

Insight From Capuchin Monkey Studies: Ingredients of, Recipes for, and Flaws in

Capuchins' success

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Many years ago, while passing in front of a group of capuchin monkeys (*Cebus apella*) at the Rome Zoo, I was lucky to see an adult male pounding an unshelled peanut with a boiled potato. Why was he behaving like this? Peanuts can be opened easily and, moreover, boiled potatoes are soft. Could it have been that he was so fond of pounding with tools that he kept doing so even in circumstances in which the function would be sheer fun rather than ... trying to achieve an impossible goal?

The fact that capuchins were doing something smart in a silly way, or something silly in a smart way, struck my interest. I was fascinated and overwhelmed by them, as many other scientists have been before me (Erasmus Darwin and Konrad Lorenz, to cite only two very famous ones). Capuchins are the right species for an enthusiastic, rational and skeptical person like me. The delicate balance between chance and necessity, doing and understanding, ingredients and outcome has, indeed, fuelled all of my future research. What I have done since then is demonstrate, on the one hand, how successful capuchins are in solving problems and, on the other, how relatively little they understand of what they do. My research has focused on sorting out the ingredients of, the recipe for and the flaws in their success. Here, I will focus on capuchins' success in using tools and solving a task cooperatively and will discuss how their behavioral traits (e.g., interest towards objects, combinatorial activities, associative learning and "chance" in the case of tool use; manipulative tendencies, high inter-individual tolerance, associative learning and "chance" in the case of cooperation) foster their success and how their

cognitive capacities constrain what they are able to understand regarding the necessary conditions for success.

Tool use

The use of tools may enable or increase the exploitation of resources, such as foods that are difficult to obtain through direct action with hands or teeth. Our contemporary fascination with tool using in nonhuman species reflects a profound appreciation of the importance of tool use to our own species. There is no doubt that the use of tools has empowered humans to diversify their way of life and to exploit resources not available to other primates. Apart from the issue of intelligence, tool using is of interest to biologists because it is a means by which an individual can extend what it can do or where it can live. In the wild, the use of tools is widespread in chimpanzees, but observed less often in other apes. However, great apes and several species of monkeys use tools readily in captivity (Tomasello and Call 1997). Among monkeys, capuchins stand out as masters of tool use. Though in natural settings they rarely use tools, in captivity capuchins, like the apes, readily and spontaneously use tools in a large variety of circumstances (Visalberghi 1990; Anderson 1996).

Biologists and psychologists have speculated widely as to how nonhuman animals arrive at the efficient and sometimes elegant and skillful use of objects as tools. One common notion is that one individual learns to use a tool by observing another, as often happens in humans. In nonhuman primates, however, recent research has shown that imitation as we typically think of it (watching and then reproducing novel actions) plays a null (monkeys) or a limited (great apes) role in learning a new tool using behavior (Visalberghi and Fragaszy 1990).

The normal way of acquiring a new tool using skill by nonhuman primates involves both social influences and individual discovery (Fragaszy and Visalberghi 1989). For example, we presented capuchin monkeys with a food (apple sauce) source inside a container. The food could be obtained only through openings too small for the monkeys' hands, but large enough to allow the insertion of sticks or straws, which were both available to them. The monkeys showed immediate interest in the food and tried to get at it in every possible way. For the capuchin monkeys, one possible way was to poke into the container with an object at hand. This behavior is often seen during normal exploration, even when food is not involved. If the object happens to be the right size, shape and strength and if it is inserted deeply enough, then the monkey will succeed in getting the food. Once a monkey has incidentally succeeded this way (and here is where "chance" comes in), it is likely to repeat the actions and associate them with success. Other monkeys in the vicinity may observe closely and even obtain some food for themselves. Although social circumstances can increase an individual's interest in the tool, the container and its environs, there is no evidence to date that capuchins can learn the specific details of how to use a tool from watching others. It is clear, however, that social influences can inhibit an individual's access to a site of particular interest to other group members, and thus decrease the probability that the individual will discover how to solve the problem. Moreover, those individuals that reliably succeed in obtaining food from others may not become tool users themselves. Overall, the ingredients that make an individual a likely tool user range from exploratory and manipulative tendencies, to persistence in trying regardless of failure, to the immediate social context and individual social relationships. The notion that individual "intelligence" is the major factor accounting for success is not supported experimentally.

Why do captive capuchins (and other primate species) use tools more in captivity than in natural settings? We can dismiss the possibility that captive animals are somehow "smarter" than their wild counterparts. Rather, it seems that the combination of abundant free time for play and exploration, little space, and few and appropriate objects and surfaces, all make discovery of tool use more likely than in nature. When a researcher places something in the cage providing an interesting new focus for activity, the monkeys or ape's natural propensity to explore the object is sufficient for the occasional incidental combination of actions and objects that produces desirable consequences (Fragaszy and Adams-Curtis 1991). The captive conditions seem to channel the individual's propensities in a way that makes the discovery of tool use more likely.

Although insight or comprehension are not *required* to use a tool, if they are present, they increase the effectiveness of tool use. The more an individual understands about the functioning of a tool, the more effectively can he or she use it or change it to improve its effectiveness. Furthermore, understanding allows an individual to deal with variations of a problem without having to resort to trial and error. The above features are indeed part of what is special about the way in which humans use and manufacture their tools.

In the past, we demonstrated that capuchins learn to use a stick to push an object out of a horizontal transparent tube. Then we wondered whether this meant that they understood the properties of the tool and the relations between their action and the outcome, that is, that the stick displaces the reward and pushes it out of the tube. To test, we varied a property of the tube: we placed a trap in the middle of it, so that the tube was now shaped like a T with a very short stem (see Fig. 1). To push something out of this tube, the monkeys had to avoid moving the object in the direction of the trap. When faced with the task, capuchins that were otherwise proficient in pushing things out of tubes suddenly performed at chance level (Visalberghi and Limongelli

1996). One monkey eventually improved, but further testing showed that she was simply introducing the stick into the side of the tube farthest from the reward, without taking the position of the trap into account.

Insert Fig. 1 (the tube task)

When chimpanzees and 3-4 year old children were presented with the same task, some of the chimpanzees and almost all the children behaved in ways suggesting an understanding of the requirements of the task (Visalberghi and Limongelli 1996). When displacing the reward with the stick, the successful individuals took into account the presence of the trap (or learned to do it) and the position of the reward in relation to the trap. These findings show that different primate species may have different levels of understanding of the same problem. We can say that their tool recipe has different ingredients and flaws. Moreover, if we limit ourselves to a description of the final outcome (i.e. whether or not they succeed in doing the task) we are going to miss those processes that lead to success and those which in other circumstances could prevent it.

The fact that capuchins are very good in using tools, though limited in their understanding of what they do, provided us with the opportunity to appreciate the ingredients needed for tool use to occur and those that, if lacking, would produce flaws. And since the latter are visible only if *ad hoc* experiments are carried out, we also learned that laboratory experiments are fundamental to assess cognitive abilities.

Cooperation

Cooperation is a topic which can benefit greatly from capuchin studies. Cooperation increases individual success and has fitness implications; most ethologists have studied cooperation from an evolutionary perspective (for a review, see Dugatkin 1997) and very few have been interested in the proximal mechanisms fostering cooperation which can be studied well in the laboratory.

Cooperation may arise because individuals are "programmed" to cooperate or as a cognitive adaptation to overcome situations in which an individual alone would not be as successful as two or more individuals acting together. In the latter case, and especially in primates where cooperation has been considered more cognitively advanced than in other animals, you would expect individuals to take into consideration how, when and where their common actions can be successful. Yet, when primates engage in most of the so-called cooperative behaviors (e.g., coalitions and alliances, grooming, defense from predators, group hunting) it is very difficult to assess exactly what each individual must do to achieve the goal, what goal is being pursued by each individual, what each individual knows and which variables it takes into account when acting. In these naturally occurring events, the scientist has little information on and no control over the many variables involved and therefore cannot assess the role played by each individual in promoting or preventing the achievement of the (supposed) goal.

This unsatisfactory condition has prompted experimental investigations on apes (Chalmeau 1994; for a review see Visalberghi 1997) and capuchin monkeys in our laboratory in Rome (Chalmeau et al. 1997; Visalberghi et al. 2000) and elsewhere (Mendres and deWaal 2000). The task that could only be solved through cooperation consisted of an apparatus that required both partners to pull a handle simultaneously in order for both to be rewarded. The

handles were less than a meter apart so that the capuchins could closely monitor what the companion was doing. In particular, we expected them to learn to pay attention to where the other monkey was (far from the handle or close to it) and to what the other monkey was doing (about to pull or do something else that would affect the handle).

Our capuchins did very well, they succeeded in the cooperation task by learning to take the spatial position of the partner into account (for a similar finding see Mendres and de Waal 2000). However, they did not consider the partner's behavior, that is whether it was pulling or not. In short, capuchins cooperated while lacking comprehension of some of the conditions for success; for example, capuchins kept pulling (hundreds and hundreds of times!) even when their companion was meters away from the apparatus or when the companion was not pulling at all. The ingredients for their success were high inter-individual tolerance (note that when chimpanzees faced the same task some individuals were so afraid of their partner that they rarely, or never, pulled the handle) and the fact that they learned to pull more when the companion was present in the area close to the handle.

Fig. 2 (cooperation task)

What is it then that capuchins are lacking? And in what circumstances would we expect them to be unable to cooperate? Cognitively grounded cooperation would call for a capuchin to pull (or learn to pull) when the partner is pulling or when the partner is at least close to the handle and about to pull the handle. If we pretend that each subject can pull the handle only 10 times; in this more demanding situation -- since they do not seem to understand that their own pulling is effective only when the companion is also pulling -- we predict little success for the capuchins.

Conversely, a human being, or a child above a certain age, will make an effort to synchronize pulling. This is what full-fledged cooperation is all about: having a goal and a companion and performing the action(s) for achieving the goal when there are greater chances of success. Another example might explain this point further; when faced with the problem of having to displace a stone too heavy for one monkey in order to be able to get at a reward underneath, macaques sometimes solve the task (Petit et al. 1992). However, most of the time each individual tries to displace the stone by pushing in a different or opposite direction from that in which the companion is pushing. In short, they show no cooperation, but since they perform so many pushing actions, a few times the macaques will, by pure chance, show "coproduction" of pushing actions. Yet, since the macaques do not understand "why" their actions were sometimes effective and sometimes not, they are unable to repeat the desired outcome.

When cooperation relies upon cognitive capacities allowing an appreciation of what is going on, then it becomes a fundamental step in evolution and strongly increases behavioral flexibility. In contrast, when animals have a poor understanding of what they do, cooperation is more a matter of chance (capuchins) or of genes (ants, honey bees, etc.).

The idea of observing what capuchins do, how they learned it and what they understand of what they do is still in my mind. The research now in progress is aimed at trying to sort out how capuchins learn to determine what they eat and the extent to which their individual learning is socially biased

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Figure captions

Fig. 1. The Trap-Tube Task. In order to solve the task, the subject must insert the stick into the side of the tube from which it can push the reward out of the tube and not into the trap. Depending on the side in which the subject inserts the tool, it can either push the reward into the trap or push the reward out of the tube and obtain it. (a) A capuchin monkey has inserted the stick into the correct side of the tube. Note that the reward is on the right side of the trap. (b) Insertion in the wrong side of the tube. A reward lost in a previous trial is already inside the trap. (Black and White pictures)

Fig. 2. To solve the cooperation task both individuals should pull their handle. (Black and White picture)