Is there a link between the crafting of tools and the evolution of cognition?

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The ability to craft tools is one of the defining features of our species. The technical intelligence hypothesis predicts that tool-making species should have enhanced physical cognition. Here we review how the physical problem-solving performance of tool-making apes and corvids compares to closely related species. We conclude that, while some performance differences have been found, overall the evidence is at best equivocal. We argue that increased sample sizes, novel experimental designs, and a signature-testing approach are required to determine the effect tool crafting has on the evolution of intelligence. © 2014 The Authors. *WIREs Cognitive Science* published by John Wiley & Sons, Ltd.

INTRODUCTION

Tools have repeatedly revolutionized human society. From the earliest stones axes through to today's mobile phones, tools have changed how we interact with each other and with our environment. While it is clear that one of the key features of humans is their high level of sociality,[1] many of the events that have had the greatest impact on our history have not been revolutions in our sociality, but in our technology. In fact, a list of the key technologies we have invented is a useful proxy for the entire history of our species: stone axes, fire, clothes, pottery, the wheel, paper, concrete, gunpowder, the printing press, the automobile, the nuclear bomb, the internet. The manufacture of these tools created revolutions in the

societies they were invented in, as each of them either redefined how humans interacted with the environment or with each other.

It is not surprising then that early attempts to define our uniqueness were based on our ability to make tools, rather than our sociality: "Man has been defined in many ways, as the talking animal, the religious animal, and so on, but the most satisfactory definition from the scientific point of view is probably Man the Tool-maker" (Oakley 1949). Evidence of hominin technology dates back to the invention of Oldowan tools at least 2.6 million years ago (mya), and possibly 3.4 mya,[2] (but see Refs 3 and 4) with the invention of Oldowan tools.[5] These tools are created by striking a hammerstone into a cobble core which creates sharp stone flakes that can be used as cutting tools. Our ancestors crafted this technology for at least 900,000 years, at which point (1.75 mya) they began creating Acheulean tools,[6,7] where cobble cores were shaped into teardrop-shaped stone tools (handaxes).

Unfortunately, it is difficult to determine the effect this stone tool crafting had on the evolution of the human mind, as we have only the stone tools our ancestors left behind. As inferences from artefacts to

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cognition can be problematic,[8] these tools provide, at best, indirect evidence for the cognition that created these tools. A further issue is that across our evolutionary history we have been highly social tool-makers. Two of the key hypotheses for the evolution of intelligence are the social intelligence hypothesis and technical intelligence hypothesis. The social intelligence hypothesis suggests that the need to navigate social interactions of increasing complexity creates selective pressure for increased intelligence.[9–12] The technical intelligence hypothesis[13] suggests that the need to efficiently organize behaviors requiring a high number of sequential operations, such as those involved in extractive foraging or tool manufacture, leads to selection for increased intelligence. As hominins were both highly social and the manufacturers of sophisticated tools across their evolutionary history,[1,5–7] it is very difficult to infer the effects of social and technical selection pressures on the evolution of intelligence by studying humans alone.

Recent brain scanning work illuminates but does not solve this problem. Functional brain imaging has shown that modern humans recruit the inferior parietal and ventral premotor elements of the parietofrontal praxis circuits when making stone tools.[14,15] While both Oldowan and Acheulean tools manufacture use areas involved in sensorimotor control and body-tool representations, only Acheulean tool making recruits areas involved in the "coordination of ongoing, hierarchically organized action sequences".[15] Interestingly, neither type of tool appears to recruit areas involved in the mental rehearsal or assessment of action plans, although it is not yet clear if this holds when the task becomes more challenging. While this work is fascinating and important, it cannot tell us if these brain areas have direct *evolutionary* links to stone tool manufacture. It cannot show if tool manufacture drove the evolution of increased sensorimotor or online hierarchical processing in humans. It could be that other selective pressures, such as the need to predict social interactions, plan in everyday life or communicate via gesture[16] were responsible for the evolution of such cognition, which was then exapted for stone tool making. In fact, it is highly likely that, within the human lineage, these pressures combined in a ratchet-like fashion,[17] such that as our tools became more complex, our level of sociality increased, which in turn allowed for the creation of even more sophisticated tools via the division of labor *et cetera*.

One way to gain insight into the role that tool manufacture may have had on the evolution of cognition is via the comparative study of animal tool manufacture. There is now evidence that a wide range of animal species are capable of tool manufacture behaviors in the wild such as detaching a tool from a substrate, removing a part of a tool, combining two objects into a tool or restructuring material into a tool.[18] These types of tool manufacture behaviors have been observed in 15 species of invertebrate, 24 species of birds, 4 species of non-primate mammals, 22 species of monkey, and 5 apes species.[18] Thus, alongside *Homo sapiens* there are a further 70 species on Earth capable of behavior that can be classified as tool manufacture. No animal species manufactures stone tools in the wild, though in highly scaffolded and enriched captive environments bonobos make stone tools after considerable training.[19]

Intriguingly, in the wild three of the 70 animal species that manufacture tools 'craft' their tools during their manufacture process in a way that seems similar to the fabrication of human stone tools (Figure 1). Tool crafting is more complex than the breaking off of a stick from a branch. It involves an animal carrying out a 'number of successive steps' to 'three-dimensionally reshape' a tool, where reshaping is defined as 'the fundamental restructuring of material'.[18] New Caledonian crows create wooden hook tools through such crafting: they strip side branches, bark, and wood from branch junction to create functional hooks.[20,21] Chimpanzees trim and sharpen the end of the sticks they use for spearing bushbabies.[22] When termite-fishing and ant-dipping they also reshape sticks by biting the end so they become split and frayed.[23] Orang-utans perform similar behavior in the wild as they also reshape the ends of sticks through biting so they resemble brushes.[24] Thus, just as with human stone tool manufacture, each of these species carries out a sequence of hierarchically structured behaviors to impose a novel, three-dimensional form onto natural material (Figure 1).

In principle, comparison of the cognitive abilities of these tool-crafting species to their close relatives should reveal if tool-crafting animal species think in more sophisticated ways about tool manufacture and the world around them. However, chimpanzees have the same problematic trait combination as humans. This species is highly social (mean group size 53.5)[25] and crafts tools.[26] Therefore, either of these two factors could have driven the evolution of the cognitive mechanisms used by chimpanzees. In contrast, both orang-utans and New Caledonian crows are relatively unsocial species. New Caledonian crows live in small family groups[27] and appear to mix closely outside of these groups with only five to six individuals.[28] Orang-utans are semi-solitary, in that they tend to range alone, but do come

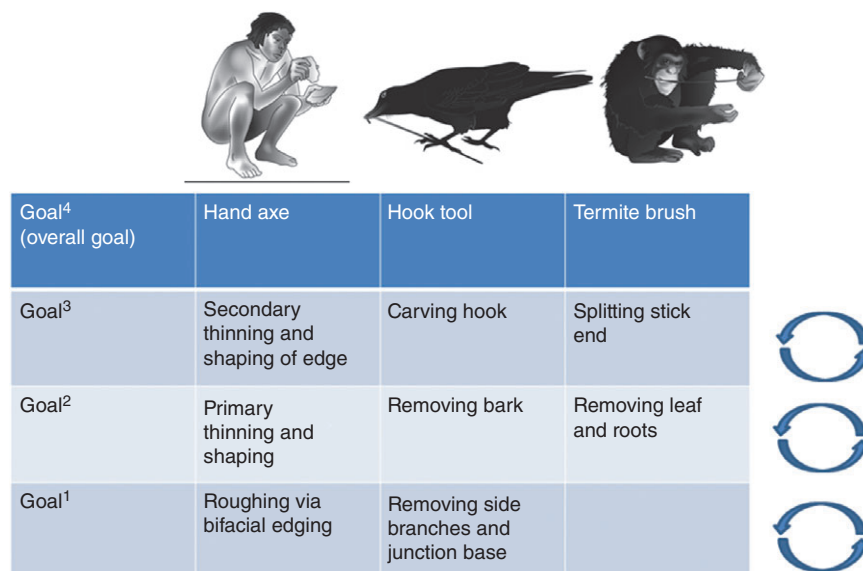| Goal[4] (overall goal)	Hand axe	Hook tool	Termite brush
Goal[3]	Secondary thinning and shaping of edge	Carving hook	Splitting stick end
Goal[2]	Primary thinning and shaping	Removing bark	Removing leaf and roots
Goal[1]	Roughing via bifacial edging	Removing side branches and junction base	

FIGURE 1 | The hierarchical organization of human stone tool crafting, New Caledonian crow hook crafting, and chimpanzee/orangutan brush crafting.

together into small groups.[29–31] These two species should therefore be considered as 'poster children' for the technical intelligence hypothesis. If they both have cognitive adaptations that are present in chimpanzees and humans, but absent in closely related non-tool-crafting species, then the most likely inference is that the evolution of these adaptations was at least initially driven by technical, rather than social, selection pressures.

Here, we examine whether there are cognitive similarities between humans, chimpanzees, orang-utans, and New Caledonian crows that are not shared by closely related non-tool-crafting species. We restrict our focus to comparison of tool crafters and non-tool crafters, due to the importance of tool crafting in human evolutionary history, rather than focus more broadly on tool behaviors (for a review of this wider area see Ref 32). We then discuss how we can increase our understanding of the effect of tool manufacturing abilities on the evolution of human and nonhuman minds.

EVIDENCE FROM METATOOL PARADIGMS

To solve a metatool problem an animal must use one tool to gain access to another, such as using a small stick tool to pull within reach a longer stick tool that can itself be used to gain food (Figure 2). It has been suggested that metatool use requires three cognitive challenges: (1) the understanding that a tool can be used on a nonfood item, such as another tool, (2)

the inhibition of actions toward the main food goal, and (3) the hierarchical organization of behavior into goals and subgoals.[33] Thus, metatool problems may require precisely the kind of hierarchical organization of ongoing behavior that is needed for stone tool manufacture. To date, studies on corvids have shown that New Caledonian crows can solve both two- and three-stage metatool problems[33–35], such as pulling up string to get a small tool, and then using this tool to get a longer tool which can be used to access food. Non-tool-making rooks can solve a two-stage metatool problem,[36] where they need to drop a large stone into a tube to gain access to a small stone that can be dropped into a thin tube and so gain food. Work on apes has shown that orang-utans and gorillas can solve a two-stage metatool problem,[37] using a short stick tool to gain a longer stick that can be used to gain food, while bonobos, chimpanzees, and orang-utans have recently been shown to solve a five-stage metatool problem where the apes had to gain progressively longer sticks in order to gain access to even longer sticks that had been placed further from them.[38]

This body of work does not suggest there is any difference in the metatool performances of tool crafters and non-tool crafters. Although gorillas do not make tools in the wild, they show no difference in performance at a two-stage metatool problem compared with orang-utans. Similarly, though tool crafting is seen in chimpanzees and orang-utans, but not bonobos, no performance difference has been found between these species. While New Caledonian crows and rooks have not been directly compared on the
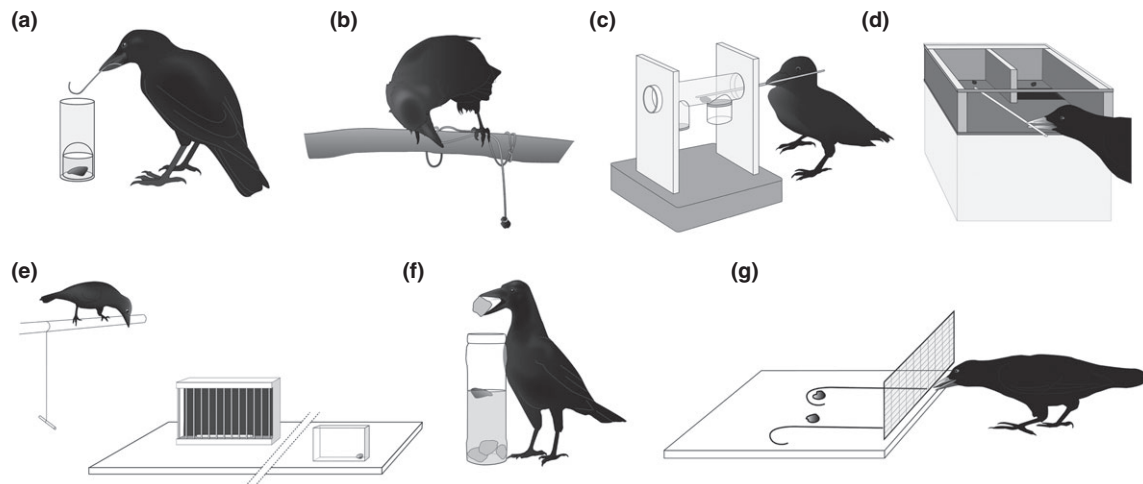
FIGURE 2 | Examples of (a) hook manufacture task, (b) perceptual-feedback task, (c) trap-tube task, (d) trap-table task, (e) metatool task, (f) water-displacement task, and (g) cane task.

same metatool task, the results found to date clearly show that both these species can solve a two-stage metatool problem. Further testing is required to see if rooks can also solve a three-stage problem. More generally, further refinement of the methodologies involved in metatool problems is required, as it has not yet been conclusively proven that these problems require the hierarchical organization of behavior, rather the lateral chaining of goals into a sequence, such that the completion of one goal triggers the behavior required for the next goal *etcetera*.[39]

THE CANE TASK

The cane task requires an animal to choose between pulling two hook-shaped tools laid flat on a surface (Figure 2). In some conditions the spatial relation between the food and the hook is varied (e.g. inside or outside of the hook), while in other the functionality of the hook is altered (e.g. broken vs solid cane). Work has shown that tool-using woodpecker finches do not outperform non-tool-using individuals of this species, or individuals of a closely related non-tool-making species, small tree finches.[40] However, a recent study provides evidence for a performance difference at this task.[41] While New Caledonian crows were able to learn to solve a cane pulling paradigm, carrion and hooded crows could not. In contrast, there was no difference between these species at a general learning task that did not require discrimination between object–object relations.

However, the New Caledonian crows performed poorly at the transfer tasks presented to them. The crows only attended to the relationship between food and hook if the food was close to the hook and

did not attend to the connectivity of the hook tool. This lack of sensitivity to connectivity mirrors the performance of New Caledonian crows at string pulling tasks.[42,43] As the authors themselves note, it is important to treat these results with caution, primarily because it is not clear the cane connectivity task actually taps into the physical cognition used in tool use and manufacture, and also because there were significant rearing differences between the New Caledonian crows and the other corvid species tested. While the New Caledonian crows tested were raised in the wild, the carrion and hooded crows were not.

Work on apes so far has not found a difference between tool-crafting and non-tool-crafting species when faced with tool functionality tasks including the cane pulling paradigm.[44] Interestingly, while all four ape species were able to solve connectivity tasks involving familiar cloth material and more novel rope material, they then all failed to choose functional cane tools over broken one. Captive sanctuary populations of chimpanzees and orang-utans were shown to also behave similarly, which suggests that these performances of these two species are not a product of experience with these materials. However, so far wild populations of non-tool-crafting ape species have not been tested to see if they also are capable of these simple discriminations.

EVIDENCE FROM HOOK MANUFACTURE STUDIES

One of the most impressive examples of tool manufacture within the Corvidae family is the manufacture of hook tools from man-made materials (Figure 2). Betty, a New Caledonian crow, was able to bend a

straight piece of wire into a hook and then use this tool to pull a bucket from within a tube.[45] While there is no evidence to date that any nonhuman great ape species is also capable of hook tool manufacture, non-tool-making rooks have recently been shown to be able to manufacture wire hook tools.[36] After experience using wooden hooks to pull a bucket from a tube, which Betty was also given in the initial study, four rooks then bent straight wire into a hook shape in order to retrieve food. The cognitive mechanism behind these performances has not yet been identified. However, what does seem evident from the results to date is that, at present, there are no differences in performance between a tool-crafting corvid and a related, non-tool-crafting species.

EVIDENCE FROM THE TRAP-TUBE PARADIGM

The trap-tube paradigm requires an animal to extract food from a horizontal tube while avoiding a trap set into its base[46] (Figure 2). Once an animal has learnt to successfully avoid pushing food into the trap during its attempts to gain food, researchers present transfer problems where a critical feature of the problem is changed. In early versions of the trap-tube paradigm the key transfer task was the inverted tube control.[46] Here, animals were presented with a trap-tube that had been flipped upside down, rendering the trap nonfunctional. An associative learning account predicts that animals should continue to avoid the trap because of its association with loss of the food when not inverted. In contrast, if the animals being tested have an understanding of the causality of the problem they should now ignore the trap, as objects cannot fall up. Chimpanzees and orang-utans have been shown to ignore the inverted trap, though only if they are able to pull rather than push the food.[47] In contrast, bonobos and gorillas did not learn to solve the initial trap-tube problem. However, it is not clear from this study if this difference is due to species differences or differences in sampling, as this study tested five orang-utans, two chimpanzees, two bonobos, and one gorilla, and found two orang-utans and one chimpanzee learnt to solve the initial problem. While New Caledonian crows ignore the inverted trap,[48,49] so do woodpecker finches, which do not craft tools.[50] Thus it is not at all clear that tool crafting is in any way linked to success at the inverted trap-tube task. Interestingly, humans continue to avoid an inverted trap when presented with this problem.[51,52]

More recent transfer tasks have examined the reaction of animals when cues associated with avoiding the trap are removed or reversed. One rook and one chimpanzee have been able to switch between treating particular visual cues as negative or positive,[53,54] but other species have not yet been tested on this paradigm. However, the fact that a non-tool-using rook performs as well as a chimpanzee rather suggests that this test requires a domain-general problem-solving ability, rather than any cognition that might have evolved specifically due to the selective pressures creating by tool crafting.[36] The trap-table paradigm involves an animal avoiding a trap embedded into a table, rather than a tube. This test can therefore be used to assess if an animal can continue to solve a problem when the cues associated with success have been removed. As the problem has the same causal structure as the trap-tube paradigm, an animal that has learn to solve the trap-tube can solve the trap-table task by transferring causal knowledge. New Caledonian crows are able to successfully solve the trap-table transfer task from the first trial while using tools,[48] as are the great apes[55,56] (but see Ref 57). In apes, transfer rates between functionally equivalent tasks increase without tools,[55,58,59] but irrespective of the task demands, no performance difference between apes have been found.

In sum, although some differences have been found between the performances of tool crafters and non-tool crafters when faced with the inverted trap-tube control, it is unclear if this is due to anything other than sampling error. The lack of differences between these two groups in their ability to transfer causal knowledge between functionally equivalent tasks supports this conclusion.

EVIDENCE FROM PERCEPTUAL-FEEDBACK STUDIES

String pulling task require an animal to pull a string with food attached to its end in order to bring the food within reach (Figure 2). The ability of birds to pull food hung vertically from a 40 cm string attached to a perch was, until, recently, thought to be product of 'insight'.[60–62] However, recent work on New Caledonian crows[42,43] suggests that such spontaneous string pulling is actually the product of heightened sensitivity to perceptual feedback. Performing two key behaviors, the pulling and stepping on a piece of string, leads the bird to gain positive feedback of the effects of their actions: the meat moves closer to the bird. This establishes a perceptual-motor feedback loop: pulling and stepping is linked to visual feedback of the food moving closer and so these behaviors are repeated. Given how useful the ability to quickly link behavior to outcome would be to tool manufacture, it is plausible that performance differences between tool

crafters and non-tool crafters might exist. The two bird species that have produced the most efficient solutions to string pulling problems are keas[63] and New Caledonian crows.[43] Both these species rapidly produced a sequence of pull-step behaviors without first carrying out any other behavior and obtained the food in only 7–15 s. In contrast, ravens presented with this problem take longer to get the food.[60] Performances of these species at various transfer tasks actually suggest that keas and ravens may have more understanding of the problem. While both keas and New Caledonian crows are able to discriminate between two slanted strings, one baited with meat and one baited with a stone, only keas and one raven have been shown to be able to discriminate between two crossed color strings. Keas did subsequently struggle with crossed string of the same color, which suggests that they did not have a full understanding of connectivity.[63] New Caledonian crows failed to discriminate colored strings of the same and different colors,[43] and they have failed other connectivity tasks.[42] This work therefore suggests that a performance difference may exist between keas, ravens, and New Caledonian crows, but in the opposite direction from that expected if tool crafting has an effect on cognition.

Evidence from the great apes also does not suggest that tool crafters have increased sensitivity to perceptual-motor feedback. When required to turn a crank handle in order to winch in food, apes required visual feedback of the effect of turning the handle on the food's position to solve the problem.[64] However, no difference in performance was found between the chimpanzees, bonobos, gorillas, and orang-utans tested, although further work with a larger sample size is required given that the success rate varied widely across the different species tested (50% for orang-utans, 33% gorillas, 25% bonobos, and 12.5% for chimpanzees).

EVIDENCE FROM WATER-DISPLACEMENT PARADIGMS

In the Aesop's fable paradigm floating food inside a tube can be brought within reach if the water level is raised (Figure 2). Ape studies to date have examined whether chimpanzees, orang-utans, and gorillas will spit water from a nearby container into the tube in order to raise the level. So far only orang-utans[65] and chimpanzees have been shown to solve this task,[66] which is precisely the kind of interspecies difference we might expect if such solutions were linked to tool crafting. However, this difference actually appears to be due to prior experience. If chimpanzees and gorillas are given water in a familiar water container they

do not solve the problem, but chimpanzees do solve the problem if they are given water in a novel water container. This suggests that functional fixedness is an issue, in that the chimpanzees have a bias to think of the water bowl in terms of its usual function (as a provider of water). So far gorillas have not yet been tested with a novel container, unlike chimpanzees and orang-utans. Further work is therefore required to establish if any interspecies differences exist.

Corvid studies with the Aesop's fable paradigm have examined whether these birds will drop stones into a tube in order to displace the water and so bring floating food within reach.[67–69] This paradigm offers great potential for examining tool-related cognition in tool-using and non-tool-using species, as it requires each species to learn a novel type of tool use that they do not perform in the wild. Additionally, unlike many other tests of animal cognition, the majority of individuals presented with the initial task can learn to solve it, which increases the effective sample size of studies. However, no large performance differences between these species have so far been found. Although Eurasian jays and rooks do not use tools in the wild, both species quickly learn to discriminate between water-filled and sand-filled tubes when stone dropping.[67–69] Similarly, rooks and New Caledonian crows quickly learn to choose large stone over small stones to drop into water, and Eurasian jays and New Caledonia crows both learn to choose floating over sinking objects. However, there may be smaller performance differences between these species, as so far, only New Caledonian crows have shown the ability to discriminate between various objects before dropping them into the water. On first trials, these crows have been shown to discard small stones and floating objects before they have actually witnessed the effect these objects have on the water level. Further sampling is therefore required in order to examine if there is a performance difference between these corvid species. However, even if such a performance difference were discovered, interpreting this difference would be highly difficult due to the different developmental trajectories of each species. At present, the New Caledonian crows that have been tested with this paradigm have grown up in the wild, while the rooks and Eurasian jays tested have grown up in captivity in single age cohorts.[67–69]

IS THERE EVIDENCE FOR ABSENCE OR ARE WE USING THE WRONG TOOL?

In summary, the majority of studies performed have not found any difference between tool-crafting and

TABLE 1 | Summary of the Performances of Tool-Crafting and Non-Tool-Crafting Species across Key Physical Cognition Tasks

Task	Description	Tool-Crafting Species Tested	Related Species Tested	Differences Found	Sampling Issues
Metatool	Use a tool on a tool	Chimpanzees	Gorillas	N	Y
		Orang-utans	Bonobos		
		New Caledonian crows	Rooks		
Hook manufacture	Make a hook	New Caledonian crows	Rooks	N	Y
Cane	Use a hook	Chimpanzees	Gorillas	Y/N	Y
		Orang-utans	Bonobo		
		New Caledonian crows	Carrion Crows		
			Hooded crows		
			Woodpecker finches		
Trap-tube	Avoid a trap	Chimpanzees	Gorillas	Y/N	Y
		Orang-utans	Bonobos		
		New Caledonian crows	Rooks		
			Woodpecker finches		
Perceptual-feedback	Link action to effect	Chimpanzees	Gorillas	N	Y
		Orang-utans	Bonobos		
		New Caledonian crows	Keas		
			Ravens		
Water-displacement	Gain out of reach floating food	Chimpanzees	Gorillas	Y/N	Y
		Orang-utans	Rooks		
		New Caledonian crows	Eurasian jays		

non-tool-crafting species (Table 1). While performance differences have been found using the cane task, inverted trap-tube control, and water-displacement paradigm (Figure 2), these differences may be due to factors such as sampling error, prior experience, and developmental history. There are three major problems that need to be resolved before any firm conclusions can be made about whether tool crafting helps drive the evolution of cognition.

Effective Sample Size

A large proportion of subjects typically fail the initial stage of many of the paradigms currently being used. In a field already rather notorious for issues with sample size, it is odd that such paradigms have been repeatedly used, as it leads to a situation where each study only has a handful of subjects (or less!) that actually learn to solve the initial problem. Only these subjects can then be given transfer or discrimination tasks in order to uncover what they have learnt. Thus sampling error becomes a major concern. One way to resolve this is to use paradigms that are sufficiently simple that the majority of individual tested can learn to solve the initial task and at least make some basic

choices correctly. The transfer tests presented can then be scaled up in their complexity, allowing us to create a gradient of performance across both individuals and species, rather than the all or nothing ratings of performance currently used.

The Aesop's fable paradigm is one test that has these characteristics.[67–69] In the studies conducted so far, animals have actually been trained to create the initial stone drooping behavior and then their performance at various discrimination tasks recorded. This training allows for the effective sample size to be close to that of the actual sample size, if not the same. Individuals from all the bird species so far tested have been able to learn stone dropping and make some correct object choices. This makes it easier to link subsequent failure to the cognitive challenge presented to subjects, rather than to other issues. It is hard to overemphasize the difference seen when comparing the Aesop's' fable paradigm to tests such as the trap-tube task or cane task. Individuals make correct choices on a range of discrimination tasks within 1–20 trials, rather than 150 trials. This speed of performance increases by an order of magnitude the number of tests that can be presented to subjects within the same time period, and thus provides us with far more

chance of finding performance differences between species. Other tests should be developed with similar characteristics, rather than relying on the unwieldy tests that have established themselves in the literature.

Linking Performance to Evolved Cognitive Differences

Differences in problem solving between species may reflect variation in learning, motivation, and development, rather than the presence or absence of tool-crafting-related cognitive mechanisms.[70] Ensuring that variables such as learning speed and inhibitory control are measured can help with this issue.[41] Another useful approach is the presentation of several tasks that tap into the same cognitive mechanism in different ways.[71] However, such extended testing is rarely carried out. The power of this approach is demonstrated by work using the Primate Cognition Test Battery (PCTB).[72,73] Interestingly, work using this test has found differences in physical cognition between orang-utans and chimpanzees. Extending this test to all the great apes could demonstrate if there are also differences between tool crafters and non-tool crafters. However, this approach cannot help if there is large variation in the developmental history of the species being compared. Captivity might lead to either an improvement or reduction in cognitive abilities, depending on the animal's experience in captivity and the task at hand. Thus, irrespective of the performance, this factor will always be able to explain behavioral differences between species when individuals of one species have been raised in the wild and the other in captivity. These problems can be overcome by acknowledging that, at best, it is only possible to compare captive populations to each other and wild populations to each other. Natural variation can then be used to address the problem of developmental history. Different populations of chimpanzees, orang-utans, and New Caledonian crows show different levels of tool use and manufacture.[74–76] Thus, one way to resolve this issue is to use within-species comparisons. By comparing isolated populations of the same species that do or do not use or make tools, it should be much easier to control for both developmental history and past experience.

Testing from First Principles

Perhaps the greatest problem with the existing paradigms is the lack of theoretical, and thus experimental, clarity. Various cognitive tests have been proposed as tests for physical cognition without reference to specific cognitive mechanisms, human-level performances, or cognitive signatures. This is best illustrated by the trap-tube and its various transfers. This test can be solved by using various cognitive mechanisms including an understanding of object–object interactions and an understanding of gravity.[53] At present none of the control tasks currently in use can unambiguously test between these two possibilities. Furthermore, humans do not react to this test appropriately,[51] which rather suggests it is not tapping into the type of sophisticated cognition we assume humans might use during tool behaviors.

The ideal way to test the technical intelligence hypothesis would be to: (1) analyze tool manufacture tasks in terms of the knowledge and planning they require, (2) identify the range of cognitive mechanisms that could be used during these tasks, including not only basic learning processes and the more sophisticated cognition used by humans but also the potential cognitive mechanisms intermediate between these two extremes, (3) develop behavioral tests for these mechanisms that could be presented to non-linguistic subjects, and then (4) present them to a series of carefully selected species, such as the tool-crafting species discussed in our introduction and their close relatives. The use of a 'signature-testing' approach,[77,78] where not only the successes of animals at cognitive tasks are studied, but also the biases, limits, and errors in their cognition would greatly inform such testing. Such an approach would allow us to identify if the same cognitive mechanisms were evolving in response to tool crafting, as cognitive similarities would be searched for along a number of dimensions (successes, biases, limits, and errors), rather than just one (successes).

In humans, stone tool crafting leads to the activation of brain areas responsible for increased sensorimotor and online hierarchical processing, but not planning or mental rehearsal.[14,15] Yet none of the animal studies mentioned above have focused on such cognition. While metatool studies have been claimed to require hierarchical processing,[33,38] they have not been designed in a way that eliminates the possibility of lateral chaining of goals into a sequence. Future studies should, therefore, use new paradigms that tap into the cognition used in human tool crafting. The battery-testing approach[72,73] could be usefully adapted in this regard. While to date the tests used in the physical domain have been based on the range of ecological tasks faced by primates in the wild, more specific tasks designed to mirror the requirements of tool manufacture, and in particular online hierarchical processing, would be very useful. Extending recent work on hierarchical planning in the great apes[79,80] would be one promising direction for future research.

CONCLUSIONS

At present we have little idea of the effect that tool crafting has had on the evolution of cognition. To make progress the field needs to develop experimental paradigms from first principles that focus on the signatures of the cognitive mechanisms underpinning tool crafting. Only if this 'signature-testing' approach is coupled with the use of appropriate sample sizes, within-species comparison and battery-testing will there be significant advances in our understanding of the effect of tool manufacture on the evolution of cognition.

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