Manuscript

Why human environments enhance animal capacities to use objects: Evidence from keas and apes

Ken Cheng[1] and Richard W. Byrne[2]

[1]Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia (ken.cheng@mq.edu.au)

[2]School of Psychology and Neuroscience, University of St. Andrews, Westburn Lane, St. Andrews, Fife KY16 8 PL, UK (rwb@st-andrews.ac.uk)

Corresponding address:

Ken Cheng
Department of Biological Sciences
Macquarie University
Sydney, NSW 2109 Australia

Email: ken.cheng@mq.edu.au
Phone: 61 2 98508613
FAX: 61 2 98509231

RUNNING HEAD: Object use in human environments

ABSTRACT

Formal training programs, which can be called education, enhance cognition in human and non-human animals alike. Even informal exposure to human contact in human environments, however, can also enhance cognition. We review selected literature to compare animals' behavior with objects in keas and in great apes, the taxa that best allow systematic comparison of the behavior of wild animals with those in human environments such as homes, zoos, and rehabilitation centers. In all cases, we find that animals in human environments do much more with objects. Following and expanding on the explanations of several previous authors, we propose that living in human environments and the opportunities to observe and manipulate human-made objects help to develop motor skills, embodied cognition, and the use of objects to extend cognition in the animals. Living in a human world also furnishes the animals with more time for such activities, in that the time needed for foraging for food is reduced, and furnishes opportunities for social learning, including emulation, an attempt to achieve the goals of a model, and program-level imitation, in which the imitator reproduces the organizational structure of goal-directed actions without necessarily copying all the details. All these factors let these animals learn about the affordances of many objects, and make them better able to come up with solutions to physical problems.

KEY WORDS: human environment; object manipulation; physical cognition; embodied cognition; extended cognition

INTRODUCTION

Explicit and sustained training programs, which can be called education, develop cognitive capacities in humans (Scribner & Cole, 1973) and in non-human animals. Pepperberg's long-term program with Alex the grey parrot evoked many remarkable cognitive achievements (Pepperberg, 2008). Immersing bonobos in what the authors called a *Pan/Homo* culture led to unexpected feats of communication and other behaviors in Kanzi the bonobo (Segerdahl, Fields, & Savage-Rumbaugh, 2005). And over three years of methodical operant conditioning in the home of Chaser the border collie led the canine to distinguish between over 1,000 objects (Pilley, 2013; Pilley & Reid, 2011). The methods and the outcomes of such cases have been well documented. Even informal contact with humans or living in human environments, however, can also lead to remarkable changes in cognition and behavior, even in the absence of explicit training. In what follows, we document some of the clearest cases and try to account for such changes.

Effects of living in human environments are curious. By human environments, we mean a heterogeneous set in which human-made objects are found, and some minimal interaction with humans is regular, including zoos, laboratories, and homes. How would simply living in human-built settings result in any changes in cognition, in the absence of explicit training? These effects promise to reveal something about the nature of cognition and its development in a number of animals—those for which suitable comparisons may be made. Scientists who have noted such differences, reviewed below, have commented on the nature of these anthropogenic effects, and we aim to add to what they have said.

We focus (1) on physical objects, and what animals can do with them, because many such instances have been reported in the literature; and (2) on species and behavior for which reasonable comparisons may be made between animals in human environments and their wild counterparts. We have not attempted an exhaustive search as we found it too difficult to come up with suitable search terms that limit the large opus on physical cognition in animals. The clearest cases come from keas and the great apes; our essay focuses on these cases. We try to make sense of the differences in object manipulations between captive and wild animals.

COMPARISONS OF OBJECT MANIPULATION BETWEEN CAPTIVE AND WILD ANIMALS

Keas

Among birds, various corvids have been observed to manipulate objects in human settings (rooks: Bird & Emery, 2009a, 2009b; Seed, Emery, & Clayton, 2008; Seed, Tebbich, Emery, & Clayton, 2006; Tebbich, Seed, Emery, & Clayton, 2007; Reid, 1982; New Caledonian crows: Weir, Chappell, & Kacelnik, 2002). But no appropriate comparisons with wild counterparts on similar tasks are available and for that reason, we will not review these cases.

A much better comparison of object manipulation in wild and captive birds comes from the research program on keas (*Nestor notabilis*) by Gajdon and associates (Gajdon, Fijn, & Huber, 2004, 2006). This case is particularly valuable for our analysis because the same task was proffered to both wild keas in New

Zealand's Mount Cook Village and captive keas in Vienna. Keas are the only alpine parrot in the world, endemic to New Zealand (Huber & Gajdon, 2006; informal summary: Cheng, 2016, ch. 14). Said to be neophilic, they take readily to human habitats, rummaging through garbage bins and sometimes twisting up windshield wipers in their exploration. They like various human foods, with butter being one of their favorites. In the task in question, butter was smeared on the outside of a hollow cylinder (Figure 1). The buttered cylinder was then inserted into an outer, hollow cylinder. The double-cylinder was in turn slid onto a long pole stuck in the ground. These steps had to be reversed to solve the task. The double-cylinder had to be pushed up the pole and over the top. The inner cylinder then had to be pushed out from its outer covering.

Figure 1 about here

All five of the captive keas tested in Vienna solved the problem (Gajdon et al., 2004). Three birds solved the tube-on-pole problem on their own, two in the first session, while the other two succeeded after observing a human model. In contrast, most wild keas in Mount Cook Village failed. Only 3 of 21 individually-banded parrots succeeded, among over 839 instances in which a bird was within a body length of the apparatus. The team then trained a demonstrator on the tube-on-pole task: but even watching a successful demonstrator did not improve the performance statistics. One caveat in comparing wild and captive keas is that the wild parrots were tested outdoors while the captive keas were tested in a Viennese laboratory. Although humans were not present, the outdoor testing condition might be more distracting in some way. Nevertheless, the contrast in performance level between wild and captive keas was stark.

Keas in Vienna also learned to lift tubes to dislodge a reward (Auersperg, Gajdon, & Huber, 2010) and wield sticks as tools to obtain rewards (Auersperg, Huber, & Gajdon, 2011). Gajdon and colleagues' Viennese keas also showed behaviors akin to tool use when simply provided with suitable objects in the lab (Gajdon, Lichtnegger, & Huber, 2014). Adolescents—although only one adult—inserted experimentally provided objects into tubes. This was play, as no extrinsic rewards were contingent on the behavior; however, most of these adolescents later inserted objects into tubes to retrieve a peanut. This task was not tested on wild keas.

In explaining differences in object-related behaviors between wild and captive keas, Huber and Gajdon (2006) invoked differences in cognitive development. They suggested that growing up in a human environment led the parrots to develop higher sensorimotor intelligence and learn more about the affordances of objects.

Great apes

Humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*) are well known for using tools (Byrne, 2016; McGrew, 1989). For our purposes, the most interesting comparisons are found in the other species, bonobos (*Pan paniscus*), orangutans (*Pongo* spp.), and gorillas (*Gorilla* spp.), animals that have only been infrequently observed to wield objects in the wild. To begin the comparison, the known cases of object handling in the wild need to be described.

Breuer, Ndoundou-Hockemba, and Fishlock (2005) reported what they considered the first observation of tool use in wild western lowland gorillas (*Gorilla gorilla gorilla*). One female used a branch to test the depth of a pool of water. Another used a tree trunk as a stabilizer, and also fashioned a bridge using a trunk. In using the trunk as a stabilizer, the wood was pushed forcefully into the ground, and the gorilla held on to it with one hand for stability while dredging with the other hand. In a later report, wild Cross River gorillas (*Gorilla gorilla diehli*) were observed to throw objects at humans (Wittiger & Sunderland-Groves, 2007).

In orangutans, Galdikas (1982) reported that the only forms of object use in the wild were found in contexts of agonistic displays, something that captive orangutans also do, and in nest-building. In agonistic displays, objects might be wielded or thrown. Subsequently, however, one population of the Sumatran orangutan (*Pongo abelii*) has been found to make and use sticks as tools, in two ways (Fox, Sitompul, & van Schaik, 1999; van Schaik, Fox, & Sitompul, 1996; Van Schaik & Knott, 2001). Arboreal bees are extracted by using a stick as a probe, manipulating it with the mouth; and the irritant hairs in the pod of the *Neesia* fruit are removed by wedging the pod open and raking out the hairs with a short stick. The researchers consider that these skills are culturally transmitted, and blocked from spreading to other populations by geographical barriers. No tool use has been found in the feeding behavior of any other population of this species or the sibling Bornean orangutan (*Pongo pygmaeus*). The newly named third orangutan species, *P. tapanuliensis* (Nater et al., 2017) has not received any systematic behavioral study as yet.

In contrast, gorillas, orangutans, and bonobos in captivity do many things with objects, resembling at times versatile tradespersons—in fact, in one study, orangutans were found to copy many of the tool-using activities of local handymen who worked where they were living in a rehabilitation camp.

Nakamichi (1998, 1999) observed 3 of 11 lowland gorillas at San Diego Zoo throw sticks at objects in trees. Fontaine, Moisson, and Wickings (1995) observed captive lowland gorillas manipulating objects in many ways. The group used sticks to reach things and as weapons. They also made rakes, and fashioned sponges. One gorilla used coconut fibers as sponging material, and used the soaked fibers for hygienic cleaning. Logs were used as ladders. And finally, one female fashioned a ball of leaves, which she placed on her neck and caught as it tumbled off. The authors suggested that this activity served as a replacement for a baby that she had lost: the mother used to catch her baby in a similar fashion.

At San Diego Zoo again, Nakamichi (2004) observed 4 of 5 Sumatran orangutans using tools. Three older ones made tools while one younger one used tools that had been made. The design of the enclosure provided incentives for making and using tools: various favorite fluid foods, such as BBQ sauce, peanut butter slurry, or apple sauce, were placed in the bottoms of pipes, out of reach of the orangutans. The tool makers fashioned food mops by picking branches, stripping off leaves and twigs, but leaving a distal end of leaves for mopping up food; one chewed and frayed the end of a stick and used the frayed end for soaking up the treats (Figure 2). Lethmate (1982) also observed object-related behaviors in captive orangutans: for instance, they covered spiky fruits (durians) with paper or leaves. Lethmate fueled object-related behaviors by posing various puzzles to the orangutans, including an out-of-reach reward: the orangutans pieced sticks together to make longer sticks (Figure 3), a form of tool manufacture.

Figures 2 and 3 about here

Extensive object use has been described in orangutans (*Pongo pygmaeus*) at a rehabilitation center in Indonesia (Galdikas, 1982; Russon, 1999; Russon & Andrews, 2011; Russon & Galdikas, 1993). Importantly, none of these acts were encouraged; indeed, since the intention of rehabilitation was to replace human-like behavior with “natural” actions, they were actively discouraged or punished. Orangutans used objects snatched from nature and objects made by humans, the latter including cups, spoons, and boats for crossing water, for which rafts and logs were also used. Like their wild counterparts, the rehabilitants brandished sticks and other objects in displays. Sticks were also used for hitting, poking, digging, reaching for objects, stirring hot liquids, or as ladders. Orangutans copied the local employees’ actions: cutting leaves from path-edges and raking them into piles, using a wooden stick rather than the local hoe; “sawing” wood, using a stick; washing clothes with soap, after paddling a canoe to reach the washing place; even trying to light a fire, by decanting paraffin with a vessel, to use as an accelerant, and fanning glowing embers with a metal plate. Coconut shells were used to scoop liquids; leaves were used as toilet paper, although such acts of wiping were not conducted after defecating. The rehabilitation center deliberately did not put bridges across a river at its boundary, to prevent its orangutans from venturing forth readily. One workman ruined that intention by plunking down a log as a bridge, once; thereafter, the orangutans copied the solution. Additionally, other materials such as vines were used as well for bridging the water. As we suggest below, such copying implies *program-level imitation* (Byrne & Russon, 1998), understanding and reproducing the organizational structure of goal-directed actions, but not necessarily minor and idiosyncratic details; and *emulation*

(Tomasello, 1998), understanding the outcome or goal of others' actions and acting to bring about a similar outcome.

Bonobos in captivity have also been observed to use objects (Jordan, 1982), in many of the ways that orangutans do. Bonobos in European zoos threw objects; sharpened sticks, and poked sticks into fissures, including their own orifices; hit objects with sticks or used them to reach and touch objects at a distance; propped branches against surfaces and used them as ladders; scooped liquids up with half a bell pepper or used a tennis ball or other absorbent materials to soak up liquids. Bonobos also played with balls, and constructed ropes out of long twigs.

EXPLAINING DIFFERENCES BETWEEN WILD AND CAPTIVE ANIMALS IN OBJECT-RELATED BEHAVIOR

Possible explanations for the recurrent finding of superior performance of captive or human-reared animals over their wild counterparts range from performance factors to various changes in cognition. On the one hand, an obvious possibility is that tame, and especially human-reared animals, are likely to be more relaxed and comfortable in the presence of experimenters or human artifacts, therefore able to deploy their full cognitive capacity. In contrast, wild animals or animals that are unwilling captives, are likely to be distracted or under stress, when their performance becomes degraded.

At the other extreme, the animal's cognition itself may change. It has been suggested that human rearing may have the power to enhance an animal's cognition to levels never typically seen in the species. This idea, termed the *enculturation hypothesis*, was proposed by Call and Tomasello (1996) to account for differences between captive and home-reared great apes in social cognition, including imitative learning of actions upon objects. Citing Vygotsky's (1962) similar hypothesis for human cognitive development, they suggested that the experience of being treated intentionally led to "a fundamental change in the social cognition of apes such that they begin to differentiate between means and ends in the behavior of others and thus view these others as intentional agents" (p. 394). At that time, as Call and Tomasello reviewed, experimental evidence from captive apes pointed to a bleak lack of understanding of others' agency, knowledge, beliefs, and false beliefs; Tomasello and Call (1997) did not accept the interpretation of observational data from wild apes that to several researchers pointed in the opposite direction (Byrne & Whiten, 1992; de Waal 1982, 1991). Suddendorf and Whiten (2001) did accept that evidence, and suggested a modification of the enculturation hypothesis, in which home-reared apes are enculturated to rich human environments, and wild apes are enculturated to rich natural environments—including complex social relationships and challenges of feeding in forest habitats. It is only captive, zoo, or laboratory-reared apes that grow up unenculturated and thus cognitively impaired.

We do not think either of these extremes provides a satisfactory explanation of the differences in object-related behavior associated with experience of humans. For instance, the hypothesis of distraction or stress from human presence does not easily account for the failures of many zoo or laboratory apes, which appear relaxed in human company, compared to human-reared apes. Nor is it really plausible that field sites such as Karisoke, Rwanda, where gorillas are relaxed enough to allow their young infants to crawl over researchers' feet (Fossey, 1983)—nowadays, greater distance is typically maintained by the researchers, for the health of the apes—are inhibiting or degrading the animals' cognitive capacities. Moreover, in some cases of the failure of wild individuals, such as the keas discussed above (Huber & Gajdon, 2006), humans were not near the test apparatus. Keas are certainly not shy of human artifacts. Indeed, wild keas have been observed to manipulate a host of human devices such as windscreen wipers, back-packs, or food containers (Huber & Gajdon, 2006; videos on the Internet of such kea behaviors can also be found readily).

Conversely, the enculturation hypothesis now seems unnecessary for what it was originally devised to explain, since the differences in social cognition between home-reared and zoo-housed chimpanzees have now disappeared, because of careful new experiments (Tomasello, Call, & Hare, 2003). One by one, the Rubicons of social cognition have been crossed. The most recent case is false-belief understanding (Krupenye, Kano, Hirata, Call, & Tomasello, 2016). Krupenye et al.'s (2016) study borrowed an experimental technique often used in infant research, observing anticipatory looking. In three great ape species, chimpanzees, bonobos, and orangutans, their looking behavior predicted correctly the behavior of another animal holding a false belief. Whether anticipatory looking reflects a full understanding of false belief may be disputed, and Krupenye et al.'s (2016) study remains the only study using the technique of anticipatory looking; the work has yet to be replicated. Nevertheless, it is consistent with other studies finding evidence that apes do represent mental states (Call & Tomasello, 2008), and we must look elsewhere for a general explanation of the beneficial effects that living with humans confers on a range of animals. An amalgam of views expressed in earlier works on this theme plus an expansion of a recent view of tool use (Mangalam & Fragaszy, 2016) might just provide the explanation.

Galdikas (1982) commented on the rehabilitant orangutans and their object-related exploits, making several suggestions still relevant today. She suggested they "probably learn some technological skills by observing the behavior of humans"; provisioning of food might also have led to more time for other activities, including activities with objects, thus furnishing learning opportunities; and she reckoned that wild orangutans possess great manipulative skills, skills that are not manifested in the wild as tool use, but shown in food processing. This latter theme has been re-iterated recently by one of us (Byrne, 2016); skillful plant-processing may be seen as a pre-adaptation to developing novel object manipulations, given the right opportunities by humans. We believe that all three of these proposals are important in understanding the effect of human exposure.

While assessing evidence for enculturation, Call and Tomasello (1996) also noted another explanation for the physical cognition of apes exposed to humans. These apes might benefit from gaining knowledge of objects, learnt by simple exposure to objects or by observation of humans interacting with objects, knowledge including object properties, relationships among objects, object affordances, and the potential benefits of using a tool. In Call and Tomasello's words, "*Exposure* to human artifacts and *emulation* of their use leads to quantitative increases in knowledge of objects and their properties and dynamic affordances" (p. 390, emphasis in the original). At that time, Call and Tomasello considered imitation to require understanding of others' intentions, and therefore beyond the capacity of great apes that had no such understanding (Tomasello, 1996). Since then, both premise and consequence have been called into question: program-level imitation may not require intentionality (Byrne, 1999a, 2003); and apes may in any case possess some intentional understanding of others (Buttelmann, Schutte, Carpenter, Call, & Tomasello, 2012; Hare, Call, & Tomasello, 2001; Schmelz, Call, & Tomasello, 2011), and can imitate arbitrary novel actions (Hobaiter & Byrne, 2010). Problem-solving routines performed successfully by humans may therefore be copied by imitation as well as emulation, augmenting the package of potential benefits from human exposure. Indeed, paying attention to human action is a useful activity to pursue (Bjorklund et al., 2002; see also Bering, 2004).

Manipulative skills also formed part of the explanation given by van Schaik, Deaner, and Merrill (1999) for the distribution of tool use across primates. All great apes possess superb manipulative skills (Byrne, 2016), and keas are manipulative. Beyond dexterity, van Schaik et al. (1999) listed "intelligence" as a contributing factor to tool use, but whether this concept is necessary, in addition to the other factors we describe, is not clear. With those two ingredients, the right kind of captive setting would deliver “enough opportunities for invention or exposure to skilled users” (p. 727), the latter conducive to social learning such as emulation or imitation. Also in van Schaik et al.’s (1999) mix is social tolerance, a trait that helps to spread skills across a population. The kinds of settings reviewed above, for human-reared keas and the great apes exposed to humans, feature the characteristics of much exposure to skilled object manipulators, humans or conspecifics, in groups of animals tolerant of each other and, importantly, of humans.

Additionally, we would stress the very extensive opportunity for practice that living with humans affords, especially for playful species. Along with the long-accepted benefits of play in developing musculature, such as the pouncing tactics of a kitten, and allowing safe practice of activities that are risky in adult life, such as play-fighting by a puppy (Bradshaw, Pullen, & Rooney, 2015), play allows individuals to build up their personal repertoire of motor skills (Byrne, 1995). Play is now thought to be widespread in vertebrate animals (Burghardt, 2015), and even in some invertebrates (Kuba, Meisel, Byrne, Griebel, & Mather, 2003; Mather & Kuba, 2013; Zylinski, 2015). Parrots, including keas, are said to be particularly playful (Burghardt, 2015). This may significantly augment their innate repertoire, especially when their juvenile experience brings them into contact with objects and situations that do not form a normal part of the species' environment, as is the case with human rearing.

Overarching all these strands, we see embodied and extended cognition expanding the cognitive ranges of these animals living in human environments. Traditionally, cognition has been viewed as an abstract, disembodied activity (Cheng, 2018; Kaplan, 2012; Michaelian & Sutton, 2013), contrasting with the lowly practicalities of deploying motor skills appropriately. This does not hold water. Cognition is boosted by engagement of motor action (embodied cognition) and by interactions with objects in the environment, some of which constitute extended cognition.

In some contexts, embodied cognition could mean actions orchestrated largely outside of the central brain (Cheng, 2018; Hochner, 2012, 2013), often with strong support from the environment; this kind of cognition outside the brain rarely applies to primates, but is not totally absent (Lavoie et al., 2018). In the context here, embodied cognition means that cognition construed as “advanced” or “complex” depends critically on the repertoire of motor actions that the subject possesses. One recent thesis claims that embodied cognition is essential for tool use (Mangalam & Fragaszy, 2016). For Mangalam and Fragaszy, tool use redistributes the degrees of freedom in deploying body parts engaged in manipulating objects, from the degrees of freedom linked with the body to the degrees of freedom linked with the body plus tool, conceived as one coherent system.

Extended cognition, in its most general description, means learning to use objects external to the individual for cognitive support (Cheng, 2018; Clark & Chalmers, 1998). For humans, such objects include a notebook (an example made famous by Clark & Chalmers, 1998) and, nowadays, a smartphone. The boundaries of extended cognition are argued over (Cheng, 2018; Michaelian & Sutton, 2013). In liberal versions, boundaries range widely. Entire institutions that humans sometimes rely on form edifices of extended cognition, social institutions such as the Internet or law (Gallagher, 2013). In conservative versions of extended cognition, links between the acting animal and the object must be tighter. Kaplan (2012) formulated the mutual manipulability criterion for extended cognition (for further refinements, see Hewitson, Kaplan, & Sutton, 2018). In mutual manipulability, the object must play a causal role in the animal’s cognition, and the animal’s cognition in turn must causally affect the object. Web-building spiders’ manipulations of their webs have been showcased as an example satisfying the mutual manipulability criterion (Japyassú & Laland, 2017; see also Cheng, 2018).

The web tension affects the attentional threshold of the resident spider: the looser the web, the larger the object impacting the web must be to catch the resident spider's attention. The spider in turn adjusts the web tension depending on its state, such as its hunger level. The animals living in human environments extend their cognition with the many objects found in their habitat, including extensions that satisfy Kaplan's mutual manipulability criterion. We expand on the notions of both embodied and extended cognition briefly as they apply to animals in human environments.

All great apes readily apply their actions in ways consistent with developing embodied cognition, suggesting that the propensity is found in the ancestor of modern great apes. Thus, a young mountain gorilla, attracted to leaves, stems, and other plant material of practical interest to adults, will by playing with them learn which actions result in tearing, stripping, rolling or accumulating the material; later in development, these actions will form the basic building blocks of the hierarchically structured, multi-stage processing skills that are essential for adult survival (Byrne, 1999b). They are predisposed to expand their embodied cognition. A human-reared animal, possessed as it will be of a richer personal repertoire of motor actions to manipulate the world of human objects and artifacts, is in a much better position to acquire and deploy successful solutions to novel problems posed by experimenters and to find new useful or playful things to do with objects.

A helpful ingredient already mentioned is spare time, which a human-provisioned environment typically allots in abundance. With spare time, playful animals get to practice. It usually takes practice to redeploy degrees of freedom

(Mangalam & Fragaszy, 2016), and a well-practiced animal is more likely to exhibit behaviors with objects, and hence more likely to be observed doing so. Spare time and the opportunity to practice might also lead playful animals to improve their exploration of new things to do with objects, perhaps reflecting practice in thinking, although this thesis remains to be explored.

The expansion of mind goes further than embodied cognition to extended cognition. Some, but not all feats that redeploy degrees of freedom in the limbs of apes, thus satisfying Mangalam and Fragaszy's (2016) conception of tool use, are accompanied by manipulations on the tool to be used. Joining two sticks together or fraying one end of a stick to mop up liquids entails the cognitive systems of the animals causally affecting the objects, the tools. These cases satisfy Kaplan's (2012) mutual manipulability criterion. Even choosing an appropriate tool out of the many objects available satisfies the mutual manipulability criterion minimally. The range of objects found in human environments fosters the development of extended cognition in great apes.

Other feats of apes reported earlier, however, hardly redeploy degrees of freedom in the limbs, and seem not to satisfy the mutual manipulabilty criterion. Throwing a log down or pushing a box to use as a ladder does not require redistributing degrees of freedom, and consequently would not count as tool use in Mangalam and Fragaszy's (2016) conception. The apes also do not shape a box or log in pushing them around; mutual manipulability fails in these cases. Nevertheless, these acts with objects expand what the apes can do; they extend cognition in an informal sense. Foraging for difficult-to-get items might well have ensured the survival of extant great apes in competing with energy-efficient monkeys (Byrne, 2016), and the challenges of foraging bring entanglements with objects, often in just getting to the food. Depending on the challenge, a mix of embodied and extended cognition and learning of the affordances of objects is encompassed by such tasks. We suggest then, that great apes are pre-adapted for embodied and extended cognition. Faced with the range of objects in human environments, in fact with a human culture that fully embraces extended cognition, and with much time on their hands, many objects end up as part of their embodied and extended cognition, mops for slushy food and logs for ladders among them.

A similar analysis could be applied to the case of keas. They too are predisposed to engage with objects and to explore relationships among objects, in the current terminology, predisposed to embodied and extended cognition. Huber and Gadjon (2006) suggest that the many opportunities in human environments to explore the properties of objects trigger cognitive development in captive-raised keas. They suggest that keas are not only interested in the effect of their action on objects, such as watching if a bit of food tossed in water sinks or floats, but also on relations between objects. They hint that practicing these aspects of embodied and extended cognition, to use our terms here, might lead to insight, imagining the outcomes of actions on objects. Whether and how human environments bring out embodied and extended cognition in certain animals deserves more study.

A methodological note from our analysis—which is not new but bears repeating—is that the rearing history of test animals matters in research on cognition. A more specific recommendation is that it would be good to test animals with a variety of rearing histories to obtain the best picture of the cognitive capacities of a species. While it is easiest to test subjects reared in the laboratory, animals caught from the wild, or even tested in field conditions, could add to the richness of the research.

In sum, we suggest that the richer basic repertoire of human-reared animals, together with their greater knowledge of human objects and artifacts—their properties and affordances, and in the case of certain species such as apes, the knowledge of effective plans of action they have acquired by observational learning, using emulation and program-level imitation—is sufficient to explain the intriguing effect of humans on object-related behavior of those animals which already possess manipulative skills.

Acknowledgements

The authors declare no conflicts of interest.

References

Auersperg, A. M., Gajdon, G. K., & Huber, L. (2010). Kea, *Nestor notabilis*, produce dynamic relationships between objects in a second-order tool use task. *Animal Behaviour, 80*, 783-789.

Auersperg, A. M., Huber, L., & Gajdon, G. K. (2011). Navigating a tool end in a specific direction: stick-tool use in kea (*Nestor notabilis*). *Biology Letters, 5*, 455-458.

Bering, J. M. (2004). A critical review of the "enculturation hypothesis": the effects of human rearing on great ape social cognition. *Animal Cognition, 7*, 201-212.

Bird, C. D., & Emery, N. J. (2009a). Insightful problem solving and creative tool modification by captive nontool-using rooks. *Proceedings of the National Academy of Sciences, 106*, 10370-10375.

Bird, C. D., & Emery, N. J. (2009b). Rooks use stones to raise the water level to reach a floating worm. *Current Biology, 19*, 1410-1414.

Bjorklund, D. F., Yunger, J. L., Bering, J. M., & Ragan, P. (2002). The generalization of deferred imitation in enculturated chimpanzees (*Pan troglodytes*). *Animal Cognition, 5*, 49-58.

Bradshaw, J. W. S., Pullen, A. J., & Rooney, N. J. (2015). Why do adult dogs 'play'? *Behavioural Processes, 110*, 82-87.

Breuer, T., Ndoundou-Hockemba, M., & Fishlock, V. (2005). First observation of tool use in wild gorillas. *PLoS Biology, 3*, e380.

Burghardt, G. M. (2015). Play in fishes, frogs and reptiles. *Current Biology, 25*, R9-R10.

Buttelmann, D., Schutte, S., Carpenter, M., Call, J., & Tomasello, M. (2012). Great apes infer others' goals based on context. *Animal Cognition, 15*, 1037-1053.

Byrne, R. W. (1995). *The thinking ape: evolutionary origins of intelligence*. Oxford: Oxford University Press.

Byrne, R. W. (1999a). Imitation without intentionality. Using string parsing to copy the organization of behaviour. *Animal Cognition, 2*, 63-72.

Byrne, R. W. (1999b). Object manipulation and skill organization in the complex food preparation of mountain gorillas. In S. T. Parker, R. W. Mitchell & H. L. Miles (Eds.), *The mentality of gorillas and orangutans* (pp. 147-159). Cambridge: Cambridge University Press.

Byrne, R. W. (2003). Imitation as behaviour parsing. *Philosophical Transactions of the Royal Society of London B, 358*, 529-536.

Byrne, R. W. (2016). *Evolving insight*. Oxford: Oxford University Press.

Byrne, R. W., & Russon, A. E. (1998). Learning by imitation: a hierarchical approach. *Behavioral and Brain Sciences, 21*, 667-721.

Byrne, R. W., & Whiten, A. (1992). Cognitive evolution in primates: evidence from tactical deception. *Man, 27*, 609-627.

Call, J., & Tomasello, M. (1996). The effect of humans on the cognitive development of apes. In A. E. Russon, K. A. Bard & S. T. Parker (Eds.), *Reaching into thought: The minds of great apes* (pp. 371-403). Canbridge: Cambridge University Press.

Call, J., & Tomasello, M. (2008). Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Sciences, 12*, 187-192.

Cheng, K. (2016). *How animals think and feel*. Santa Barbara: ABC-CLIO.

Cheng, K. (2018). Cognition beyond representation: Varieties of situated cognition in animals. *Comparative Cognition & Behavior Reviews, 13*, in press.

Clark, A., & Chalmers, D. (1998). The extended mind. *Analysis, 58*, 7-19.

de Waal, F. B. M. (1982). *Chimpanzee politics*. London: Jonathan Cape.

de Waal, F. B. M. (1991). Complementary methods and convergent evidence in the study of primate social cognition. *Behaviour, 118*, 297-320.

Fontaine, B., Moisson, P. Y., & Wickings, E. J. (1995). Observations of spontaneous tool making and tool use in a captive group of Western lowland gorillas (*Gorilla gorilla gorilla*). *Folia Primatologica, 65*, 219-223.

Fossey, D. (1983). *Gorillas in the mist*. London: Hodder & Stoughton.

Fox, E., Sitompul, A., & van Schaik, C. P. (1999). Intelligent tool use in wild Sumatran orangutans. In S. T. Parker, H. L. Miles & R. W. Mitchell (Eds.), *The mentality of gorillas and orangutans* (pp. 99-116). Cambridge: Cambridge University Press.

Gajdon, G. K., Fijn, N., & Huber, L. (2004). Testing social learning in a wild mountain parrot, the kea (*Nestor notabilis*). *Learning & Behavior, 32*, 62-71.

Gajdon, G. K., Fijn, N., & Huber, L. (2006). Limited spread of innovation in a wild parrot, the kea (*Nestor notabilis*). *Animal Cognition, 9*, 173–181.

Gajdon, G. K., Lichtnegger, M., & Huber, L. (2014). What a parrot's mind adds to play: The urge to produce novelty fosters tool use acquisition in kea. *Open Journal of Animal Sciences, 4*, 51-58.

Galdikas, B. M. F. (1982). Orang-utan tool-use at Tanjung Puting Reserve, Central Indonesian Borneo (Kalimantan Tengah). *Journal of Human Evolution, 10*, 19-33.

Gallagher, S. (2013). The socially extended mind. *Cognitive Systems Research, 25-26*, 4-12.

Hare, B., Call, J., & Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour, 61*, 139-151.

Hewitson, C., Kaplan, D. M., & Sutton, J. (2018). Yesterday the earwig, today man, tomorrow the earwig? *Comparative Cognition & Behavior Reviews, 13*, in press.

Hochner, B. (2012). An embodied view of octopus neurobiology. *Current Biology, 22*, R887–R892.

Hochner, B. (2013). How nervous systems evolve in relation to their embodiment: What we can learn from octopuses and other molluscs. *Brain, Behavior and Evolution, 82*, 19-30.

Hobaiter, C., & Byrne, R. W. (2010). Able-bodied wild chimpanzees imitate a motor procedure used by a disabled individual to overcome handicap. *Public Library of Science One, 5*, e11959.

Huber, L., & Gajdon, G. K. (2006). Technical intelligence in animals: the kea model. *Animal Cognition, 9*, 295–305.

Japyassú, H. F., & Laland, K. N. (2017). Extended spider cognition. *Animal Cognition, 20*, 375–395.

Jordan, C. (1982). Object manipulation and tool-use in captive pygmy chimpanzees (*Pan paniscus*). *Journal of Human Evolution, 11*, 35-39.

Kaplan, D. M. (2012). How to demarcate the boundaries of cognition. *Biology & Philosophy, 27*, 545–570.

Krupenye, C., Kano, F., Hirata, S., Call, J., & Tomasello, M. (2016). Great apes anticipate that other individuals will act according to false beliefs. *Science, 354*, 110-114.

Kuba, M., Meisel, D. V., Byrne, R. A., Griebel, U., & Mather, J. A. (2003). Looking at play in *Octopus vulgaris*. In K. Warnke, H. Keupp & S. von Boletzly (Eds.), *Proceedings of the International Symposium Coleoid Cephalopods Through Time* (pp. 163-169). Berlin: Weinert GmbH.

Lavoie, E. B., Bertrand, J. K., Stone, S. A., Wispinski, N. J., Sawalha, J., & Chapman, C. S. (2018). Examining the "species" of situated cognition in humans. *Comparative Cognition & Behavior Reviews, 13*, in press.

Lethmate, J. (1982). Tool-using skills of orang-utans. *Journal of Human Evolution, 11*, 49-64.

Mangalam, M., & Fragaszy, D. M. (2016). Transforming the body-only system into the body-plus-tool system. *Animal Behaviour, 117*, 115-122.

Mather, J. A., & Kuba, M. (2013). The cephalopod specialties: complex nervous system, learning, and cognition. *Canadian Journal of Zoology, 91*, 431–449.

McGrew, W. C. (1989). Why is ape tool use so confusing? In V. Standen & R. A. Foley (Eds.), *Comparative socioecology: The behavioural ecology of humans and other mammals*. Oxford: Blackwell.
Michaelian, K., & Sutton, J. (2013). Distributed cognition and memory research: History and current directions. *Review of Philosophy and Psychology, 4*, 1-13.
Nakamichi, M. (1998). Stick throwing by gorillas (*Gorilla gorilla gorilla*) at the San Diego Wild Animal Park. *Folia Primatologica, 69*, 291–295.
Nakamichi, M. (1999). Spontaneous use of sticks as tools by captive gorillas (*Gorilla gorilla gorilla*). *Primates, 40*, 487-498.
Nakamichi, M. (2004). Tool-use and tool-making by captive, group-living orangutans (*Pongo pygmaeus abelii*) at an artificial termite mound. *Behavioural Processes, 65*, 87–93.
Nater, A., Mattle-Greminger, M. P., Nurcahyo, A., Nowak, M. G., de Manuel, M., Desai, T., . . . Krützen, M. Morphometric, behavioral, and genomic evidence for a new orangutan species. *Current Biology, 27*, 3487-3498.e3481-e3410.
Pepperberg, I. M. (2008). *Alex and me*. New York: HarperCollins.
Pilley, J. W. (2013). Border collie comprehends sentences containing a prepositional object, verb, and direct object. *Learning and Motivation, 44*, 229-240.
Pilley, J. W., & Reid, A. K. (2011). Border collie comprehends object names as verbal referents. *Behavioural Processes, 86*, 184-195.
Reid, J. B. (1982). Tool-use by a rook (*Corvus frugilegus*), and its causation. *Animal Behaviour, 30*, 1212-1216.
Russon, A. E. (1999). Orangutans' imitation of tool use: a cognitive interpretation. In S. T. Parker, H. L. Miles & R. W. Mitchell (Eds.), *The mentalities of gorillas and orangutans* (pp. 117-146). Cambridge: Cambridge University Press.
Russon, A. E., & Andrews, K. (2011). Orangutan pantomime: elaborating the message. *Biology Letters, 7*, 627-630.
Russon, A. E., & Galdikas, B. M. F. (1993). Imitation in free-ranging rehabilitant orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology, 107*, 147-161.
Schmelz, M., Call, J., & Tomasello, M. (2011). Chimpanzees know that others make inferences. *Proceedings of the National Academy of Sciences USA, 108*, 3077-3079.
Scribner, S., & Cole, M. (1973). Cognitive consequences of formal and informal education. *Science, 182*, 553-559.
Seed, A. M., Clayton, N. S., & Emery, N. J. (2008). Cooperative problem solving in rooks (*Corvus frugilegus*). *Proceedings of the Royal Society of London B: Biological Sciences, 275*, 1421-1429.
Seed, A. M., Tebbich, S., Emery, N. J., & Clayton, N. S. (2006). Investigating physical cognition in rooks, *Corvus frugilegus*. *Current Biology, 16*, 697-701.
Segerdahl, P., Fields, W., & Savage-Rumbaugh, S. (2005). *Kanzi's primal language: The cultural initiation of primates into language*. Houndmills, UK, New York: Palgrave Macmillan.
Suddendorf, T., & Whiten, A. (2001). Mental evolution and development: evidence for secondary representation in children, great apes, and other animals. *Psychological Bulletin, 127*, 629-650.

Tebbich, S., Seed, A. M., Emery, N. J., & Clayton, N. S. (2007). Non-tool-using rooks, *Corvus frugilegus*, solve the trap-tube problem. *Animal cognition, 10*, 225-231.

Tomasello, M. (1998). Emulation learning and cultural learning. *Behavioral and Brain Sciences, 21*, 703-704.

Tomasello, M., & Call, J. (1997). *Primate cognition*. New York: Oxford University Press.

Tomasello, M., Call, J., & Hare, B. (2003). Chimpanzees understand psychological states — the question is which ones and to what extent. *Trends in Cognitive Sciences, 7*, 153-156.

van Schaik, C. P., Deaner, R. O., & Merrill, M. Y. (1999). The conditions for tool use in primates: implications for the evolution of material culture. *Journal of Human Evolution, 36*, 719–741.

van Schaik, C. P., Fox, E. A., & Sitompul, A. F. (1996). Manufacture and use of tools in wild Sumatran orangutans. Implications for human evolution. *Naturwissenschaften, 83*, 186-188.

van Schaik, C. P., & Knott, C. D. (2001). Geographic variation in tool use on *Neesia* fruits in orangutans. *American Journal of Physical Anthropology, 114*, 331-342.

Vygotsky, L. (1962). *Thought and language*. Cambridge, MA: MIT Press.

Weir, A. A. S., Chappell, J., & Kacelnik, A. (2002). Shaping of hooks in New Caledonian crows. *Science, 297*, 981.

Wittiger, J., & Sunderland-Groves, J. L. (2007). Tool use during display behavior in wild Cross River gorillas. *American Journal of Primatology, 69*, 1307–1311.

Zylinski, S. (2015). Fun and play in invertebrates. *Current Biology, 25*, R10-R12.

Figures

Figure 1. The cylinders-on-pole problem presented to wild and human-reared keas. Butter, a favourite food of keas, is smeared on the outside of a hollow cylinder (inset right). The buttered cylinder is placed inside another hollow cylinder. The two cylinders are then placed on a pole stuck into the ground. The bird must push the double-cylinder off the pole, and then push the inner cylinder out of the outer cylinder. From Gajdon, Fijn, and Huber (2004), Figure 1. With permission from authors and publisher. Reprinted by permission from Springer, *Learning & Behavior, 32*, pp. 62-71, Testing social learning in a wild mountain parrot, the kea (*Nestor notabilis*), Gajdon, G. K., Fijn, N., and Huber, L. (2004).

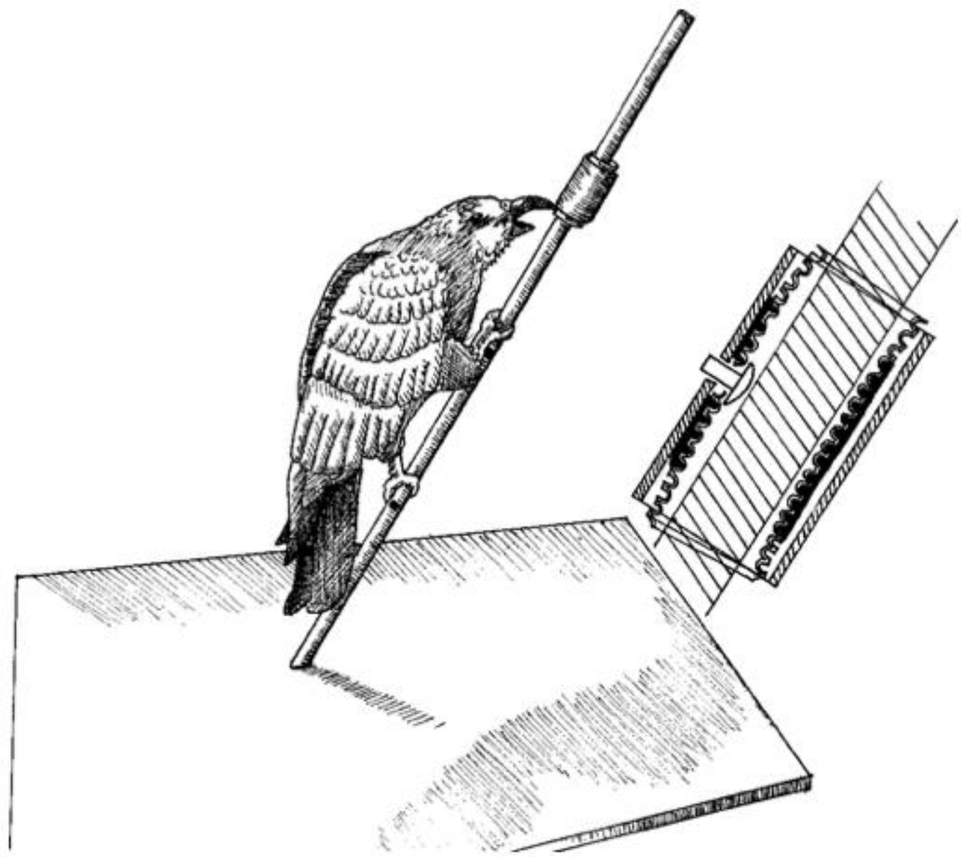

Figure 2. An orangutan at San Diego Zoo using a tool to extract orange-juice concentrate. Author: William H. Calvin, August 7, 2005. Nakamichi (2004) observed a number of orangutans at San Diego Zoo using fashioned tools to extract treats such as peanut butter slurry or BBQ sauce from the bottom of deep containers. In color online. Photo from Wikimedia creative commons: https://commons.wikimedia.org/wiki/File:Orangutan_using_precision_grip.jpg. Licence: https://creativecommons.org/licenses/by-sa/4.0/deed.en.

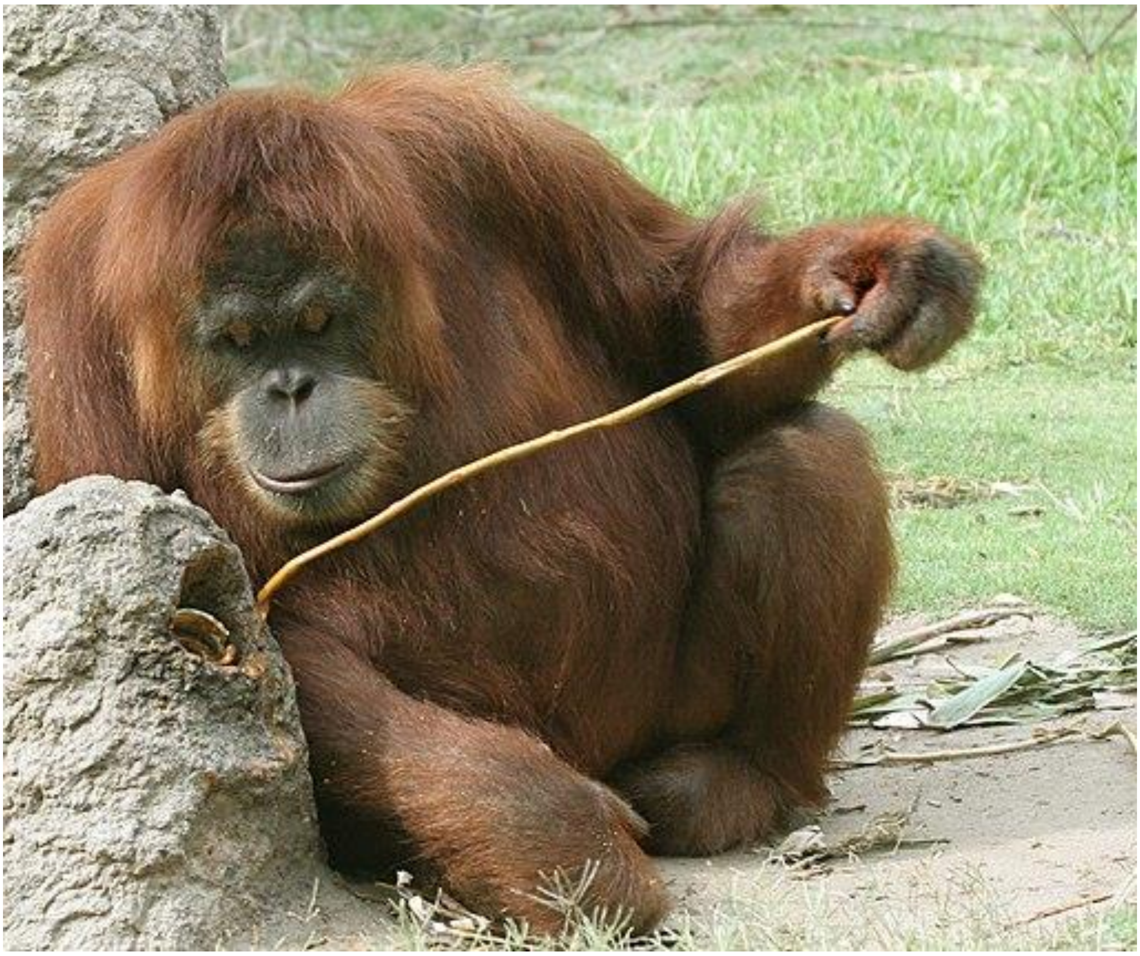

Figure 3. An orangutan called Mano solving a physcial problem. In the top photo, he has tapered one stick and split another stick, and is joining the two together to form a longer stick. In the bottom photo, he is using the longer stick to reach for food. From Lethmate (1982) Plate 2. Reprinted from *Journal of Human Evolution, 11*, Jürgen Lethmate, Tool-using skills of orang-utans, pp. 49-64, Copyright 1982, with permission from Elsevier.

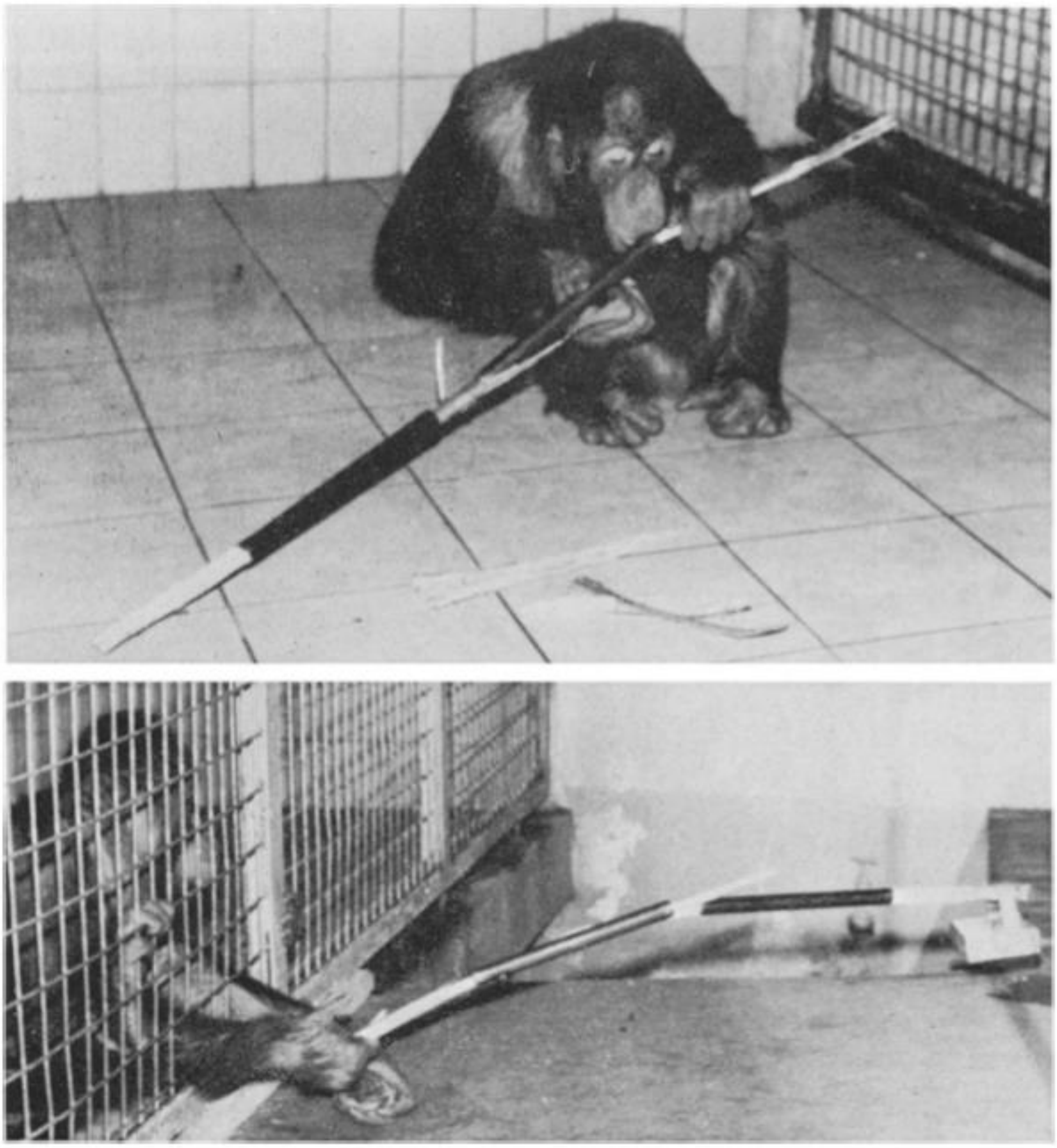

Figure 1

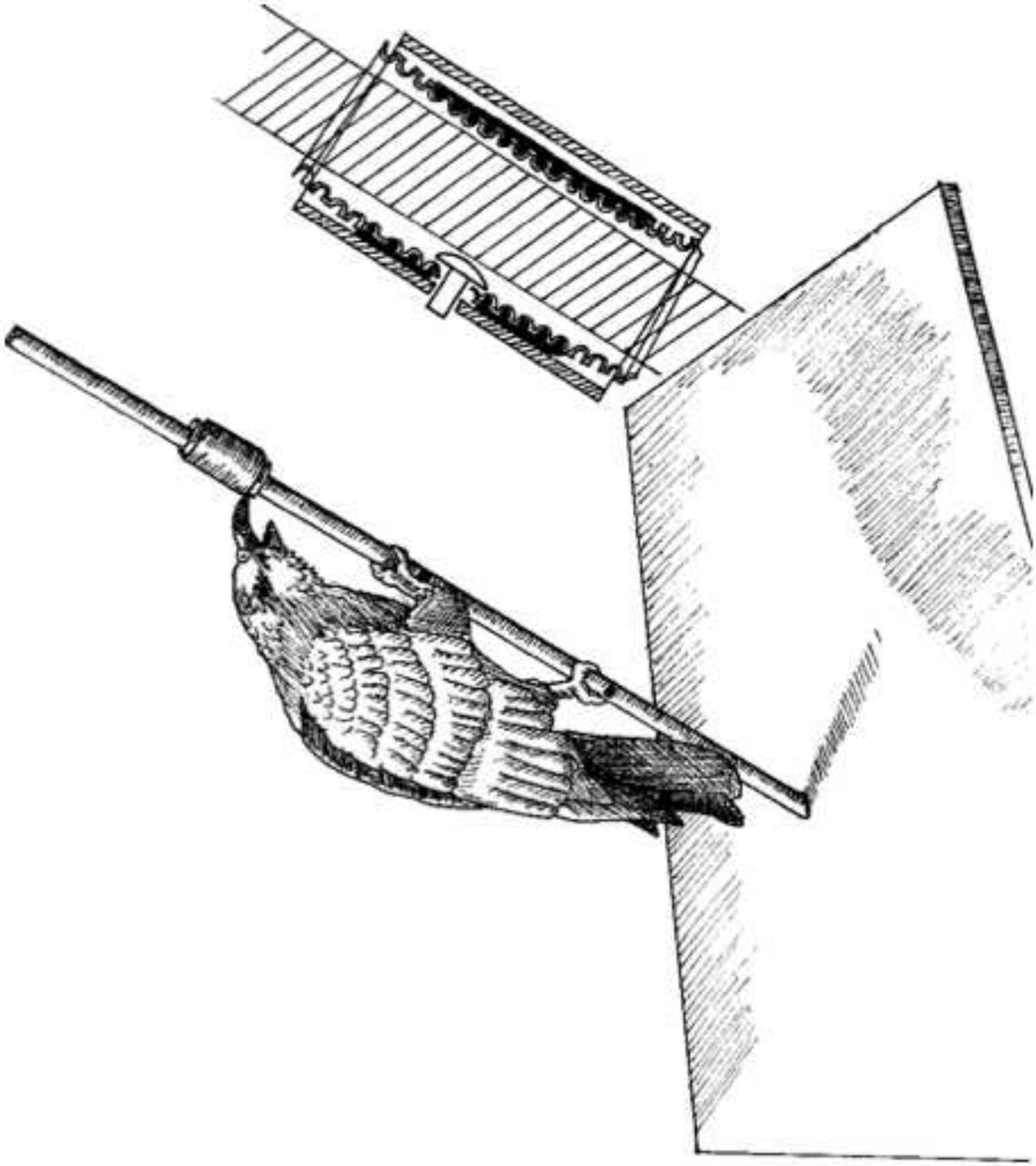

Figure 2

Figure 3