were associated with food in the same context. Moreover, a pigeon placed in an experimental box experiences reduced attentional competition for stimuli. In fact, the experimenter selects for the pigeon both what stimuli to pay attention to and what responses to produce. This is obviously a much simpler problem than the one faced by chimpanzees because the number of possible combinations is greatly reduced. The real challenge would be to know whether pigeons placed in the same situation as chimpanzees and left to their own devices would produce a solution to the problem on their own.

The previous discussion, however, should not be taken as evidence that chimpanzees can engage in reasoning whereas other animals such as pigeons or rats cannot. On the contrary, there is evidence from other studies suggesting that rats use reasoning in spatial navigation tasks. In fact, Thorpe (1963) noted that insightful problem solving (and perhaps reasoning in general) may be widespread among animals and not restricted to a few species like chimpanzees that have been traditionally considered “smart” ones.

Is tool use a cognitive specialization?

To answer this question we have to go back to a distinction we made earlier in the chapter. For some species, tool use is best understood as a specialization analogous to other behavioral specializations, such as a fear grin in macaques, or morphological specializations such as the elongated beaks of hummingbirds (*Trochilidae*). In this sense, the use of stones in Egyptian vultures (*Neophron percnopterus*) to crack open ostrich's eggs, and the use of stones in digger wasps (*Sphex* spp.) to block the entrance of their burrows would qualify as tool-use specializations. Specializations are extremely efficient at accomplishing a particular function, typically hardwired, perhaps even based on a modular architecture, but they are also relatively inflexible.

Labeling cases of tool use as behavioral specializations should be revised if it can be shown that those species could spontaneously (without human intervention) apply their tool-using skills outside of their canonical ecological contexts. A first step toward increased flexibility and away from specialization consists of using tools for more than one function, especially when those new uses can be classified as innovations. For instance, if Egyptian vultures were to use the stone to cover the food from the prying eyes of competitors, or drop the stone against a predator/competitor to drive them away. In such cases, the label “specialization” that we have provided should be revised, especially if multiple non-canonical uses are observed.

Those cases in which individuals use multiple tools for multiple functions represent an even stronger challenge to the notion of specialization. Note that the key here is not displaying multiple cases of one tool for one function, but cases in which multiple tools are used for multiple functions, that is, when a tool and its function appear dissociated. Particularly interesting are double dissociations in which a particular tool is used for multiple functions (e.g., a stone to crack open nuts, to throw during agonistic displays) and a function is served by multiple tools (e.g., nut cracking with a stone or log). Such means–ends dissociation is one of the key indicators of intentional and flexible behavior. For those species displaying this kind of flexible tool use, it is unlikely that tool use is based on a narrow cognitive specialization as it was just described for Egyptian vultures and digger wasps. Instead, it is likely that tool use in these species is based on the same sensorimotor and conceptual abilities that can be recruited to solve a variety of problems, not just tool-using problems.

Seemingly distinct tasks such as spatial detours and tool use are considered equivalent from the point of view of problem solving (e.g., Köhler, 1925). Although some may argue that this putative similarity is purely functional, there is evidence showing that spatial and stimulus discrimination problems may recruit some of the same cognitive resources in terms of inhibitory and motor control (Walker *et al.*, 2006). Another case in point is the relation between gesture production and tool use. Focusing on apes, many of the features that enable flexible tool use can also be found in the way they use gestures. Not only do gestures display a means–ends dissociation like the one described for flexible tool use (Call & Tomasello, 2007), some neurophysiological evidence indicates that the same motor control areas are recruited both to use tools and to produce gestures (Roby-Brami *et al.*, 2012). Moreover, although much of the work on problem solving in rodents was mainly based on spatial tasks, the conclusions were similar to those arrived at by those scholars investigating tool-using primates.

Contrasting species that routinely use tools with their close relatives that do not use them can also be very informative. Although bonobos (*Pan paniscus*) and rooks do not normally use tools to obtain food in their natural habitats, they can do so if the situation (in the laboratory) requires it. In fact, they can be as proficient as chimpanzees and New Caledonian crows, respectively, which are habitual tool users in the field. Tebbich (Chapter 7) also found that woodpecker finches (*Cactospiza pallidus*), which use tools quite proficiently, do not appear to differ in cognitive abilities from small tree finches (*Cactospiza parvulus*), a species that does not use tools. Although future research may uncover differences between species, currently tool use in this taxon may be best conceived as a manifestation of the existing cognition rather than a specialization that evolved to use tools. Reader and Laland (2002) reached a similar conclusion when they argued that tool use and social learning were best understood as manifestations of general intelligence rather than special processes. Reader and Laland (2002) also showed a correlation between innovation, tool use and social learning in primates. This finding is interesting because it relates acquiring information (via social learning) with using information in innovative ways, of which tool use is just one manifestation. It would be equally interesting to know whether those species also show a strong exploratory tendency and play behavior.

The previous discussion, however, should not be taken as evidence that all species process information in the same way. Differences between species do exist (but see Macphail, 1987), but they have not evolved as a consequence of tool use. At the risk of oversimplifying the issue, this means that our rook–pigeon dichotomy is more virtual than real. If a rook could see the world through a pigeon’s eyes, it would behave like a pigeon. This idea is certainly attractive from the point of view of simplicity: a common processing architecture for all species paired with a different input system. However, and without denying the importance of selecting certain types of information, one cannot ignore the fact that information still undergoes massive processing after input has occurred. Even if two individuals paid attention to the same stimuli, the way they were later processed may produce very different representations. Moreover, even if two individuals created equivalent representations, they may also differ both in what representations they chose to use and in their ability to relate them with other existing representations. Making a clear-cut distinction between input and processing becomes even more problematic when one considers that input can also largely be determined by the pre-existing representations that lead organisms to perceive stimuli in certain ways.

Psychological ingredients to be(come) a creative tool user

Spontaneity, innovation and flexibility are some of the key labels that we have used to characterize the behavior of species that solve problems in creative ways. Such labels apply not just to tool-using problems but also to other kinds of physical and social problems. In this last section of the chapter we re-focus our attention on tool use in particular, and list three key ingredients that would make a species an adaptable and creative tool user.

Information hoarding

The first ingredient is information seeking and hoarding. Many species acquire responses based on positive or negative reinforcement. Acquisition of responses by secondary reinforcement (i.e., features associated with features that are associated with reinforcement) would also belong to this category. Thus, learning based on reinforcement is an important source of useful knowledge. However, information can also be acquired in the absence of reinforcement. In fact, for some species this non-reinforced pathway may be its major source of information. Therefore, a predisposition for exploration and latent learning are important sources of information even in the absence of reinforcement. In fact, information acquired in non-goal-directed contexts is often crucial to later solve goal-directed problems. For instance, Birch (1945) reported that chimpanzees that were given the opportunity to manipulate objects in the context of play were more skillful at later solving tasks that involved those objects than chimpanzees that did not have that experience. Similarly, there is a literature on latent learning showing that rats that are given the opportunity to explore a maze (in the absence of reinforcement) prior to being tested on that maze learn faster than rats that

are naive to the maze (see Thorpe, 1963). Moreover, the use of the information is quite flexible as they can solve problems that involve connecting different experiences to produce the most efficient solution.

Some authors (e.g., Thorpe, 1963) have established a strong connection between latent learning and insightful problem solving since latent learning may be the basis for deploying adequate information. Information acquisition can occur by observing the consequences of our own or others' behavior. Even actions that fail to produce the desired outcome are often a good source of information to reach adequate solutions because they can reveal relations that we had not mentally entertained, but once they are perceived, they can be comprehended and used. Learning about the consequences of others' behavior is an equally good source of information since others' behavior can also reveal relations between the elements of a problem. In fact, such appreciation of information is the basis for emulation learning.

One advantage of information acquired in the absence of reinforcement is that it may be more amenable to being used in more flexible ways when the situation demands it. In other words, knowledge that is associated with the delivery of a reward may become encapsulated and therefore less accessible than knowledge based on exploration and play. That play and exploration may perform a crucial role in the acquisition and storage of information that can be used for later problems is not a new idea (e.g., Bruner, 1972). However, knowledge acquired by exploration in the absence of reinforcement may also have its limitations since it may be difficult to recruit for solving problems compared to knowledge that has been associated with reinforcement, which works well with familiar problems and may even generalize to similar problems.

The information stored, however, can be of different types. Two organisms witnessing the same event, even if they belong to the same species, may encode it in different ways. Upon witnessing an experimenter hiding a toy under one of three distinct containers, one-year-old human infants, just like non-human great apes, focus on the spatial coordinates of the hidden toy when they are allowed to retrieve it. In contrast, three-year-old children focus on the features of the container and they search for the toy under the container where the object was hidden, regardless of its current spatial position (Haun *et al.*, 2006). Of particular interest in the case of tool use is information about object–object relations, or so-called structural representations which deal with relations between objects (Seed & Call, 2009). These representations specify functional properties of objects, typically in relation to other objects (e.g., solidity, connectivity). These structural representations contain different information from so-called perceptual representations, which refer to the configuration or appearance of objects, not their functional properties. Thus, one can represent one object next to, on top of, or affecting the position of, another object. In all cases, the perceptual information is the same but the representation formed differs dramatically.

There is some evidence showing that animals differ on how much they use these two different types of information. Presented with the string task, pigeons solve the problem by encoding the configural information, whereas apes encode not just the perceptual appearance—their analysis is also about object–object interactions (Seed *et al.*, in press). Apes interpret the food as the cause of the noise made by a baited cup when it is shaken, whereas dogs do not

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