

“UNWILLING” VERSUS “UNABLE”: UNDERSTANDING CHIMPANZEES’ RESTRICTIONS IN COGNITION AND MOTIVATION

Shinya YAMAMOTO

Kyoto University, Japan

Human uniqueness and its evolutionary basis are explored through a comparison between humans and our closest evolutionary animals. With this approach, any behavior not demonstrated by non-human animals is considered unique to humans. We often attribute human uniqueness to a highly sophisticated cognitive ability that seemingly exists only in humans. However, even though non-human animals do not demonstrate a certain behavior, it is too early to say that they cannot demonstrate it. In this article, I introduce some examples in which chimpanzees have a cognitive basis for some social or cultural behaviors but do not perform these in their everyday lives, which urges us to consider not only cognitive restrictions but also motivational restrictions. I propose four hypotheses to explain their inaction. This type of “growth allowance” of cognitive abilities may help animals survive when they are challenged under a novel selective pressure during the exploration of a new environment.

Key words: unwillingness, inability, cognition vs. motivation, theory of mind, prosociality, social learning, cumulative culture, apes, human evolution

INTRODUCTION

The Evolution of Human Uniqueness

Human beings are spreading globally. Even in Antarctica, although there are no permanent settlers, hundreds or seasonally thousands of people live there. In contrast, most non-human primates inhabit only tropical and semi-tropical zones, with only a few exceptions in the temperate zone. The Japanese macaque is known as a primate species that lives in the northern limit of non-human primate habitats. The chimpanzee and bonobo, our evolutionarily closest-living relatives, live only in the tropical region of Africa. Regarding population, humans are unique compared to our close relatives. The global human population in 2021 was estimated at 7,875 million people (United Nations Population Fund, 2021), while great apes remain in units of tens of thousands to hundreds

Shinya Yamamoto, Institute for Advanced Study, Kyoto University, Japan, and Wildlife Research Center, Kyoto University, Japan.

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Correspondence concerning this article should be addressed to Shinya Yamamoto, Institute for Advanced Study, Kyoto University, Yoshida Ushinomiya-cho, Sakyo-ku, Kyoto 606-8501, Japan (e-mail: shinyayamamoto1981@gmail.com).

Table 1. Comparison Between Bonobos, Chimpanzees, and Humans Regarding Traits That Used to Be Considered Unique to Humans

	Bonobo	Chimpanzee	Human foragers
Extractive foraging	Only captivity	Frequent	Frequent
Non-conceptive sexual behavior	Frequent	Absent	Frequent
Lethal aggression between groups	Absent	Present	Present
Mother's importance to adult offspring	High	Low	High
Infanticide/Female coercion	Absent	Present	Present
Levels of adult play	High	Low	High
Cooperative hunting	Absent	Present	Present
Sharing between strangers	Present	Absent	Present
Male-male alliances	Absent	Frequent	Frequent
Female gregariousness	High	Low	High

Note. Adapted from Hare and Yamamoto (2015, 2017).

of thousands; the latter are all listed as endangered or critically endangered animals in the International Union for Conservation of Nature's Red List.

Comparative cognitive studies have struggled to investigate the cognitive properties that enable humans to prosper and to reveal the evolutionary basis for human uniqueness in non-human animals. Their efforts to date have revealed many similarities and differences between humans and non-human animals. Hare and Yamamoto (2015, 2017) listed some characteristics that used to be considered unique to humans and showed that some of these are shared with chimpanzees and others are shared with bonobos (Table 1). One of the most conspicuous behavioral differences between these ape species is the rarity of tool use in feeding contexts among wild bonobos (Ingmanson, 1996; Hohmann & Fruth, 2003) compared to chimpanzees, one of the most prolific and skilled tool users in the animal kingdom (McGrew, 1992; Whiten et al., 1999). Researchers have proposed several hypotheses to explain the differences between these sister species (Furuichi et al., 2015). The necessity hypothesis posits that tool use is a behavioral response to a scarcity of ecological resources; that is, low resource availability encourages animals to exploit novel food items with tools (Fox et al., 1999). The opportunity hypothesis proposes that the frequency of exposure to appropriate conditions, such as encounters with target items and the availability of tool materials, is the key to the emergence and maintenance of tool use (Fox et al., 1999). The relative profitability hypothesis emphasizes the comparison of profitability between tool-assisted feeding and conventional methods without tools. If tool-assisted feeding strategies targeted at embedded food items are more profitable than gathering more accessible foods, tool use is expected to evolve (Rutz et al., 2010). Shifting the viewpoint from ecological to social factors, the invention hypothesis predicts that, given that the invention of new tool use is rare in natural environments, the spread

and maintenance of tool use require sufficient opportunities for observational learning via proximity to conspecifics (Fox et al., 2004). Furuichi et al. (2015) proposed another hypothesis, suggesting that differences in tool-use behavior between bonobos and chimpanzees might not be explained by the current ecological or social conditions, but rather by circumstances during the Pleistocene epoch. Although these hypotheses are still controversial and we need more empirical data to examine them, investigation of the similarities and differences among species, including humans, should lead to a deeper understanding of how our common ancestors behaved and how specific behaviors evolved.

Distinction Between “Can” and “Do”

This kind of comparative study is essential for investigating human uniqueness. People often consider that if a certain behavior is observed in humans, but not in non-human animals, only humans are equipped with the behavior's sophisticated underlying cognitive abilities. However, especially when animals do not demonstrate a specific behavior, we need to be cautious about two possibilities: that the animals are unable to perform the behavior or that they can do it but are just unwilling. Bonobos' tool use is a typical case that requires attention to these possibilities. Wild bonobos virtually never use feeding tools in their natural environment. In contrast, captive bonobos have been observed to use a variety of tools, including stone tools, without intensive training by humans (Jordan, 1982; Gruber et al., 2010; Toth et al., 1993). This shows that bonobos are cognitively capable of using tools to obtain food. Thus, when we explain the rarity of feeding-tool use in wild bonobos, motivational restriction, rather than cognitive restriction, seems to matter.

Keep in mind that animals sometimes do not demonstrate specific behavior even when it is something that they can do (Fig. 1). This is not surprising because a behavior only appears as an action when a cognitive or neural foundation is in place, not the other way around (see also Leavens et al., 2019, for a discussion on the relationship between cognition and behavior from different viewpoints). This is analogous to cases of physical abilities in which, for example, a cheetah has the potential to run at a speed of over 100 km/h but does not run as fast during normal travel. The problem is that we sometimes assume that animals *cannot* do something when their performance is bad (or no different from a baseline or control condition) in a cognitive task and ignore the possibility that the animals are *not willing* to do that particular thing, despite being able. We often think that animals act to maximize the amount of food they earn per unit of time with minimum effort, which is often a prerequisite for assessing their performance in a cognitive task, but this is not always true. Animals sometimes show contradictory behaviors like *contrafreeloading*, in which, when offered the choice between provided food or food that requires effort to obtain, they prefer the food that requires effort (Osborne, 1977). Further, animals are sometimes highly motivated for non-food reasons, such as social interactions, and their performance in cognitive tasks that use food as a reward does not necessarily reflect their cognitive level accurately since the value of food varies according to social contexts (e.g., the same food was evaluated low in an inequity

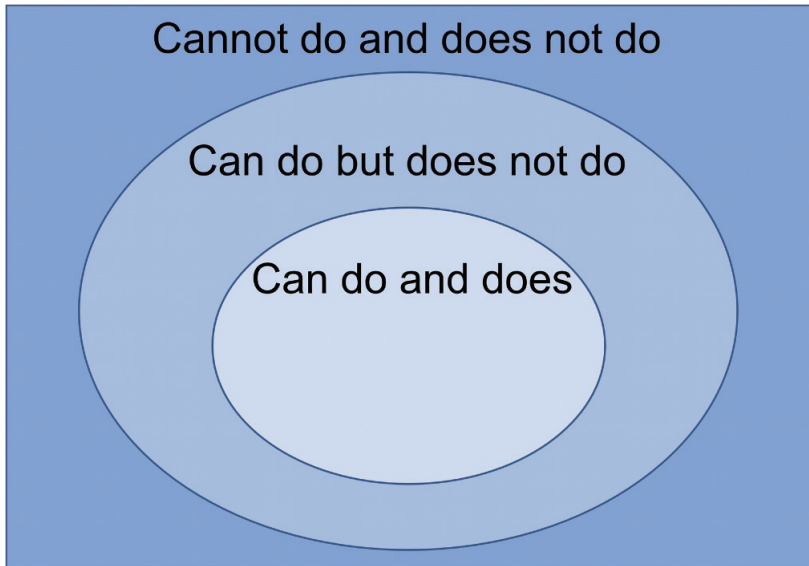


Fig. 1. Concept of the Area of Latent Cognitive Abilities (“Can Do but Does Not Do”)

situation in chimpanzees: Brosnan et al., 2005). Thus, cognitive and motivational restrictions should be considered equally but separately.

This difference between “can” and “do” is also seen in the developmental process of human behavior and cognition. Regarding the theory of mind, for example, many previous studies have shown that children over four years old can pass false belief tasks with verbal instructions and verbal responses (Wellman et al., 2001; Wimmer & Perner, 1983). However, recent studies suggest that children aged two years old or younger can pass non-verbal false belief tasks in which their non-verbal responses such as looking behavior were coded (Onishi & Baillargeon, 2005; Southgate et al., 2007). This suggests that children younger than four years old have already implicitly acquired a theory of mind, although they cannot demonstrate appropriate responses explicitly in verbal communication. Thus, although interpreting the results of the studies measuring looking behavior requires caution (Kulke et al., 2018), young children may have good cognitive abilities to understand the knowledge state of others, but they need to overcome other challenges (e.g., linguistic understanding; Bloom & German, 2000) for this ability to be exerted properly. Another example of a discrepancy between cognition and behavior can be observed in moral development. Previous studies have suggested a gap between what children believe they should do and what they actually do when given the chance to follow or violate moral norms. In a classic study, most children engaged in some form of deceit despite knowing that their actions were wrong, and cooperation varied widely by situation despite a common belief in doing good for others (Hartshorne et al., 1929). The gap between moral knowledge and behavior is also evident in resource distribution tasks, which are a core component of the early theories of moral development, and some changes in cognition and behavior (e.g., self-regulation, social distance, and social

learning) close this gap with age (Blake, 2018).

Enculturation and the Zone of Proximal Development/Evolution

This section introduces a similar but not identical concept that is often discussed in the context of human education. Children can sometimes do things with the help of an adult that they cannot do on their own. A Russian psychologist, Lev Vygotsky, emphasized that, in addition to the mature cognitive function acquired at some point in growth, children have a cognitive level that can be reached through “scaffolding” (Wood et al., 1976), such as assistance from others. He called this cognitive function reaching toward maturity the “zone of proximal development.” Vygotsky argued that education should be based on the child’s zone of proximal development—that is, on a level that is developing, but not on the child’s current level of development (Yasnitsky, 2018).

Gómez (2004) argued that “enculturation” functions as scaffolding and extends the area of cognitive-ability exertion in chimpanzees. It is known that encultured chimpanzees raised by humans in a human environment demonstrate highly sophisticated human-like social behaviors such as social reference (Russell et al., 1997) and communication with gestures or lexigrams (Gardner & Gardner, 1969; Savage-Rumbaugh, 1986), which are not normally observed in their natural environment. Gómez thought that this extensible area of cognition might suggest the direction in which the apes’ intelligence would evolve under novel evolutionary selection pressure and called it the “zone of proximal evolution.” Although this idea is still under speculation (Tomonaga, 2006), it suggests that the chimpanzee, as a species, is equipped with a cognitive basis that is not exerted in their natural daily life.

This article will introduce several examples in which chimpanzees have cognitive abilities but do not express them as behaviors beyond the context of enculturation. This article, titled “‘Unwilling’ versus ‘unable’: understanding chimpanzees’ restrictions in cognition and motivation,” is done so after the title of a famous study conducted by Call and his colleagues (2004), “‘Unwilling’ versus ‘unable’: chimpanzees’ understanding of human intentional action,” in which they showed that chimpanzees behave differently depending on whether a human is unwilling or unable to give them food, which suggests that chimpanzees understand the intentional actions of others. While the original paper focused on human intentions, this paper focuses on the unwillingness and inability of the chimpanzees. It discusses why non-human animals do not engage in a specific behavior even though they are capable of the behavior. This study will hopefully raise important points to be addressed in comparative cognitive studies and provide deeper insights into our understanding of human evolution.

CHIMPANZEES CAN DO IT, BUT DO NOT DO IT

This section will introduce some examples in which chimpanzees may plausibly possess cognitive abilities but do not exert them in action. There should be many more, but this work will focus only on the contexts of the understanding of others, prosociality,

and culture. These traits are still sometimes considered to be unique to humans, and thus, this choice is also helpful for thinking about the evolution of human uniqueness.

Theory of Mind

Researchers have discussed whether chimpanzees have a theory of mind ever since the first study of this kind was published in 1978 (Premack & Woodruff, 1978). Although several studies, such as those introduced above (Call et al., 2004), suggest that chimpanzees can understand others' behavioral intention, it was considered that a full-fledged theory of mind that enables us to comprehend reality-incongruent mental states (e.g., false beliefs) of others is unique to humans, as chimpanzees failed to make explicit behavioral choices that reflect false-belief understanding in several food-choice tasks (Kaminski et al., 2008; Krachun et al., 2009). Krachun et al. (2009) tested chimpanzees, bonobos, and human children in a competitive situation with a human competitor. In their research, a competitor witnessed an experimenter hiding a reward in one of two containers. The experimenter switched the locations of the containers when the competitor left the room or turned around. The competitor returned and reached with effort, but unsuccessfully, toward the incorrect container. During this process, apes did not display an understanding of the competitor's false belief, failing to choose the other container to find the reward, while children did. However, apes looked more often at the unchosen container in false belief trials than in true belief control trials, and the authors pointed out the possibility that the apes understand the competitor's false belief implicitly or uncertainly. Krupenye et al. (2016) confirmed this implicit understanding of false beliefs in apes by investigating their anticipatory looking behavior in a non-verbal false belief task that was modified for apes, from a task used for human two-year-old children (Southgate et al., 2007). Based on this evidence, chimpanzees seem to be able to understand other's mental states, but do not necessarily behave according to this understanding.

The exertion of this cognitive ability may also depend on context. Hare and Tomasello (2004) tested chimpanzees in two cognitive tasks, an object-choice task and a discrimination task, and examined whether the chimpanzees utilized social signals from another individual. This study aimed to compare the performance of chimpanzees in two contexts of cooperation and competition. They found that chimpanzees performed better in cognitive tasks when competing than when cooperating with others. The same individuals were tested in these two contexts, so this result shows that their exertion of cognitive ability is context-dependent and suggests that chimpanzees' social cognition evolved to outcompete conspecifics rather than to cooperate in their natural life.

Prosociality

Based on the above, chimpanzees' social cognition in cooperative contexts was investigated further. The question was whether chimpanzees do not understand others' goals or whether they understand them but do not behave accordingly. Previous studies empirically revealed that chimpanzees are cooperative to some extent (Warneken & Tomasello, 2006; Yamamoto et al., 2009). However, they found discrepancies in

prosociality between humans and chimpanzees regarding the range of prosocial application (Silk et al., 2005; Warneken & Tomasello, 2006) and proactivity (Yamamoto et al., 2009), which were reasoned as being due to chimpanzees' total lack or insufficient understanding of others' goals in some situations (Warneken & Tomasello, 2006). Yamamoto et al. (2012) examined chimpanzees' understanding of others' goals in a helping task in which a chimpanzee helper had to select an appropriate tool that worked to solve a partner's problem-solving situation from seven objects. The results showed that chimpanzees could understand their partner's goal by selecting an appropriate tool to give to their partner when they could visually inspect the partner's situation; nevertheless, they did not help proactively but mostly upon the partner's explicit request. Thus, the implication is that many chimpanzees' limitations in cooperation and prosociality are more motivational than cognitive (see also Melis & Tomasello, 2013).

Social Learning

Chimpanzees are known to be excellent social learners, while they are also considered to be conservative in their behavioral flexibility. Previous studies have shown that chimpanzees can learn a variety of behaviors from other individuals, such as the manipulation of a novel device (Whiten et al., 1996), the selection of tools and target foods (Biro et al., 2003; Hirata & Celli, 2003), and even tool-use techniques (Yamamoto et al., 2013). In Yamamoto et al.'s (2013) study, captive chimpanzees were provided with a straw tube; the chimpanzees spontaneously demonstrated two different techniques in obtaining juice through a small hole: "dipping" and "straw-sucking." Both the "dipping" and "straw-sucking" techniques demand that the same tool (straw-tube) for the same target (juice) be accessed from exactly the same location (small hole 1 cm in diameter). Therefore, the difference between "dipping" and "straw-sucking" was only in "technique." Although the two techniques differed significantly in their efficiency, their cognitive and perceptuomotor complexities were comparable. All five chimpanzees who initially performed the "dipping" technique switched to using the more efficient "straw-sucking" technique after observing a conspecific or human demonstrate the latter. This social learning of "technique" cannot be explained by the simple mechanism of local or stimulus enhancement and is a case of faithful, high-fidelity social transmission, which is considered to be the basis for human culture (Tennie et al., 2009).

There is considerable evidence showing chimpanzees' abilities in social learning; however, there are also many studies suggesting chimpanzees' conservatism. When chimpanzees are provided with multiple options to solve a problem, their previous knowledge either hinders the acquisition of a more optimal solution (Bonnie et al., 2012; Hanus et al., 2011) or prevents them from trying the novel (more rewarding) alternative that another is demonstrating (Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008). Another investigation (Yamamoto, 2013) of the tool-use behavior of chimpanzees was done in the Kumamoto Sanctuary of Kyoto University, the first and only sanctuary for chimpanzees and bonobos in Japan (Hirata et al., 2020; Morimura et al., 2011). Thirty-four chimpanzees were placed in 4–6 groups (15 individuals were grouped into 1–3 groups in which the composition varied daily, and the other 19 individuals were separated

into three constant groups). The chimpanzees were provided with a juice bottle attached to the outside of their enclosure fence and could drink the juice with tools made of natural plants or branches that were provided in the enclosure. The chimpanzees used two types of tools: stick and brush. Brush-type tools are much more efficient than stick-type tools because they can catch more juice at one time. Chimpanzees often chewed the tip of a twig to turn it into a brush before their first trial of drinking juice, which suggests that the brush-type tools were created intentionally and not as a by-product of chewing the juice from the tools. Interestingly, the two tool types co-existed in the same group. During the two-year observation, the tool types were consistent from individual to individual. Clearly, the chimpanzees had ample opportunity to observe each other (the juice drinking activities were provided regularly, twice a week, as one of the measures for environmental enrichment), and that all the chimpanzees were equipped with the physical skill to make the brush-type tool (they just chewed the tip). Considering the chimpanzees' (potential) social learning abilities introduced above, the chimpanzees can learn other types of tool-use by observing others, but they did not do so in practice.

One plausible explanation for this disagreement about chimpanzees' social learning is that chimpanzees apply a copy-if-dissatisfied strategy, rather than a copy-if-better strategy, in their social learning. If animals adopt a copy-if-better strategy, they switch their behavior if the returns of the adopted behavior exceed those of their original behavior, while animals applying the copy-if-dissatisfied strategy copy the action of a demonstrator only when they are not satisfied with the returns of their own current behavior (Laland, 2004). Compared to the copy-if-better strategy, which requires animals to make a judgment regarding whether a novel solution to a problem generates better returns than an established behavior does, the copy-if-dissatisfied strategy is simpler to implement because it does not require an assessment of the relative profitability of alternatives. Laland (2004) anticipated that the copy-if-dissatisfied strategy is likely to be more widespread in nature. The chimpanzees' conservatism, even with their abilities of social learning, can be explained by this strategy; that is, chimpanzees may not copy the behavior of others when they are satisfied with their own behavior, even though the alternative can produce more. In Hirata and Morimura's (2000) study, naïve chimpanzees frequently observed experienced tool users just after their failed attempts but never after their own success. van Leeuwen and Call (2017) suggested that chimpanzees adopt a copy-if-better strategy, demonstrating that chimpanzees forgo personal behavior in favor of relatively better variants observed in others. In their experiment, after being trained on one token-type, chimpanzees were confronted with a conspecific demonstrator who either received the same food reward as the subject (control condition) or a higher value food reward than the subject (test condition) for exchanging another token-type. However, the chimpanzees' behavioral shift in the test condition can be explained by the more parsimonious copy-if-dissatisfied strategy. Considering chimpanzees' sense of fairness (Brosnan et al., 2005), the subjects would feel dissatisfied in front of a conspecific that received a better reward for the same labor.

Cumulative Culture

Human uniqueness can be seen in the cumulative nature of culture. With successive generations building on earlier achievements, human culture accumulates modifications over time (“ratchet effect;” Tennie et al., 2009; Tomasello, 1999), arguably lacking an equivalent in other species, including our closest living relative, the chimpanzee, a species that otherwise demonstrates a variety of cultural traits such as tool use. For cultural accumulation, two important phases should be considered: the invention or modification phase and the transmission phase. In the transmission phase, faithful social learning of more profitable behavior invented by others is important, and the copy-if-better strategy is a plausible key element (Tennie et al., 2009). Chimpanzees’ conservatism or copy-if-dissatisfied strategy may hamper the accumulation of modification in their culture.

Despite many arguments and empirical evidence on the differences between humans and chimpanzees in the transmission phase of culture, there has been comparatively less discussion on the invention/modification phase that can be achieved individually. By invention or modification, new behaviors drive changes in culture when they are transmitted among group members at a later phase, which enhances cultural variation as well as cultural accumulation. Although it is difficult to detect the invention phase, there have been a few examples of chimpanzees engaged in invention. Yamamoto et al. (2008) observed a wild juvenile chimpanzee in Bossou invent an ant-fishing tool use in trees and modify his tool use for two years. Ant-fishing had never been observed in this community during the preceding 27 years. During the first session, at the age of five, he employed wands of a similar length used for ant-dipping on the ground, a customary tool-use behavior of his community, for ant-fishing in trees. Two years later, at the age of seven, his tools for ant-fishing were shorter and more suitable for capturing carpenter ants in trees. Biro et al. (2003) experimentally introduced an unfamiliar species of nuts to the Bossou chimpanzees, which are known to be skillful nut-crackers, and found that the individuals’ responses toward the novel items differed markedly with age, with juveniles being the most likely to explore the items. In both cases, the novel behaviors did not spread to the whole community, thus providing no evidence for cumulative culture, plausibly because of the low profitability (Yamamoto et al., 2008) and/or the limitation of direction in social observation that occurred only from younger to older individuals (Biro et al., 2003).

Based on the above facts, there seem to be three important points to understand about chimpanzees’ innovation in culture. First, they sometimes invent new behaviors, but the inventors are normally young individuals. Second, the young individuals involved in inventing do not make a good model for the other, especially elder, group members. Third, the newly invented behavior may possibly be less profitable than the chimpanzees’ traditional behaviors. Taken together, these points show that, although chimpanzees’ potential innovative nature, in combination with their abilities for faithful social learning, may consist of a cognitive basis for cumulative culture, this may be hampered in their real lives in their natural environments.

WHY DO CHIMPANZEES NOT DO IT WHEN THEY CAN DO IT

As listed above, there is evidence supporting the idea that chimpanzees sometimes do not exert their cognitive abilities in action. Then, I discuss why this phenomenon can be observed from two aspects.

When They Can Do It, Why Not Do It?

Several hypotheses can be considered to explain chimpanzees' inaction, despite their abilities in the above examples. This section considers four possible hypotheses: additional cognition, relationship, context, and profitability hypotheses, which are not mutually exclusive (Table 2).

The additional cognition hypothesis attributes chimpanzees' inaction to their lack of necessary additional cognitive abilities. This may explain the cases in the theory of mind and social learning. To exert a theory of mind—especially an understanding of others' false beliefs—in action, animals are required to relinquish their own knowledge or attraction toward a preferable resource. For example, when they are provided with two options of food in front of a dominant competitor, one is a preferred food, and the other is a less preferred food; a subordinate, with a theory of mind, should choose the less preferred food and give up the preferred food. For this choice, another cognitive ability of self-control is essential. In the social learning case, to adopt the copy-if-better strategy, rather than the copy-if-dissatisfied strategy, animals are expected to be able to ascertain with sufficient reliability whether the behavior of another individual is more profitable than their own and to make a judgment as to how much better the alternative is, which is an ability considered to be absent in non-human animals (Laland, 2004).

The other three hypotheses are more related to animals' motivation than cognition. The relationship hypothesis predicts that prosociality and social learning can be observed only in limited dyads with highly affiliative and tolerant relationships since animals need to be proximate with others in either case (e.g., education by master-apprenticeship; Matsuzawa et al., 2008; bonding- and identification-based observational learning; de Waal, 2008). Evolutionary viewpoints suggest that prosociality, especially altruism, among non-kin should be maintained reciprocally, but this relationship might be rare in

Table 2. Four Hypotheses to Explain Why Chimpanzees' Cognitive Abilities Are Present but Are Not Exerted in Their Ordinary Lives

Hypotheses	Theory of mind	Prosociality	Social learning	Innovation
Additional cognition	✓		✓	
Relationship		✓	✓	
Context	✓			✓
Profitability		✓	✓	✓

Note. "✓" means that the hypothesis plausibly explains the chimpanzees' inaction even with the cognitive ability.

non-human animals, even in chimpanzees (Brosnan et al., 2009; Yamamoto & Tanaka, 2009, 2010). In chimpanzees, social learning can occur only in younger individuals absorbing from older individuals; older individuals tend to be more conservative, which suggests that social learning can only be observed where young naïve individuals learn an existing (but not innovative) behavior from older group members. All of these viewpoints support the relationship hypothesis to explain the chimpanzees' inaction in their prosociality and social learning.

The context hypothesis emphasizes the importance of ecological or social validity for the exertion of cognitive abilities. Chimpanzees may exert sophisticated social cognitive abilities, such as a theory of mind, in competition to outstrip others but not in cooperative contexts (e.g., Hare & Tomasello, 2004). Innovation may occur only in an environment that provides animals with ecological variability. If there is little chance for animals to be placed under a novel ecological requirement, animals do not need to change their behaviors. Parsimoniously speaking, necessity can be the mother of innovation by stimulating the animals' motivation.

The profitability hypothesis predicts that a behavior can be observed in action only when it produces good profitability for animals. Prosociality can be profitable only when it is reciprocated, so proactive helping is risky, considering the possibility that it is not appreciated by others. The reluctance toward proactive helping is cognitively parsimonious since individuals should assess others' goals only when they receive an explicit request. Innovation can be profitable only when the benefit of a novel behavior exceeds its cost and still produces the same or more benefits than those gained by their traditional behavior. This might be difficult to achieve in a stable environment. It also influences the occurrence of social learning; if another's behavior is not more profitable, social learning cannot increase the learner's fitness.

In sum, these three hypotheses (i.e., the relationship, context, and profitability hypotheses) can be grouped in terms of motivation: Animals are motivated to demonstrate a behavior in action only with a conspecific sharing a good relationship in limited social and ecological contexts with profitable outcomes.

While They Do Not Need to Do It, Why Can They Do It?

A more fundamental question is why chimpanzees are equipped with cognitive abilities that are not required or exerted in their everyday lives in their natural environments. This is a difficult question to answer presently, but there are some possible explanations. One possibility is that cognitive ability can be useful only in limited situations (i.e., with specific conspecifics, in specific contexts, etc.), but not in most others. More broadly, cognitive ability might be a byproduct of another cognition that is developed for a completely different purpose. Another possibility is that cognitive ability was tuned to tackle challenges during previous generations, so it might just be the remains of past heritage. Plasticity, when the demands are high enough, may be another answer. It may be very costly for chimpanzees to fully exert their cognition, but it is worthwhile in some circumstances. They may have evolved plasticity to enable themselves to solve new challenges when necessary. These speculations are possible but

lack a solid knowledge base or clear evidence for further discussion; therefore, future comparative cognitive studies should strive to answer this question.

FUTURE PERSPECTIVES

What Can and Should Comparative Cognitive Studies Do?

Chimpanzees can discriminate between inability and unwillingness in humans (Call et al., 2004). Now, the question is whether and how we can discriminate between inability and unwillingness in non-human animals. As the Introduction discussed, we often consider the cognitive inability of non-human animals when they do not pass a cognitive task, but we should consider the possibility that they are just unwilling to perform a given task even though they have the requisite cognitive ability.

Taking the above into account, the point should be whether and how we can measure motivation in non-human animals. Of course, many studies (although, ideally, it should be all studies) applying cognitive experiments set a criterion to confirm that animals are well motivated to participate in a training or pre-test phase or a control condition. However, it seems that a set test condition is normally cognitively or physically demanding or time-consuming, which may diminish subjects' motivation in the task. Thus, subjects' poor performance in a test condition does not necessarily represent their poor cognitive ability but may reflect their low motivation in the task. We need to measure subjects' motivational levels independently, apart from their performance in the task. Measuring their attentiveness or duration of participation in a task could be one solution to overcome this. Itakura (1996) investigated gaze-following behavior in 11 species of non-human primates and found a high correlation between correct responses in the gaze-following task and the length of time that the subject continuously concentrated on the experiment. Ringhofer et al. (2021) tested 38 horses in a guesser-knower task (Povinelli et al., 1990) to investigate their understanding of the knowledge state of humans and found that horses that sustained high attention levels toward human behavior could pass the test, while individuals with low attention levels did not. When all the subjects were analyzed together, there was a non-significant trend that the horses would make the correct choices, which may mislead our understanding of the horses' social cognition. Instead, the interpretation should be that horses, as a species, are equipped with social cognition, but whether this cognition is exerted in action depends on the motivation of individuals.

Another promising way to measure non-human animal internal states is a combination of measuring behavioral and physiological responses. Even when non-human animals do not explicitly express their response in behavior, their recognition of an external stimulus may change their physiological state. Recent advances in technology enable researchers to measure physiological responses such as pupillary reaction (Hepach et al., 2021; Kret et al., 2014) and facial temperature (Kano et al., 2016; Sato et al., 2019) in non-invasive ways without restraining the movement of the animals and sometimes even remotely. This combination of traditional behavioral experiments and physiological measurements

could be a powerful means to investigate the latent cognitive abilities of non-human animals.

Research on captive animals' cognitive abilities has a strong advantage in this kind of study that requires strict control of conditions. Occasionally, captive studies are criticized for their ecological validity of what the findings mean when their experimental conditions are unnatural and do not consider the animals' individual learning histories in specific ecological circumstances (Leavens et al., 2019) or when they find cognitive abilities in captive non-human animals that are not seemingly exhibited in the wild (e.g., symbolic communication in early ape language studies; Gardner & Gardner, 1969; Savage-Rumbaugh, 1986; tool use studies with captive bonobos; Jordan, 1982; Gruber et al., 2010; Toth et al., 1993). However, such findings in captivity also have significance and solicit our understanding of non-human animals' latent abilities. Further intensive exploration could reveal the reasons why these abilities are latent in the animals' natural environments as well as the conditions under which they exert these abilities.

Conclusion and Insights Into Human Evolution

This article focused on chimpanzee-related examples and advocates that cognitive abilities are not necessarily represented in behavioral responses under certain conditions. We should bear in mind the possibility that animals sometimes do not act even though they can do so. While their performance may require additional cognitive abilities to be in place first, as proposed in the additional cognition hypothesis, the other three hypotheses (the relationship, context, and profitability hypotheses) assume that motivation explains animals' inaction in many cases. With this in mind, there are some avenues for future studies in comparative cognitive science to measure the motivational level of non-human animals, which is suggestive, or sometimes essential, for understanding their cognition properly.

Although we do not know exactly why animals are equipped with latent cognitive abilities that are not seemingly demonstrated in natural environments, it is natural to consider that these latent abilities are exerted under a novel selection pressure and help animals survive. This trend can provide insight into human evolution. From the above evidence, it seems clear that chimpanzees have a variety of latent cognitive abilities, which suggests that the common ancestor of humans and chimpanzees (and bonobos) was also equipped with such flexibility in their cognition. As in Gómez's (2004) idea of "zone of proximal evolution," developed based on Vygotsky's "zone of proximal development" (although we should be cautious about an easy application of the concept from development to evolution since there is theoretically no fixed direction for evolution), understanding the area and direction in which latent cognitive abilities spread may lead to understanding the potential direction of evolution under a new evolutionary selective pressure. In chimpanzees, populations living in harsh or unstable environments have a larger repertoire of tool use (Kalan et al., 2020). Understanding the environments and situations in which latent cognitive ability is converted into action in this way, is rich in important suggestions when considering human evolution. Archeology can read the "expression" of cognitive function in archeological materials but cannot decipher the

latent cognitive function. Comparative cognitive science, in collaboration with neuroscience and physical anthropology, helps clarify not only the behaviors of the common ancestor of humans, chimpanzees, and bonobos, but also their cognitive abilities, including latent ones, and thus is expected to clarify how such cognitive abilities have evolved and what role they play in the great human journey with environmental cataclysms.

CONFLICT OF INTEREST

There are no conflicts of interest to declare.

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