Tool use and physical cognition in birds and mammals

Nathan J Emery[1] and Nicola S Clayton[2]

In the wild, chimpanzees are the most prolific and proficient tool users, yet their understanding of tools in the laboratory is surprisingly poor. Although this apparent lack of understanding might be interpreted as a reflection of a general failure of animals to appreciate 'folk physics', recent studies suggest that some non-tool using species perform rather well on such laboratory tasks. In some animals, tool use and manufacture may also engage aspects of planning, but some non-tool using species have also been shown to demonstrate prospective cognition. Consequently, we argue that habitual tool use is not a clear predictor of physical intelligence, for either instrumental tool tasks or tests of planning.

Addresses
[1] School of Biological & Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, UK
[2] Department of Experimental Psychology, University of Cambridge, Downing Street, Cambridge CB2 3EB, UK

Corresponding author: Emery, Nathan J (n.j.emery@qmul.ac.uk) and Clayton, Nicola S (nsc22@cam.ac.uk)

Introduction

Many species habitually use tools to obtain food that would otherwise be unattainable. Classic examples include chimpanzees stripping the leaves off sticks and poking them into termite mounds to 'fish' for insects, sea otters hitting shellfish onto stones resting on their stomachs and herons using bait to catch fish [1]. Many species also use tools in captivity or can be trained to use them [2]. However, only two non-human species regularly make tools; chimpanzees and New Caledonian crows. Although tool-use has been reported in all the major animal groups, including a number of invertebrates, it is not clear whether such tool-using ability is an indication of a species' physical intelligence or merely a reflection of their specialised feeding mechanism [3].

Within mammals, primates are the most proficient tool-users, both in the wild and in captivity [4]. Habitual tool use was first described for chimpanzees, the most famous examples being termite-fishing [5] and nut-cracking [6], but recently capuchins have also been observed using stone tools to crack nuts [7] and orangutans using a variety of tools [8]. The other major vertebrate group that contains species that use tools are birds [9], where the most complex tool-use and manufacture is found in New Caledonian crows that construct stepped-cut Pandanus leaves and hooked twigs for use in retrieving insects [10]. Pandanus leaf tools display great diversity depending on the number of steps needed to make them [11]. The crows also make stick tools that they sculpt into hooks by tearing off side twigs at the end and then chipping away at the end until they create a hook [12,13].

Does tool use reflect physical intelligence?

It has long been argued that tool use is a reflection of physical intelligence, and this is supported by a strong correlation between tool use and brain size in both birds [9] and primates [14]. Additional support comes from the fact that chimpanzee infants require years of observation to learn how to make tools, about five and a half years to fish for termites [15] and three to five years to crack nuts using hammers and anvils [16]. However, in woodpecker finches tool-use develops through individual trial-and-error learning rather than social learning [17] and New Caledonian crows spontaneously insert sticks into crevices irrespective of whether they observe a tool-user [18]. However, social learning may be essential for the transmission of subtle tool-manufacturing techniques, as different crow populations make and use different tools [19].

Experiments on woodpecker finches have attempted to test what these birds know about the properties of stick tools, such as their length, whether they need to be modified, the consequences of inserting a stick into a tube with a trap in the centre, and whether pushing a food into the trap can be avoided [20]. The finches performed similarly to capuchins and chimpanzees [4]. New Caledonian crows have also been examined for their folk physics using similar tasks. For example, crows were presented with a selection of sticks of different lengths and a tube with food in the centre. The crows chose a tool of either the appropriate or greater length [21]. In another task in which food was located behind a small opening, the crows chose a tool narrow enough to pass through the hole and push the food out. If the crows chose a tool that was too wide, they often modified the tool to make it fit [22]. Betty, a New Caledonian crow, spontaneously modified a functional hook out of wire in order to pull up a small bucket containing food [23].

Figure 1
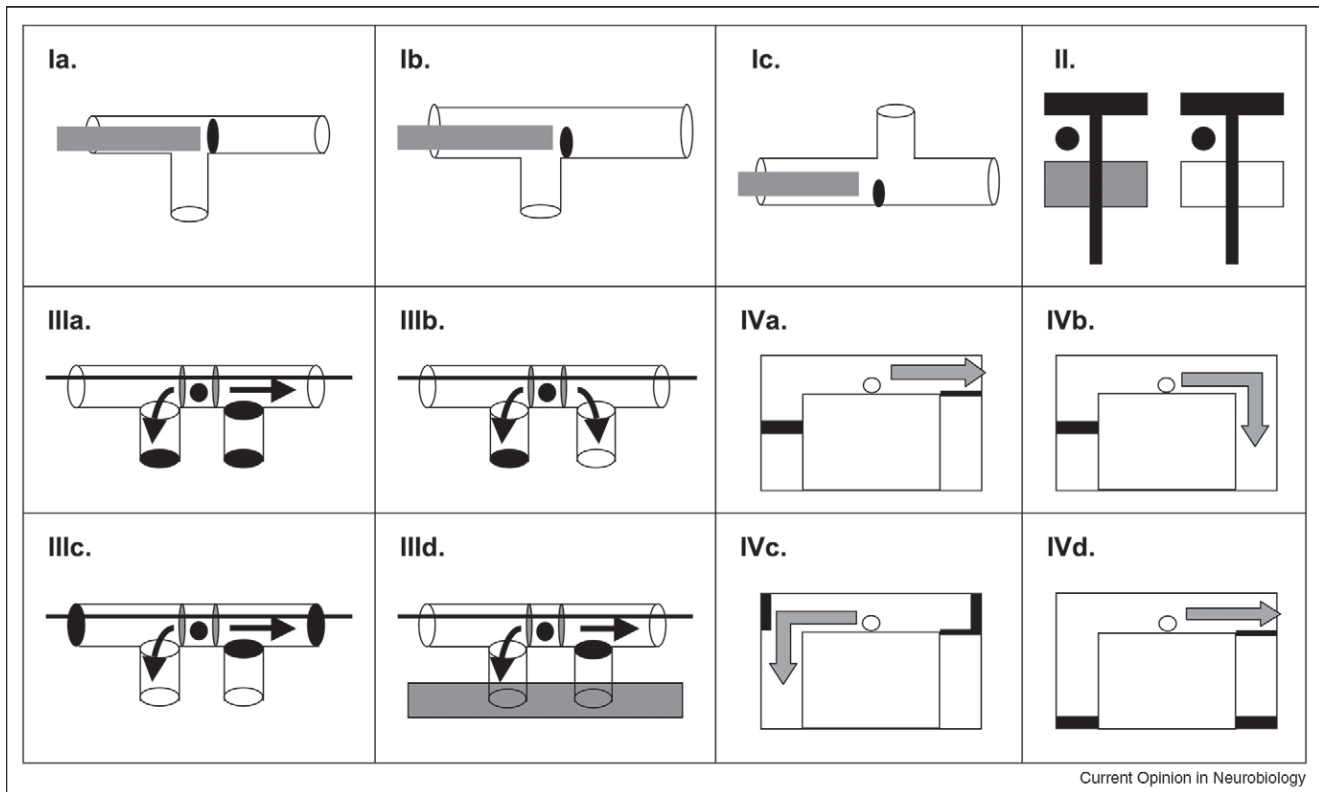
Drawings of various trap problems. **(Ia)** Original trap-tube [20,33–35,43]. **(Ib)** Modified trap-tube [37••]. **(Ic)** Inverted modified trap-tube [37••]. **(II)** Trap-table [27,38,44]. **(IIIa)** Two-trap tube (Tube A) [31••]. **(IIIb)** Two-trap tube (Tube B) [31••]. **(IIIc)** Two-trap tube (Tube C) [31••]. **(IIId)** Two-trap tube (Tube D)[31••]. **(IVa)** Two-trap-box (Box A) [26]. **(IVb)** Two-trap box (Box B) [26]. **(IVc)** Two-trap box (Box C) [26]. **(IVd)** Two-trap box (Box D) [26].

Further support for the argument that tool-users are intelligent comes from studies of innovative tool use such as Mendes and co-workers' adaptation of an old Aesop's fable of the crow and the pitcher for apes [24••]. Rather than having to drop stones into a pitcher to raise the water level, they provided a treat at the bottom of an empty tube and the subject had to develop a method for raising the treat to within reaching distance. An orangutan collected water in her mouth and spat it into the tube, raising the water level so that the treat could be reached. In the absence of knowing the precise reinforcement history of this animal, however, it is not clear that this was the first instance of this behaviour, thereby questioning whether this example is a true case of innovation.

Many non-tool-using species spontaneously use tools in captivity [25] when given tool-choice tasks, such as selecting a tool with the hook end surrounding a reward as opposed to a tool with the food placed outside the hook end. Other non-tool-using species (e.g. *Degus octagon*) can be trained to use tools and then choose the most appropriate tool for the job (e.g. a solid rake versus a rake with prongs so food passes through [2]). Experience is also important for tool-using species, however. For example, chimpanzees with experience of trap tube problems were quick to learn a different trap box problem whereas those with no experience of trap problems failed to solve the task [26]. The provision of tools also plays a role because the chimpanzees' performance was compromised if they had to use a tool in the trap problems compared to those subjects that could manipulate the food (or container holding the food) directly [26], and this might explain why others have found that apes fail to transfer their understanding of trap problems (trap tube) to a different trap table problem that required the use of a tool [27].

The fact that a species does not use tools in the wild does not necessarily compromise that species' physical intelligence. Indeed both non-tool-using primates [28–30] and corvids [31••,32] have been found to have a level of reasoning comparable, if not superior to, the tool-using primates on laboratory tests. However, what these findings do challenge is the relationship between tool use and intelligence, specifically the hypothesis that animals that habitually use tools in the wild are more intelligent, or better at physical intelligence tasks, than those that do not.

The comparative study of folk physics

Although field and captive studies of tool-use are extremely important, they cannot answer questions about an animal's intuitive understanding of the forces acting on tools, so-called folk physics. To do so, one needs to adopt an interventionist approach and develop tasks that test an animal's understanding of folk physics. Experiments on primates have focused on chimpanzees and capuchins. Povinelli [33] tested seven chimpanzees on a variety of physical tasks and found that although some of the chimps could learn many of these tasks, their performance appeared to be based on reasoning about observable rather than the unobservable principles of the tasks, such as contact, connectedness, causality and support. With respect to trap problems (Figure 1), some chimpanzees learn to avoid losing the food, but could do so using a simple rule such as 'move' the food away from the trap [33–35] and have difficulties transferring across functionally equivalent trap tasks [27].

Their failures have been attributed to a number of factors, including the suggestion that Povinelli's chimpanzees may have had an impoverished cognitive and social development [36]. The way in which the task is administered can also have a major effect on performance. For example, chimpanzees find it much easier to solve a trap tube task in which the food can be pulled towards the animal as opposed to pushed away [37••], and success on the trap table task was constrained by subtle differences in tool types, reinforcement contingencies, position of tools and the number of tables [38]. Chimpanzees show enhanced performance on support problems (cloth), connectedness problems (rope & banana) and food retrieval problems (rakes & canes), provided there is contact between the tool and the reward, whereas both bonobos and rooks failed to spontaneously solve a task in which they had to determine which side of an apparatus to pull a stick tool to move a food reward into reach, predicting the consequences of contact rather than which objects were currently in contact [32,39].

There may also be methodological and conceptual problems with Povinelli's studies, as adult humans performing the same trap and connection problems do not always act rationally. For example, continuing to avoid a trap even when it cannot possibly function as a trap [40,41] or pulling a rope placed multiple times over a banana rather than a rope placed under a banana, even when the rope under the banana is the only tool that will result in retrieving the banana [42•]. In this latter case, the subjects rationalise their behaviour by stating that they chose the rope placed on top of the banana because it contacted it more than the other choices.

## Is there any evidence for causal reasoning in animals?

Although the trap tube task is typically seen as the benchmark test for causal understanding, it is not without its problems. In the traditional configuration, a single trap is either offset to one side with the food located next to the trap or in the centre of the tube, or the trap is located in the centre of the tube with the food offset. The subject then either has to insert a tool into the correct side of the tube to dislodge the food without it falling into the trap [33–35] or a tool is already inserted and the subject has to pull the tool to move the food [43]. A control procedure is then provided in which the tube is inverted so that the trap is no longer functional. If the subject continues to move the tool so as to avoid the trap even though the trap will have no effect on the reward, the subject is deemed to have failed to understand the task. However, if they chose to move the tool randomly from either side of the inverted trap, then the subject is said to have understood that the trap is longer relevant.

The modified two-trap tube task [31••] was designed to test for causal reasoning in non-tool-users, as the tool used to move the food in the tube is already placed inside the tube, with two discs attached in the centre of the stick tool, and the food is located between the discs, a task that rooks rapidly learned. To obtain the food, the bird must pull the stick in the correct direction. The second trap (functional or non-functional) was added as a control to eliminate the use of simpler cues for learning or the application of a simple rule, namely 'pull the food away from the trap'. A horizontal tube was mounted on a wooden platform, with two traps positioned either side of centre. One trap was functional (i.e. had a solid base), one was non-functional (either Tube A with raised base so food passes over or Tube B with no base so food falls through). Additional novel tube configurations (C and D) were provided to test for causal reasoning without recourse to alternative associative explanations. Seven rooks rapidly learned Tubes A and B, and one rook, Guillem transferred immediately to Tubes C and D (Figure 2).

Taylor and co-workers [44] utilised these two-trap designs to test for causal reasoning in New Caledonian crows. Only three out of the six crows learned the initial tube configuration (pull across non-functional trap), compared to seven out of the eight rooks and could transfer to similar tubes retaining arbitrary features. Surprisingly, all crows failed to transfer to a novel configuration with a fall down non-functional trap (compared to seven out of eight rooks that immediately transferred). All three crows solved a novel trap table problem (having to pull one of two rakes to avoid pulling a reward into a trap), suggesting that the crows could transfer to a problem with functionally equivalent causal properties. However, it is not clear that this task could not be solved by generalizing the properties of holes across tasks. Without testing the crows on Tubes C and D, it is not clear that they have demonstrated the causal reasoning that the authors suggest. Perhaps the best evidence for causal

Figure 2
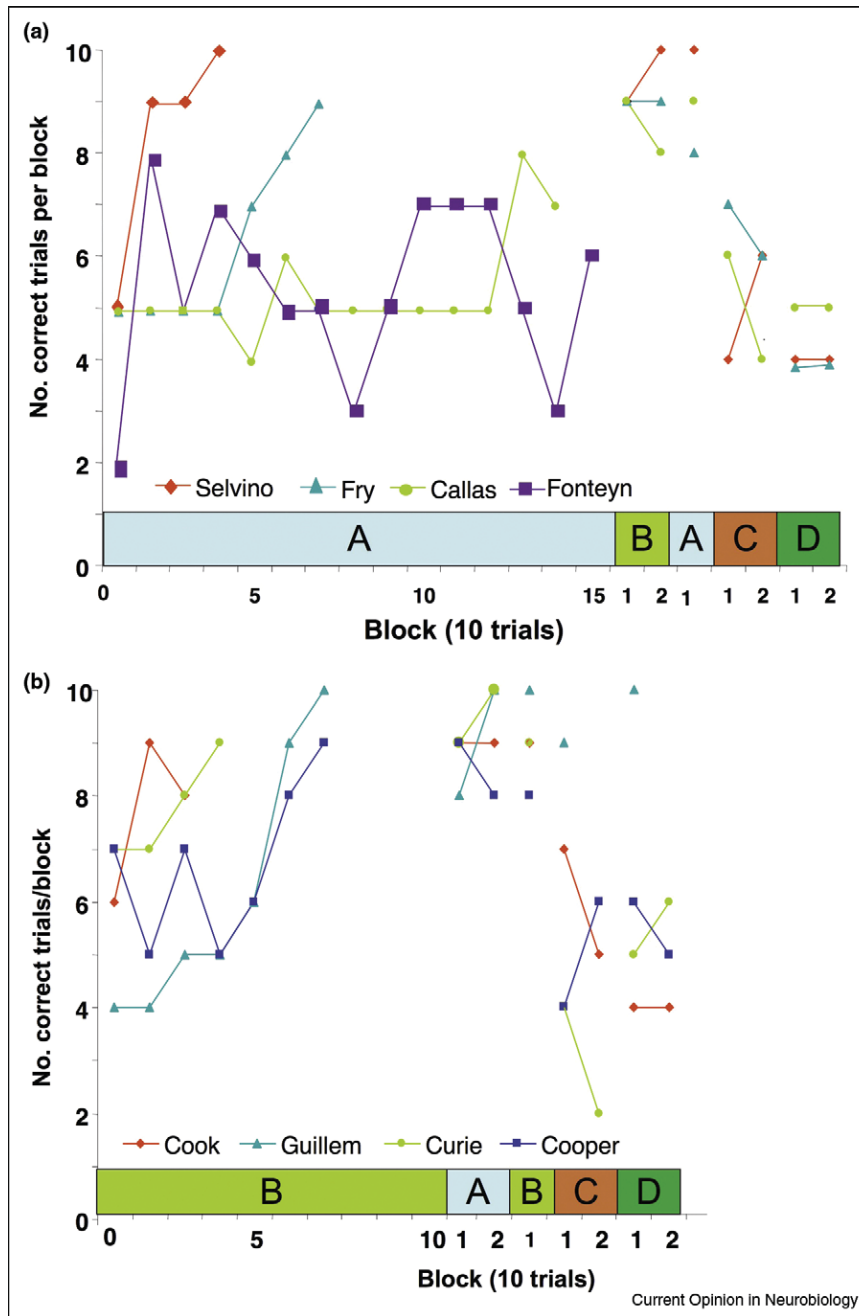
The two-trap tube task. In a modification of the original trap-tube design, an additional non-functional trap was added to the tube. (**I**) In Tube A, the subject could pull the food across a raised base and (**II**) in Tube B the base was removed so that the food would fall through the hole. Half the subjects received Tube A then Tube B then a re-test of Tube A, and half the subjects received Tube B then Tube A then a re-test of Tube B. Seven out of eight rooks rapidly learned either Tube A or B and transferred immediately to the novel configurations of the tube (A or B) [31**••**]. To further examine whether the rooks' behaviour was the result of causal reasoning rather than the use of a conditional rule such as pull the food away from the trap with a solid base, the two previously rewarded non-functional traps (drop down and pull across) were added together in the same tube, so that pulling towards either trap would result in a reward. Then one of the traps was made functional. In Tube C, a rubber bung with a hole through the centre was added to each side of the tube, so that pulling food towards the trap resulted in the food becoming trapped behind the bung. In Tube D, the entire tube was lowered onto a wooden platform, so that the platform effectively acted as a base to the open trap, thus trapping any food pulled into the trap. One rook, Guillem, spontaneously performed the task successfully on both Tubes C and D.

reasoning in tool use in birds still lies with a rook, Guillem. However, two out of eight chimpanzees have also shown similar transfers in equivalent configurations of the two-trap box problem [26].

Planning and thinking about future tool use

A cognitive approach to tool use should not focus exclusively on folk physics. Tool use and manufacture may also suggests aspects of prospective cognition; the delay of gratification until a tool is made and then used to gain a reward (self-control), forming mental representations of the goal that allows the animal to use one tool to access another that can reach the goal (sequential or meta-tool use) and either short- or long-term planning (e.g. transporting tools to the food site or saving tools for future use). Chimpanzees carry stone tools to food sites for nutcracking [45]. Although wild capuchins only carry food to stone sites [46], captive capuchins carry stones and probing tools to appropriate food sites, even when the sites are out of view [47]. There is also evidence that captive capuchins display self-control in tool use. When provided with edible rod-shaped tools (celery or pretzel) and a tube either baited with peanut butter located 1 m or 10 m away, the monkeys used the tools to extract the peanut butter; whereas in the un-baited control condition, they ate the tools immediately [48•].

A final aspect of short-term planning is sequential or meta-tool use; using tools in a series to achieve the goal of retrieving food. Both monkeys [49] and New Caledonian crows [50•] can use a short tool to pull in a longer tool and then use the longer tool to retrieve food that would be out-of-reach with the shorter tool.

Although wild chimpanzees carry stone tools short distances (∼100 m), possibly forming a representation of the goal (e.g., using the stone hammer to crack nuts), is there any evidence that non-human animals can form long-term representations of goals, for say the next day? Mulcahy and Call [51] presented orangutans and bonobos with a tool use task in which they had to select the appropriate tool to use either 1 or 14 h later in order to obtain a reward from an apparatus. Although some of the apes were successful in selecting and saving an appropriate tool for later use (see also [52]), the way that the experiments were conducted cannot exclude the possibility that the apes' behaviour was due to simpler associative learning or that their behaviour was cued by their current motivational state.

More convincing evidence of future planning comes from a recent study with apes that controlled for alternative explanations based on current versus future motivational states, where the apes could suppress an immediate reward in favour of a tool that would lead to a larger reward in the future [53•]. Although tool-using crows have not been tested on such tasks, there is evidence that another non-tool-using corvid, the western scrub-jay, will cache for a future need independent of their current motivational state (e.g. [54]).

Some speculations on the neural basis of tool use

Although the neural circuitry of human tool use has been extensively mapped out using neuroimaging techniques [55], our understanding of the neural basis of tool use in birds and mammals is largely speculative. There is a strong relationship between the frequency of 'true tool use' and brain size in birds [9] and neocortex size in primates [14], with tool-using species having the larger brains, and so by implication, greater intelligence to control tools in a goal-directed manner. The most extensive studies into the neural control of tool use in animals have been performed on Japanese monkeys, who can be trained to use a simple raking tool to access out-of-reach food ([56] for review). Like humans, complex cortical networks, focusing on the motor and premotor cortices, control the fine movements required to use a tool. Although the nomenclature of the avian brain has recently changed to reflect our modern understanding of brain connectivity and neurochemistry, finding that the basic sensory and motor connectivity patterns are homologous in birds and mammals [57]. Our lack of understanding of what cognitive operations the different parts of 'an intelligent' birds' brain do, rather than being restricted to less cognitively-sophisticated pigeons and chickens, will rapidly curtail any conclusions we can draw.

Interestingly, another brain area that controls motor skill learning in humans, also visually controls fine movements of the beak (cerebellar trigeminal and visual parts) in birds and is probably used for object manipulation and tool use. These parts of the cerebellum are larger in crows, parrots and woodpeckers than other species that do not use fine movements of the beak during instrumental actions, independent of body size or overall brain size [58]. By contrast, the vestibular and tail somatosensory cerebellar regions are larger in owls reflecting their role as nocturnal predators. Although the relationship between the size of parts of the cerebellum and tool use remains speculative, the size of the cerebellum does correlate with another form of fine motor control; bower design complexity [59]. What about other forms of fine object manipulation, such as nest building or food processing? Future studies will be important to determine whether there is something special about tool use and whether neural control of tool use is different from the neural control of tool manufacture or other forms of complex object manipulation, particularly relating the goal-directed actions of one object (e.g. stick tool) towards a second object (e.g. food). Without detailed neuroanatomical and neurophysiological studies of object manipulation, including tool use in birds, these questions will never be answered.

Conclusions

In short, the evidence to date that animals have an understanding of folk physics is at best mixed. The successes of corvids and chimpanzees, on both tool choice and transfer tests on trap problems, contrast with their performance on other tasks that suggests that they cannot discriminate between the functional and non-functional properties of tools [e.g. 60]. However, one thing is clear: to date we cannot find strong support for the hypothesis that tool-users are better than non-tool-users at tests that tap either folk physics or future planning.

Acknowledgements

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