



The interplay between psychological predispositions and skill learning in the evolution of tool use

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Tool use behaviours tend to be split into cases that appear to entail complex cognitive abilities and that are highly reliant on learning to be acquired (e.g. flexible tool use), and into others that seem to be more genetically canalized (e.g. stereotyped tool use). However recent evidences suggest that the differences between these forms of tool use are more nuanced than previously assumed, as in both cases tool use can entail some degree of both inborn predisposition and learning. Here, we particularly discuss the role played by intrinsic (e.g. not socially induced) motivation towards the manipulation of objects, in the emergence of flexible tool use. We highlight the importance of focussing on these psychological predispositions to understand the rarity of tool use among wild animals, as well as the higher proficiency in using tools that some species non-tool users express in captivity.

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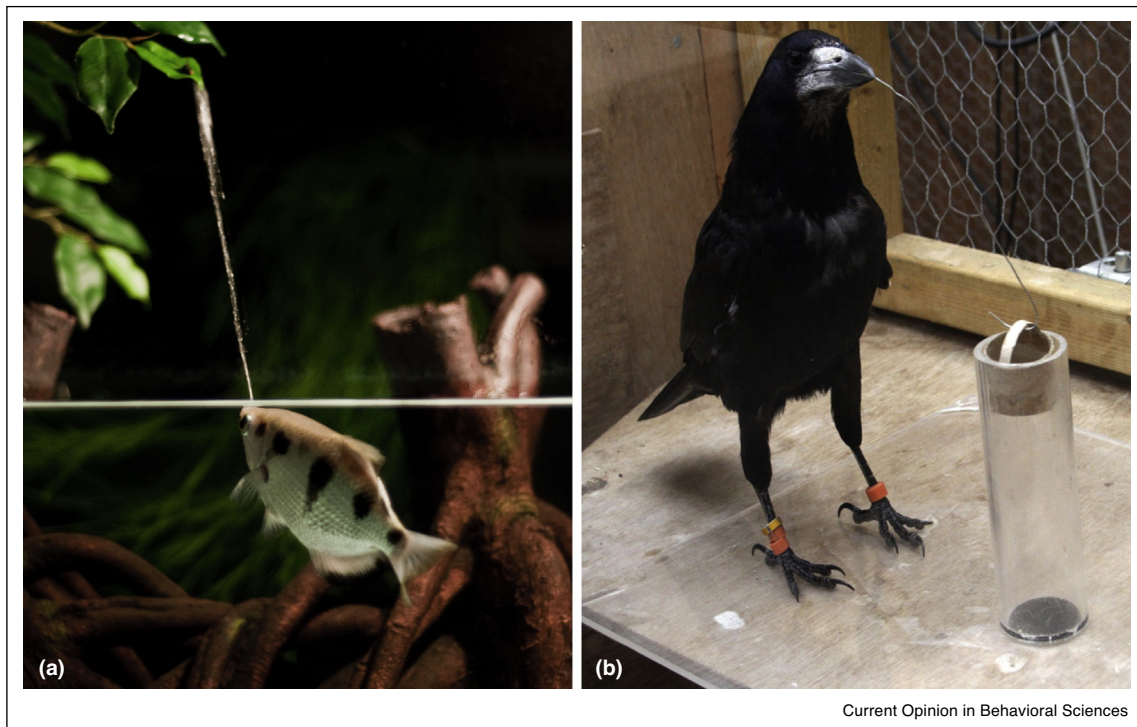
Introduction

Tool use has most commonly been defined as the ‘employment of an unattached or manipulable attached environmental object to alter . . . another object . . . when the user holds and directly manipulates the tool during or prior to use . . .’ ([1], pp. 5). Once viewed as one of the most iconic expression of humans’ intelligence, the ability to use tools has since been revealed to be widespread within the animal kingdom. From insects to fishes, and from birds to apes, non-human animals use tools for distinct purposes. For instance, sea snails use pebbles as leverage devices to restore their normal posture when they have been turned upside-down [2] and boxer crabs use stinging anemone to deter being attacked [3], while capuchin monkeys and Egyptian vultures use stones to crack respectively, nuts or eggs [4,5].

Despite fulfilling the same operational definition, these tool use behaviours are likely to vary dramatically in their cognitive underpinnings as well as in the role played by learning processes in the acquisition of tool use proficiency. With this in mind, researchers often split tool use behaviours into cases that appear to involve greater cognitive abilities and cases that do not. For example, according to Hunt *et al.* [6] tool use behaviours can be classified as either stereotyped or flexible. Stereotyped tool use behaviours emerge in the absence of prolonged individual practice or social inputs, they show little variation within species or genera, and they do not require any cognitive sophistication to evolve. In contrast, flexible tool use is acquired through long periods of apprenticeship, is highly variable among individuals and populations, and involves multiple cognitive skills. In a similar vein, ethologists often distinguish between customary and habitual tool use [7,8], with customary tool use consisting of more hard-wired behavioural specializations and habitual tool use being an expression of cognitive flexibility, reliant on social learning to be acquired [9]. Typically, stereotyped tool use is attributed to invertebrates and fishes and refers to behaviours observed in highly specific contexts only [6]. Conversely, flexible tool users, most notably chimpanzees and New Caledonian crows, can use (or even manufacture), a single tool for different purposes, or several tools to achieve a particular goal [10–15].

Important to stress however, is that, although flexible and stereotyped tool use behaviours differ substantially in several respects, both forms of tool use entail some degree of both inborn predispositions and learning. For instance, the spitting of water at prey by archerfish (Figure 1) is viewed as a textbook example of stereotyped tool use behaviour [6,10]. Nevertheless, it has been shown recently that these animals learn to hit rapidly moving targets at great heights through both individual and social learning [16] and flexibly shape their underwater jets according to the features of the substrate in which the food is buried [17]. Similarly, when presented with a set of artificial materials differing in soaking properties (e.g. sponge, plastic film), funnel ants maximize the amount of liquid food that they can transport to their nests by developing a preference for objects with good soaking properties [18]. Thus, animals that acquire tool use in absence of extensive practice may still be able to fine-tune these behaviours through learning. From the other perspective, examples of flexible tool use will also be underpinned by innate predispositions, to varying

Figure 1



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Photograph of (a) an archerfish spitting water at a target; (b) a rook using a hook-like tool. Photographs courtesy of Stefan Schuster (a) and of Nathan Emery (b).
b reprinted from [32].

degrees. For example, among New Caledonian crows, basic manipulation of tools emerges spontaneously during the first weeks post-fledging [19]. However, individual practice and social inputs appear to be essential for juveniles to acquire some of the more complex tool behaviours performed by this species, such as the manufacture of hooked stick tools or stepped pandanus tools [20,21]. Among primates, recent findings indicate that the dramatically more complex tool use repertoire of chimpanzees compared to that of bonobos [22], may be supported by a stronger attentional and motivational predisposition in using tools in the former species [23^{••},24^{••},25[•]], findings which we discuss in more depth in section two. Hence, although thinking about tool use in terms of sharp dichotomies is, to some extent, ideal to subsume the key differences among tool use behaviours, this approach requires caution. By doing so, we may risk to exacerbate the differences between these two forms of tool use, thus overlooking the role played by inborn predispositions in flexible tool use, as well as the involvement of learning processes in stereotyped tool use. Importantly, understanding what behavioural or cognitive building blocks support the emergence of flexible tool use in a given species can help us to develop more nuanced evolutionary explanations for why some animals use tools and some don't.

Here, we discuss the involvement of psychological predispositions in the evolution of flexible tool use. In the first part of the paper, we review the major categories of explanations for the rarity of flexible tool use in the wild and highlight how the investigation of psychological predisposition can provide key answers to this question. Subsequently, we turn our attention to animals that do not use tools in the wild, yet show remarkable tool use skills in captivity. We suggest that specific features of non-natural settings (e.g. absence of predators, human-provisioned food) may reduce the relevance of psychological predispositions in the acquisition of tool use behaviours (e.g. because more time and attention can be dedicated to explore objects), thus participating in explaining this apparent paradox.

Understanding the patchy distribution of flexible tool use

In the wild, the routine occurrence of flexible tool use is rare. It is most notably expressed in chimpanzees and New Caledonian crows (see [26] for a review), and a small number of other species. This is intriguing for two reasons. First, tool use is sporadic or absent in a large number of taxa that show outstanding complex cognition in other domains. For example, various parrot species excel in their physical cognition [27,28] and show striking skills

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