

Animal Tool-Use

Minireview

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The sight of an animal making and using a tool captivates scientists and laymen alike, perhaps because it forces us to question some of our ideas about human uniqueness. Does the animal know how the tool works? Did it anticipate the need for the tool and make it in advance? To some, this fascination with tools seems arbitrary and anthropocentric; after all, animals engage in many other complex activities, like nest building, and we know that complex behaviour need not be cognitively demanding. But tool-using behaviour can also provide a powerful window into the minds of living animals, and help us to learn what capacities we share with them — and what might have changed to allow for the incontrovertibly unique levels of technology shown by modern humans.

The notion of ‘man the tool maker’, that we alone in the animal kingdom manufacture and use tools, has long been known to be false. The first blow was struck by chimpanzees, which Jane Goodall famously described fashioning tools to fish for termites [1]. Since then the flood-gates have opened. Chimpanzee technology has received the most attention and is wide-ranging: for example, they use stone tools to crack open hard nuts, strong sticks to dig in the ground for tubers and underground bee hives, and sharpened sticks to spear bush babies sleeping in tree holes (for a recent overview see [2]). Perhaps unsurprisingly primates stand out among mammals as the most frequent tool-users. Like chimpanzees, capuchin monkeys use stones both for nut cracking and digging [3]. Tools can extend the reach of the senses as well as the grasp: gorillas, when wading through water, use stick tools to test its depth. Acts of communication can also be enhanced by tools: orangutans use a handful of leaves to deepen the pitch of one of their calls. Tools can be protective: a chimpanzee may use a stick to investigate a fire (Figure 1), and orangutans use small sticks to rid *Neesia* fruits of their irritant hairs when extracting the seeds inside. And protection can also be important when catching prey, as when chimpanzees dip with long sticks for ferocious driver ants marching along the forest floor. Dolphins in Shark Bay carry sponges over their rostrums when foraging on the ocean floor, perhaps for a similar reason (Figure 2) [4].

Such remarkable behaviour is not the sole preserve of primates or even mammals: some of the most impressive non-human tools are made by New Caledonian crows, a member of the Corvidae, a large-brained family of birds. New Caledonian crows extract grubs from tree holes using two distinct kinds of tool [5]. One variety is cut from the leaves of *Pandanus* (Figure 3). The other variety is made from twigs by removing all side branches from the central stem except one at the distal end, which is instead cut near the base and then sharpened to form a hook.

Defining Tool-Use

A case of tool-use seems intuitively easy to identify, but a suitably precise definition has actually proved hard to pin down because of the problem of borderline cases. For instance, a widely-used definition is the use of an object “to alter ... the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use” [6]. Several species (chimpanzees, capuchin monkeys and elephants) use branches or leaves to rid themselves of flies or parasites; but some chimpanzees use a vine for this purpose. The vine is not a detached object and would not ‘count’ as a tool, but is there a meaningful difference? Yet if we admit the vine, then perhaps the use of a scratching post by a cow or horse should count, and tool-use starts to bleed into any behaviour involving the external environment (for example, climbing a tree or building a nest). Water is another slippery case, as revealed by a problem-solving task given to orangutans and later to rooks. In both studies, a food reward was placed at the bottom of a transparent tube, out of reach of the subject, floating in a small volume of water [7]. Orangutans brought the food within reach by spitting more water into the tube, while rooks added stones, raising the level of the water until they could reach the reward with their beaks [8]. Were the rooks displaying tool use but the orangutans not? Archer fish, which spit jets of water to dislodge insects from the vegetation above them, are not usually considered tool-users. Nor are birds, such as seagulls and ravens, that drop encased food (shellfish, nuts, eggs or bones) from a height onto a hard surface to crack them open; but is this really different from capuchin monkeys or chimpanzees throwing sticks and stones, or using stones to smash open nuts [9]?

Despite the seemingly arbitrary nature of the distinction, using a tool as *an extension of the body* may have particular consequences for psychological processes such as perception, attention and cognition, because the periphery of the body is thereby changed in mechanical and sensory capabilities. Recent research suggests that, in humans and monkeys, this extended motor capability is followed by changes in specific neural networks that hold an updated map of body shape and posture [10]. As such, the classic definition retains its usefulness. Some borderline cases, such as sea otters smashing shellfish on a hard surface, are sometimes referred to as ‘proto-tool-use’: this identifies potentially interesting behaviour in which an outcome is achieved via a secondary object or substance, albeit not something defined as a tool. (And the usefulness of this distinction is reinforced by finding that, among birds, ‘true’ tool-users have larger brains relative to their bodies than proto-tool-users [9].) For the comparative psychologist, the semantics of which behaviour should ‘count’ seems less important than finding candidate cases of an animal solving a problem for which evolution has not provided a rigid morphological or behavioural adaptation: a context in which general cognitive abilities, like learning and reasoning, may be recruited.

Tools and Cognition

Human tool-making is characterized by an understanding of the physics of our bodies and surrounding objects, and an

ability to plan a complex sequence of actions to achieve a distal goal. Tool-use can result from far simpler mechanisms, such as inborn dispositions and trial and error learning [11]: but can all animal tool-use be explained in that way? Or do we see the evolutionary roots of human cognition in animal tool use?

Causality

We can recognize an animal's target outcome: when it pursues that outcome directly, and ceases to act when it has been achieved. But does that mean that the animal has an internal *representation* of the goal 'in mind', and *knows* that its actions will cause it to follow? The difficulty is captured by two examples. Baboons throw rocks at predators, with the result that the predator is deterred. Do baboons recognize that being pelted with stones would cause the predator to flee, and throw them with that intention? With a primate, the tendency is to assume that the answer is yes, based on their large brains and their close relationship to humans. But what about the ant-lion larva, which flicks grains of sand at prey on the edge of its trap, causing them to fall in? Our intuition is that this behaviour, despite its surface similarities, has a different underlying cognitive mechanism: but does it? An isolated observation of tool-using behaviour cannot tell us much about the animals' appreciation of the underlying causality.

A case for goal-directedness has been made for laboratory rats by training a pair of instrumental actions, such as chain-pulling for one food type and lever-pressing for another. When one food was devalued, for example by pre-feeding it to the rats, they homed in on the action that produced the other food: their action was therefore not triggered simply by force of habit, but by the context in which they were previously rewarded. Similarly, if the food linked to one action began to appear just as often when the rat performed the action as when it did not, the rats gave up that action but continued to perform the other; but if the delivery of 'free', non-contingent food was preceded by a signal, both actions continued to be performed. The rats' actions satisfy the criteria for goal-directedness: sensitivity to the incentive value of the rewards on offer and the causal relationship between their actions and their specific outcomes [12]. In other words, rats represent what they want and what they have to do to get it.

If the behaviour of the ant-lion larva is hard-wired or habitual rather than goal-directed, we would expect the larva to behave differently to the rats: it might continue flicking sand at insects appearing at the edge of its trap even if they had become inedible, or if the contingency between flicking sand and insects falling was disrupted. That would suggest that tool-use in this species is inflexible and non-selective; unfortunately, these sorts of experimental manipulations are difficult to carry out in natural settings and have seldom been done. The tool-use of chimpanzees, capuchin monkeys and New Caledonian crows, at least, displays the hallmarks of goal directedness: selectivity, choosing or tailoring the tool to suit the specific goal at hand, and flexibility, such as using several means to achieve the same end [13,14]. But there is an inborn component to the tool-using behaviour of even these accomplished and relatively large-brained tool-users. They begin manipulating tool objects (sticks or stones) from a young age, even in the absence of a goal object [15,16]; and, despite the impressive ability of New Caledonian crows to use up to three tools in

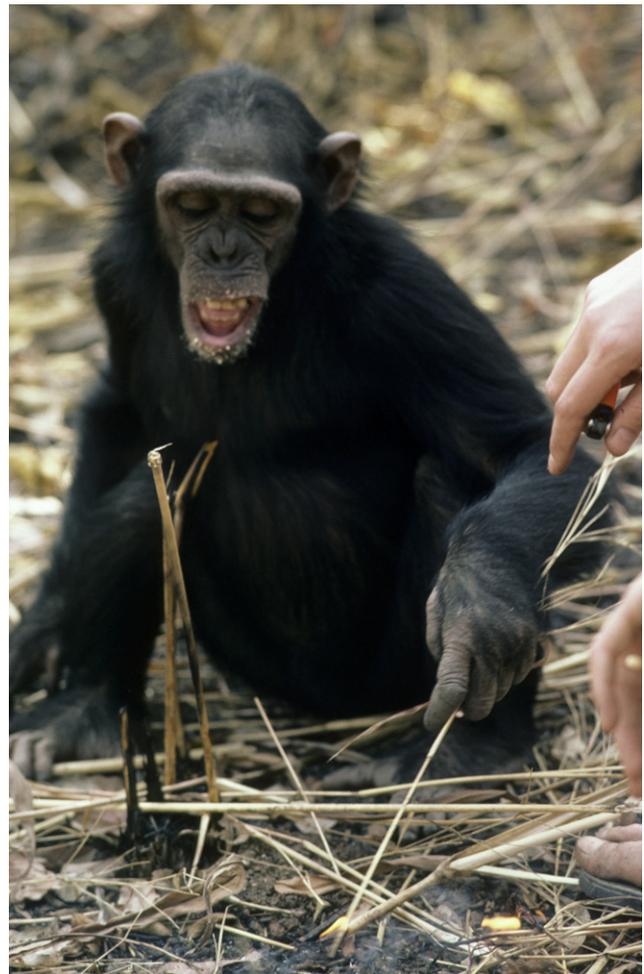


Figure 1. A chimpanzee uses a stem to poke a small fire.

Lit by a person, a small grass fire interests but frightens a rehabilitant chimpanzee, whose first reaction is to use a tool for investigation. (Photo: Richard Byrne.)

sequence in laboratory experiments (using smaller tools to gain tools long enough to reach a reward), they will sometimes use small tools to fish for longer ones when there is no ultimate food reward present [17]. Goal-directedness is not a simple all-or-nothing issue.

Physical Reasoning

A special case of causal reasoning concerns the physical process by which a tool effects its outcome. Even a goal-directed tool-user might know that her action caused an outcome, without knowing how or why it worked; in fact this is how the less technologically-minded among us use sophisticated tools like laser pointers or microphones. But humans are also capable of physical reasoning, for example unbending a coat-hanger to fish for keys that have fallen out-of-reach: fashioning a tool with the right physical properties to solve a problem. Betty the New Caledonian crow showed the same creative modification in the laboratory, bending (and unbending) wire to make a suitable hook or probing tool [18]. Selective tool modification is also seen in primates (Figure 4): Gombe chimpanzees, for instance, famously convert a leafy vine into a thin, flexible probe-tool for



Figure 2. A dolphin 'sponging'.

It is thought that dolphins at Shark Bay, Australia, have developed a tradition of using sponges to protect their sensitive rostrums when foraging on abrasive parts of the sea floor. (Photo: Michael Krutzen.)

termite-fishing, but make a stiffer rod for ant-dipping [1]. Behaviour like this raises the intriguing possibility that the animals represent the physical properties and forces involved in the tool-using event in an abstract, conceptual way: in terms of properties such as rigidity, continuity, and connectedness. The simpler alternative is that the animals' thinking is grounded in perceptual features of the objects (their shape, feel, or spatial orientation). Psychological experiments have often capitalized on tool-using (or proto-tool-using) behaviour to try to tease these alternative explanations apart.

For many years, laboratory studies gave results supporting the simpler explanation. Even chimpanzees seemed to be using perceptually-based information rather than an abstract notion of object properties [19]; for example, in the 'trap-tube' task, in which the subject needs to push a piece of food out of a horizontal tube away from a trap, the one chimpanzee that learned to do so continued to use this strategy even when the tube was inverted and the trap was non-functional. A capuchin monkey that solved the trap-tube task did likewise [20], as did a New Caledonian crow [21]. It seemed that even these successful individuals had avoided the trap as a perceptual feature but had not encoded its functional significance. Similarly, although chimpanzees would choose a complete tool over a broken one when the break in the wrong tool was clearly visible, they chose indiscriminately if the ends of the broken tool were aligned in front of them [19]. New Caledonian crows, required to make a tool to fish for food in transparent wells, first made a tool of intermediate length and only made a longer one if the first one was too short [22]. When presented with a tool made from barbed *Pandanus* leaves, positioned in the baited hole but with barbs pointing in the wrong direction, these crows first attempted to use the tool, and then either abandoned it or only switched it around after several unsuccessful attempts, even over repeated trials. In the wild, it seems that their successful use of the barbed leaves comes from the procedure by which they rip the tool from the leaf and insert it into the hole [23]. Yet when the same experiment was run with hooked stick-tools, most of the same crows

immediately repositioned the tools before attempting to use them: the picture is not straightforward.

The fact is that the use of simple heuristic procedures does not preclude the capacity for more sophisticated strategies. Quick and simple strategies offer evolutionary advantages for animals in a harsh and competitive natural environment. Humans can also use 'fast and frugal' heuristics to solve problems, rather than slow and effortful reasoning processes, and indeed this approach is often more efficient [24]: how many of us have tried a key

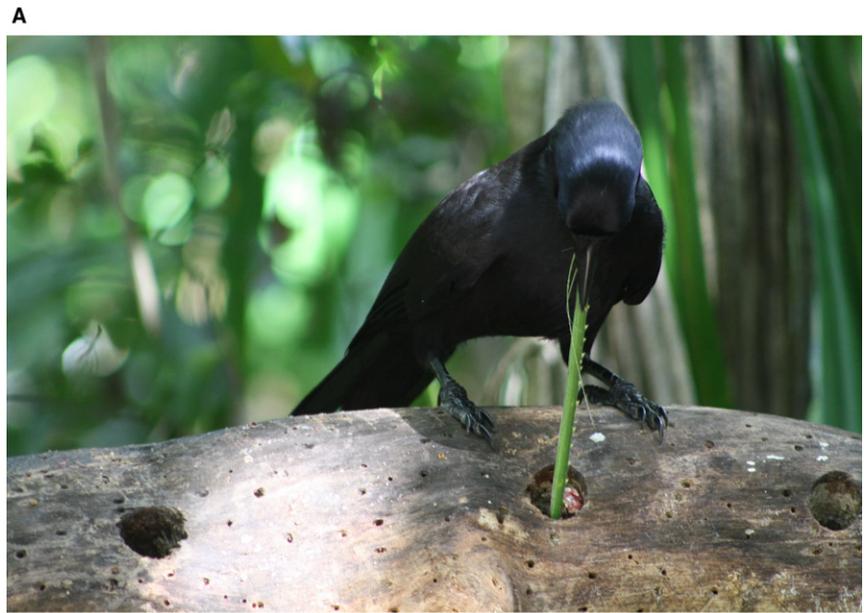
without bothering to check first which way up it needed to be used? Perhaps the most powerful illustration of the danger of reliance on negative results comes from a study in which adult humans were given the trap problem: just like the tool-using animals, most continued to avoid the inverted trap [25]! And indeed, it does no harm to do so. Although humans would no doubt use more sophisticated strategies in many of the other situations in which animals 'fail', would this reflect a qualitative difference in our cognitive make-up or a difference in our tendency to employ effortful thought? Are there any contexts in which animals go beyond simple strategies?

A re-designed trap task, which pitted physical reasoning against perceptually based strategies, was used with rooks [26] and chimpanzees [27]. To avoid a trap, in some conditions subjects had to move the food across a plastic surface to an exit at the side, and in others they had to push it down an uninterrupted channel to an exit at the bottom. In a critical contrast, the same feature (the plastic surface) had to be treated differently depending on whether it played the role of a supporting surface (when the side exits were open) or barrier (when they were closed). Most chimpanzees and rooks did not make this distinction, suggesting reliance on the surface-level appearance of the task; but one animal from each group did, apparently having encoded something about the key physical properties. Chimpanzees (and also New Caledonian crows) were able to transfer their success in one trap problem to another one with very different perceptual features, also implicating abstract representational capacities [27,28]. Nevertheless, in all of these studies there is notable individual variation, the cause of which remains to be investigated.

Capuchin monkeys have also been shown to treat the same visual feature differently depending on task-relevant physical properties [29]. Wild capuchins were presented with stones at some distance from a nut-cracking anvil: they quickly selected large, heavy, robust stones to transport, seemingly identifying the effective stones through visual inspection. When presented with novel, man-made 'stones', which looked identical but differed in density and

Figure 3. Tool use by crows.

(A) A New Caledonian crow uses a *Pandanus* tool. (B) A selection of step-cut *Pandanus* tools made by the crows. New Caledonian crows cut tools from the leaves of *Pandanus*, which are edged with a convenient row of spiny hooks. The most complex of these tools are broad at the base and narrow at the distal end, providing a precision tip without compromising tool rigidity. Tapering is achieved by tearing the tool from the leaf in a step-wise fashion, with as many as four steps along the length of the tool. (Photos: panel A, Mick Sibley, University of Auckland; panel B, Gavin Hunt.)



weight, the capuchins tapped and gently moved the stones before transporting the heavy, effective tool. They even chose correctly when the heavy tool was smaller than the other alternatives.

Insight

If animals do know something about the physics of their environment and their actions, can they use this knowledge productively, to reason about new applications for tools or new means to reach their goals? The question of animal insight dates back to Koehler's experiments at the beginning of the 20th century, in which chimpanzees were given the task of obtaining out-of-reach rewards. The rapid emergence of a fully-formed solution, such as stacking boxes to climb on or combining short sticks to produce a long tool, prompted Koehler to apply the term 'insight' as an alternative mechanism to blind trial-and-error. However, the fact that chimpanzees exhibit many of these behaviours when the objects are presented without an out-of-reach reward points towards a simpler explanation: perhaps the 'spontaneity' of the chimpanzees' solution and its suitability to the task at hand was a case of one lucky trial and no error [30].

In a recent revival of insight experiments, rooks, normally a non-tool-using species, were presented with a tube containing a collapsible platform with a food reward resting on it — the platform would collapse under slight pressure so that the food would fall out [31]. At first the rooks did not solve the problem, but after experience of nudging stones into the tube from a ledge next to the opening they began to bring stones to drop into it, and generalised their solution to pushing down on the platform with sticks. In a subsequent experiment they even made a hook to lift a bucket of food from a tube: they put a wire into the tube, bent it over the lip, reversed the wire and used it to pull up the bucket. Impressive as this undoubtedly is, in all cases the solution, as in the rooks' training, involved adding an object to the tube; and the items to be used were placed beside it, increasing the likelihood that the 'correct' action would be



the first one attempted in the face of the new problem. Without another group of naïve birds for each stage, it is impossible to know how important that cumulative experience was [30]. Regardless, the rooks displayed sensitivity to the task requirements, quickly developing a preference for heavy stones over light ones and using thin stones in preference to wide ones when the mouth of the tube was narrowed. In the platform-collapsing task, New Caledonian crows generalised from the experience of pecking at the platform through a small-necked tube to dropping objects into it when the neck was longer; though note that these birds, unlike the rooks, already have tool-use in their behavioural repertoire [32].

In his later writings, Koehler made a distinction between insight (quickly recognising when the right solution has been stumbled upon in the course of exploration, leading to a sudden disappearance of further trial-and-error), and 'foresight' (sizing up a problem in advance through physical reasoning and bringing a new solution to it fully formed). To



Figure 4. A Goualougo chimpanzee with a brush-tipped tool.

Chimpanzees in the Goualougo Triangle make a range of tools when fishing for termites: they select robust plants for making digging sticks, stripping side branches and sharpening one end before puncturing a fishing hole into subterranean termite nests; they also split stems lengthwise to use as flexible fishing lines for angry termites to bite onto; and form brush-tipped twigs by raking the tip through their teeth, providing a greater surface area for termite attachment. (Photo: Ian Nichols.)

date, there seems to be clearer evidence for the former ability than for the latter in animals such as chimpanzees and corvids. The exact cognitive mechanisms underpinning both sorts of accomplishment are yet to be formalised, but examining the sorts of experience needed for the emergence of such seemingly ‘insightful’ solutions seems to be a fruitful beginning [30].

A powerful illustration of the role of immediate feedback about an action’s effect comes from a study investigating one of the most famous cases for insight in animals: birds pulling up a reward on the end of a string tied to a perch in increments, trapping successive lengths under their feet. Strikingly, most naïve New Caledonian crows produced the complete solution in one fluid attempt from the first trial. However, when deprived of visual feedback (through the use of a horizontal occluder with a hole just large enough for the reward to pass through), naïve New Caledonian crows tugged at the string but did not pull up the reward. Even the performance of the experienced subjects was disrupted [33]. This experiment neatly exemplifies how even rapidly emerging solutions need not have been planned out in the mind. What role, if any, did physical knowledge play? Visual feedback was shown to be necessary, but is it sufficient — would any action with a contingent effect on the reward be repeated?

Planning

One reason that tools have had such a high profile in the study of human evolution is the evidence they give about ancient hominins’ ability to plan ahead. Reconstructions of knapped flint from over two million years ago show a detailed sequence of detachments that can only result from mentally ‘looking ahead’ in the manufacture process [34]; later in human evolution, raw material for stone tools has been found transported from sites miles away from the point of manufacture and use [34]; later still, hand axes were retained for use over long periods of time. Does the evidence from non-humans suggest any similar kinds of foresight and planning?

Several authors have suggested that apparent evidence of anticipatory planning in animals can be explained another

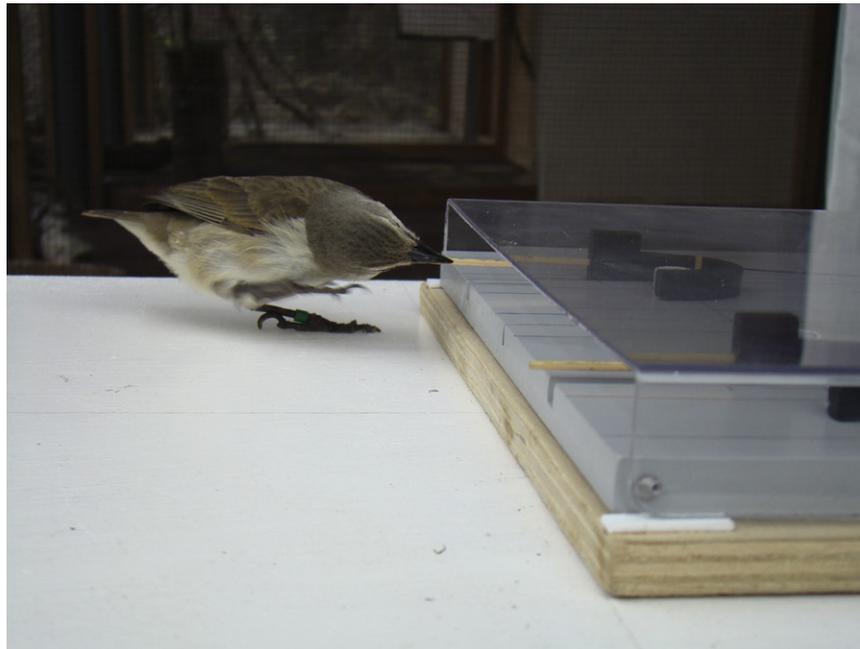
way. When you take a canvas bag with you to work in anticipation of a later shopping trip, this could result from an imagination of your future-self standing at the check-out with items to transport. But alternatively it might be that packing your bag was habitual, triggered by the context of getting ready for work. That habit might have been shaped by associative learning, and not reflect any imagination of yourself in the future or memory of yourself in the past: without the chance to ask, it would be hard to tell. With this concern in mind, much of the evidence that suggests anticipatory planning in animals is ambiguous [35]. We should also note that there is no way in principle of telling whether non-humans imagine themselves personally in the past or projected into the future, as humans do; all we can do is to discover whether current behaviour is based on representation of past or future states.

Chimpanzees, New Caledonian crows and capuchin monkeys are all known to transport their tools over relatively long distances (roughly 50–200 m). For instance, when a chimpanzee is seen to bite off several vine or herb stems, strip off the side leaves, bite the tips neatly and tuck them into her mouth, observers can be sure she has termite-fishing in mind, even if no termite mound is in sight. That might be explained as a learnt habit, triggered by feeling in the mood for a termite snack. In the laboratory, however, apes are found to select tools for future use even in cases that cannot be explained this way. Instead of a tasty grape, they will select a tool they will need to gain a large reward in an hour’s time; and yet with the tool in hand they will reverse their preference and take the grape, instead of the now-superfluous tool [36].

It has long been noticed that chimpanzees make tools in advance, where appropriate raw material is not available at the site of use, sometimes out of sight of the place of use. A particularly striking case is that of the chimpanzees of Goualougo, which use two different tools in sequence to fish for underground termites. First, they puncture the ground using a digging stick, and then use a flexible tool to fish. The robust digging stick is usually left at the site, and so it is the *second* tool of the sequence that the chimpanzees often arrive carrying with them. Apparently they think through their regular tool-using routine in advance: just as we might think through a familiar recipe, and remember to soak the currants a day in advance of starting cooking. All these examples could be retrospectively ‘explained’ as the result of associative learning, but the plausibility of doing so

Figure 5. Woodpecker finch chooses the correct raking tool.

Interestingly, the relatives of these tool-using birds, small and large tree finches, solve this task equally quickly, despite not using tools in the wild. (Photo: Irmgard Teschke and Sabine Tebbich.)



decreases as the degree of elaborateness of the anticipation increases [37].

Tools and Evolution

Why Has Tool-Use Evolved in Some Species?

Using tools to get food involves costs: direct costs of time and effort, and opportunity costs if simpler-to-access foods are missed while struggling with the harder task. Candidates for environmental features that might outweigh these costs include: lower availability of directly accessible foods compared to ‘defended’ ones; high nutritional quality of defended foods; and unpredictability from seasonal variation or rapid environmental change, selecting for flexibility in food-getting. (These candidate features are not mutually exclusive: need and opportunity can act in combination, and different features may have acted at different points during the evolution of a species.)

Some support for these ideas can be found in recent field studies. For example, Tebbich and Taborsky [38] found that woodpecker finches prefer to use tools to probe tree holes for invertebrates, specifically in arid habitats and in the dry season: then, availability of surface prey is low but availability and nutritional content of embedded prey remains high. Similarly, capuchin monkeys use stones to dig for high-quality tubers in arid environments, but have not been reported to do so in habitats rich in other food sources [39]. But orangutans use tools to access insects most often where the insects are most abundant, even when other resources are freely available [40]. More generally, ecological hypotheses remain untested because of the inherent difficulty of doing so. In order to assess the relative nutritional value and availability of competing food sources, animal diet and environmental distribution of food have to be studied in tandem, at the level of specific nutrients, over at least a year cycle: that has seldom been done for tool-using species.

Tools for Thought?

Although tool-use can result from simple strategies, sophisticated ones might have advantages: making tool-use more selective, flexible, and innovative. The cognition actually involved in animal tool-use is far from being well-understood, but there are indications that some animals other than humans know something about the functionality of their tools, and can take steps in the present in order to gain a reward in the future. Could the pressure to exploit resources using tools have provided the selective pressure for the evolution of those abilities?

Rates of tool-using and of innovation correlate with relative brain-size in birds and primates, supporting a causal

link; but these correlations do not rule out the alternative, that selection in some *other* domain created minds capable of innovation and tool-use. One important line of evidence is comparison between pairs of closely related species which differ in few traits other than tool-use: a systematic difference across such pairs would point to a role for tools in cognitive evolution. As yet, there are very little data of this kind available. So far, there is no evidence that New Caledonian crows outperform other, non-tool-using corvids such as rooks on physical tasks; and some of the best evidence for future planning comes from scrub jays [35], another non-tool-using corvid. Among the great apes, some populations of chimpanzees and orangutans are the only habitual tool-users in the wild; but in tests of physical reasoning or planning they do not systematically outperform bonobos and gorillas (for example [41]). In a direct comparison between tool-using woodpecker finches and two closely related but non-tool-using species of Darwin’s finch, no differences in physical problem-solving skills were found. All three species rapidly solved problems such as pulling an effective rather than an ineffective tool to bring food within reach (Figure 5) [11].

Why Is Tool-Use So Widespread and Sophisticated in Humans?

The technology of modern humans remains unique in its breadth and sophistication. What mental adaptations made this possible? Several psychological faculties have been suggested to have changed since the human and ape lineage diverged: the representational abilities discussed above, such as conceiving of the future or abstract physical properties [42]; executive functioning abilities such as working memory that allow for information to be held in mind and manipulated [43]; sensorimotor capabilities that allow for the coordination of perception and action during complex behaviour such as stone-knapping [44]; the cognitive skills and motivations underpinning collaborative culture, which gives rise to a ratcheting-up of tool complexity [45]. Did one

small change make the crucial difference? If so, what feature of the early hominid niche prompted its evolution? In reality, these hypotheses are not mutually exclusive, and several effects might ramify with each other over the course of human evolution. However, a quantitative change in working memory capacity could facilitate changes in several other abilities, so it is interesting to note support for this way of thinking from the developmental and comparative literature.

The theory, inspired by the changes in the types of tools made by hominids, suggests that greater working memory size would allow modern humans to hold representations of multiple states of reality in mind *at one time*: important for theory of mind, symbolic thought, analogical reasoning and planning [43]. Executive control certainly seems to play a crucial role in limiting the problem-solving abilities of young children. Two-year-olds fail to locate a ball that is rolled behind an occluder and stopped by a visible wall which protrudes above the occluder, yet their failure seems to have little to do with physical reasoning. They make as many search errors when the occluder is partly transparent, and their looking-patterns reveal that they correctly anticipate it to stop in front of the wall. Instead, coordinating perception, attention, knowledge, prediction and action may overload immature executive resources [46]. Interestingly, adult monkeys make similar search errors to human toddlers, despite looking longer, like the toddlers do, at displays that violate physical principles [47]. Adult apes, in contrast, are more successful [48]. Using a tool may pose even steeper challenges to executive resources than other actions, both because of the increase in the number of items that need to be held in mind, and the intricacy of the action itself [49]. The majority of chimpanzees and three- to four-year-old children fail to solve the traditional trap task when required to use a tool, but successfully move the food away from the trap if small holes allow them to use their fingers to move the reward [27]. But five-year-old children solve the task easily, even when using a tool [50]. Thus, there is tentative support for the notion of an evolutionary trajectory toward greater executive capacities, mirrored in human ontogeny, which allowed humans to make ever more complex tools to solve new problems.

The nature of the cognition underpinning uniquely human tool-use is still hotly debated, but one thing is clear, understanding the cognition underpinning animal tool use is a critical piece of the puzzle. The more we study tool-use and manufacture in strikingly large-brained animals such as chimpanzees, capuchin monkeys and crows, the more it seems that physical reasoning and planning abilities may have originated deeper in the phylogenetic record than previously thought, and perhaps more than once. But we still know very little about the exact nature of these representational capacities, and how they interact with other psychological abilities such as memory and attention during problem-solving. Solving these puzzles is as important to understanding human evolution as studying the tools left behind by extinct hominids.

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References

- Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior* (Cambridge, MA, US: Harvard University Press).
- McGrew, W.C. (2010). Chimpanzee technology. *Science* 328, 579–580.
- Ottoni, E.B., and Izar, P. (2008). Capuchin monkey tool use: overview and implications. *Evol. Anthropol.* 17, 171–178.
- Mann, J., Sargeant, B.L., Watson-Capps, J.J., Gibson, Q.A., Heithaus, M.R., Connor, R.C., and Patterson, E. (2008). Why do dolphins carry sponges? *PLoS ONE* 3, e3868.
- Hunt, G.R. (1996). Manufacture and use of hook-tools by New Caledonian Crows. *Nature* 379, 249–251.
- Beck, B.B. (1980). *Animal Tool Behavior: The Use and Manufacture of Tools by Animals* (New York: Garland).
- Mendes, N., Hanus, D., and Call, J. (2007). Raising the level: orangutans use water as a tool. *Biol. Lett.* 3, 453–455.
- Bird, C.D., and Emery, N.J. (2009). Rooks use stones to raise the water level to reach a floating worm. *Curr. Biol.* 19, 1410–1414.
- Lefebvre, L., Nicolakakis, N., and Boire, D. (2002). Tools and brains in birds. *Behaviour* 139, 939–973.
- Maravita, A., and Iriki, A. (2004). Tools for the body (schema). *Trends Cogn. Sci.* 8, 79–86.
- Tebbich, S., Sterelny, K., and Teschke, I. (2010). The tale of the finch: adaptive radiation and behavioural flexibility. *Phil. Trans. R. Soc. B* 365, 1099–1109.
- Dickinson, A., and Balleine, B. (2000). Causal cognition and goal-directed action. In *The Evolution of Cognition*, C. Heyes and L. Huber, eds. (M.I.T Press).
- Hunt, G.R. (2008). Introduced *Lantana camara* used as tools by New Caledonian Crows (*Corvus moneduloides*) New Zealand. *J. Zool.* 35, 115–118.
- Sanz, C., and Morgan, D. (2009). Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. *Int. J. Primatol.* 30, 411–427.
- Kenward, B., Weir, A.A., Rutz, C., and Kacelnik, A. (2005). Tool manufacture by naive juvenile crows. *Nature* 433, 121.
- Visalberghi, E., and Guidi, C. (1998). Play behaviour in young tufted capuchin monkeys. *Folia Primatol.* 69, 419–422.
- Wimpenny, J.H., Weir, A.A.S., Clayton, L., Rutz, C., and Kacelnik, A. (2009). Cognitive processes associated with sequential tool use in New Caledonian crows. *PLoS ONE* 4, e6471.
- Weir, A., and Kacelnik, A. (2006). A New Caledonian crow (*Corvus moneduloides*) creatively re-designs tools by bending or unbending aluminium strips. *Anim. Cogn.* 9, 317–334.
- Povinelli, D.J. (2000). *Folk Physics for Apes: The Chimpanzee's Theory of How the World Works* (Oxford: Oxford University Press).
- Visalberghi, E., and Limongelli, L. (1994). Lack of comprehension of cause-effect relations in tool-using capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* 108, 15–22.
- Kacelnik, A., Chappell, J., Weir, A.A.S., and Kenward, B. (2006). Cognitive adaptations for tool-related behaviour in New Caledonian crows. In *Comparative Cognition: Experimental Explorations of Animal Intelligence*, E.A. Wasserman and T.R. Zentall, eds. (Oxford, UK: Oxford University Press), pp. 515–528.
- Hunt, G.R., Rutledge, R.B., and Gray, R.D. (2006). The right tool for the job: what strategies do wild New Caledonian crows use? *Anim. Cogn.* 9, 307–316.
- Holzhaider, J.C., Hunt, G.R., Campbell, V.M., and Gray, R.D. (2008). Do wild New Caledonian crows (*Corvus moneduloides*) attend to the functional properties of their tools? *Anim. Cogn.* 11, 243–254.
- Gigerenzer, G., and Brighton, H. (2009). Homo heuristicus: why biased minds make better inferences. *Top. Cogn. Sci.* 1, 107–143.
- Silva, F.J., Page, D.M., and Silva, K.M. (2005). Methodological-conceptual problems in the study of chimpanzees' folk physics: how studies with adult humans can help. *Learn. Behav.* 33, 47–58.
- Seed, A.M., Tebbich, S., Emery, N.J., and Clayton, N.S. (2006). Investigating physical cognition in rooks, *Corvus frugilegus*. *Curr. Biol.* 16, 697–701.
- Seed, A.M., Call, J., Emery, N.J., and Clayton, N.S. (2009). Chimpanzees solve the trap problem when the confound of tool use is removed. *J. Exp. Psychol. Anim. Behav. Process* 35, 23–34.
- Taylor, A.H., Hunt, G.R., Medina, F.S., and Gray, R.D. (2009). Do New Caledonian crows solve physical problems through causal reasoning? *Proc. R. Soc. Lond. B* 276, 247–254.
- Visalberghi, E., Addessi, E., Truppa, V., Spagnoletti, N., Ottoni, E., Izar, P., and Frigaszy, D. (2009). Selection of effective stone tools by wild bearded capuchin monkeys. *Curr. Biol.* 19, 213–217.
- Shettleworth, S.J. (2009). Animal cognition: deconstructing avian insight. *Curr. Biol.* 19, R1039–R1040.
- Bird, C.D., and Emery, N.J. (2009). Insightful problem solving and creative tool modification by captive nontool-using rooks. *Proc. Natl. Acad. Sci. USA* 106, 10370–10375.
- von Bayern, A.M.P., Heathcote, R.J.P., Rutz, C., and Kacelnik, A. (2009). The role of experience in problem solving and innovative tool use in crows. *Curr. Biol.* 19, 1965–1968.
- Taylor, A.H., Medina, F.S., Holzhaider, J.C., Hearn, L.J., Hunt, G.R., and Gray, R.D. (2010). An investigation into the cognition behind spontaneous string pulling in New Caledonian crows. *PLoS ONE* 5, e9345.

34. Roche, H., Blumenschine, R.J., and Shea, J.J. (2009). Origins and adaptations of early *Homo*: what archeology tells us. In *The First Humans – Origin and Early Evolution of the Genus Homo*, F.E. Grine, J.G. Fleagle and R.E. Leakey, eds. (Netherlands: Springer), pp. 135–147.
35. Raby, C.R., and Clayton, N.S. (2009). Prospective cognition in animals. *Behav. Process* 80, 314–324.
36. Osvath, M., and Osvath, H. (2008). Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: self-control and pre-experience in the face of future tool use. *Anim. Cogn.* 17, 661–674.
37. Byrne, R.W., and Bates, L.A. (2006). Why are animals cognitive? *Curr. Biol.* 16, R445–R448.
38. Tebbich, S., Taborsky, M., Fessel, B., and Dvorak, M. (2002). The ecology of tool-use in the woodpecker finch (*Cactospiza pallida*). *Ecol. Lett.* 5, 656–664.
39. Moura, A.C.d.A., and Lee, P.C. (2004). Capuchin stone tool use in Caatinga dry forest. *Science* 306, 1909.
40. Fox, E.A., van Schaik, C.P., Sitompul, A., and Wright, D.N. (2004). Intra- and interpopulational differences in orangutan (*Pongo pygmaeus*) activity and diet: Implications for the invention of tool use. *Am. J. Phys. Anthropol.* 125, 162–174.
41. Mulcahy, N.J., and Call, J. (2006). Apes save tools for future use. *Science* 312, 1038–1040.
42. Penn, D.C., Holyoak, K.J., and Povinelli, D.J. (2008). Darwin's mistake: explaining the discontinuity between human and nonhuman minds. *Behav. Brain Sci.* 37, 109–130.
43. Coolidge, F.L., and Wynn, T. (2005). Working memory, its executive functions, and the emergence of modern thinking. *Camb. Archaeol. J.* 15, 5–26.
44. Stout, D., and Chaminade, T. (2007). The evolutionary neuroscience of tool making. *Neuropsychologia* 45, 1091–1100.
45. Tomasello, M., Carpenter, M., Call, J., Behne, T., and Moll, H. (2005). Understanding and sharing intentions: the origins of cultural cognition. *Behav. Brain Sci.* 28, 675–735.
46. Keen, R., and Shutts, K. (2007). Object and event representation in toddlers. In *Progress in Brain Research*, Volume 164, C. von Hofsten and K. Rosander, eds. (Elsevier), pp. 227–235.
47. Santos, L.R. (2004). 'Core knowledges': a dissociation between spatiotemporal knowledge and contact-mechanics in a non-human primate? *Dev. Sci.* 7, 167–174.
48. Cacchione, T., Call, J., and Zingg, R. (2009). Gravity and solidity in four great ape species (*Gorilla gorilla*, *Pongo pygmaeus*, *Pan troglodytes*, *Pan paniscus*): vertical and horizontal variations of the table task. *J. Comp. Psychol.* 123, 168–180.
49. Byrne, R.W. (2004). The manual skills behind hominid tool use. In *Evolutionary Origins of Great Ape Intelligence*, A.E. Russon and D.R. Begun, eds. (Cambridge: Cambridge University Press), pp. 31–44.
50. Horner, V., and Whiten, A. (2007). Learning from others' mistakes? Limits on understanding a trap-tube task by young chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *J. Comp. Psychol.* 121, 12–21.