Research Article

Monkey See, Monkey Plan, Monkey Do

The End-State Comfort Effect in Cotton-Top Tamarins (*Saguinus oedipus*)

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ABSTRACT—*The way human adults grasp objects is typically influenced by their knowledge of what they intend to do with the objects. This influence is reflected in the end-state comfort effect: Actors adopt initially uncomfortable postures to accommodate later task demands. Although many experiments have demonstrated this effect, to the best of our knowledge its phylogenetic roots have not been investigated. In two experiments, we tested whether 9 cotton-top tamarin monkeys would show the end-state comfort effect. We did so by presenting the monkeys with a small cup containing a marshmallow. The cup was suspended in different orientations. The monkeys inhibited their natural grasping tendencies and adopted unusual grasping postures to accommodate subsequent task requirements, thus demonstrating the end-state comfort effect. This outcome provides evidence for more sophisticated motor planning than has previously been ascribed to this and related species.*

The motor planning necessary to grasp an object is more complex than one might suppose. Taking hold of an object (prehension) requires selecting a specific sequence of hand and arm postures from a nearly infinite number of possible alternatives. Previous observations have indicated that a constraint operates in such planning. People tend to grasp objects in uncomfortable ways if the initially uncomfortable grasp affords a more comfortable or more easily controlled final position. Thus, a waiter will pick up an inverted glass with the thumb pointing down if he plans to pour water into the glass. Grabbing the glass with the uncomfortable thumb-down posture allows the waiter to hold the glass with a more comfortable and more easily controlled thumb-up posture when the water is being poured.

A number of laboratory experiments have demonstrated the robustness of this effect, which Rosenbaum et al. (1990) called the *end-state comfort effect* (see Rosenbaum, Cohen, Meulenbroek, & Vaughan, 2006, for a review). The end-state comfort effect reflects planning. It shows that the way an object is taken hold of does not depend solely on the object's immediate appearance. Instead, the way the object is grasped also reflects knowledge of what the actor plans to do with it. Given the cognitive abilities reflected in the end-state comfort effect, it is natural to ask how it develops in individuals and whether it is found in nonhuman animals.

Recent research with human infants has shown that the cognitive capabilities linked to anticipatory effects in prehension appear at a young age. One series of studies showed that 19- to 24-month-old infants orient their hands appropriately for the task of grasping a spoon, whereas younger infants (9- to 12-month-olds) do not show such task-appropriate hand orientations (McCarty, Clifton, & Collard, 1999, 2001), although providing training can facilitate performance in 12-month-olds (McCarty & Keen, 2005). Claxton, Keen, and McCarty (2003) also found that 10-month-old infants reach more quickly for a ball when engaging in an activity that requires less precision (throwing) than when engaging in an activity that requires more precision (fitting the ball into a tube). These demonstrations do not involve the end-state comfort effect per se, but they do show that the anticipatory abilities exemplified by the effect begin to take hold around the end of the first year of life.

Although there has been some research on the ontogeny of anticipation in prehension, there has been much less work on the phylogenetic parallels of such anticipation. Many neurophysiological investigations have concerned reaching behaviors in monkeys; for example, some studies have included qualitative

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evaluations of the grasping of objects of various shapes and sizes (e.g., Gardner, Ro, Debowy, & Ghosh, 1999; Rizzolatti et al., 1988). However, no studies have investigated the cognitive components of more sophisticated reaching behaviors. In particular, no study that we know of has investigated whether monkeys grasp objects differently depending on what they plan to do with the objects. The present study is the first to do so, to the best of our knowledge.

We sought evidence for the end-state comfort effect in cotton-top tamarins (*Saguinus oedipus*). Tamarins are small, arboreal New World monkeys and are interesting subjects for this line of research because they are believed not to use tools in the wild, though in captivity they can learn functionally relevant properties of simple tools, such as canes or cloths, which can be used for dragging food (Hauser, 1997; Hauser, Kralik, & Botto-Mahan, 1999; Hauser, Pearson, & Seelig, 2002; Santos, Pearson, Spaepen, Tsao, & Hauser, 2006; Santos, Rosati, Sproul, Spaulding, & Hauser, 2005). The latter findings indicate that tamarins can learn means-end relationships, which are a cognitive prerequisite for the end-state comfort effect.

If tamarins were found to demonstrate the end-state comfort effect, this would signify that they have the capability for a more advanced level of motor planning than has been reported in earlier studies of these monkeys. It would indicate that tamarins can depart from their normal preferred mode of grasping (with a thumb-up or palm-down hand orientation) for the sake of a future state. Such a change in motor activity for the sake of a later state would not be expected if the motor planning for future body states constitutes a necessary and sufficient mental condition for tool use (Johnson-Frey, 2004).

EXPERIMENT 1

In Experiment 1, we asked whether cotton-top tamarins would invert their hands when reaching for an inverted cup in order to extract a marshmallow stuck inside the cup. Because tamarins are known to have difficulties interacting with transparent containers (Santos, Ericson, & Hauser, 1999), we first familiarized the monkeys with the cup (a plastic champagne glass with the base cut off) by allowing the monkeys to remove a marshmallow from the cup when it was not inverted. During this familiarization period, the monkeys received no directed, explicit training. Instead, they were allowed to use any method they wished to get the marshmallow. After this familiarization phase, the monkeys were tested in the same free-form way, only with the cup presented in an inverted orientation.

Next, we presented the cup, in either an upright or an inverted orientation, in an apparatus that required sliding out the cup if the marshmallow was to be extricated (Fig. 1). The cup had to be slid out because its open surface abutted a platform, which precluded directly grasping the marshmallow. We expected the monkeys to slide the cup by pulling on its stem, and we were especially interested in the hand orientations the monkeys would use when doing so. We expected the monkeys to grasp the stem with a thumb-up orientation when the cup was upright in the apparatus. This hand orientation is one that tamarins normally assume when grasping objects (the other hand posture they use is one in which the thumb is turned inward toward the body midline). In contrast, we predicted that the monkeys would grasp the stem with a thumb-down orientation when the cup was inverted in the apparatus. This is an awkward hand position,

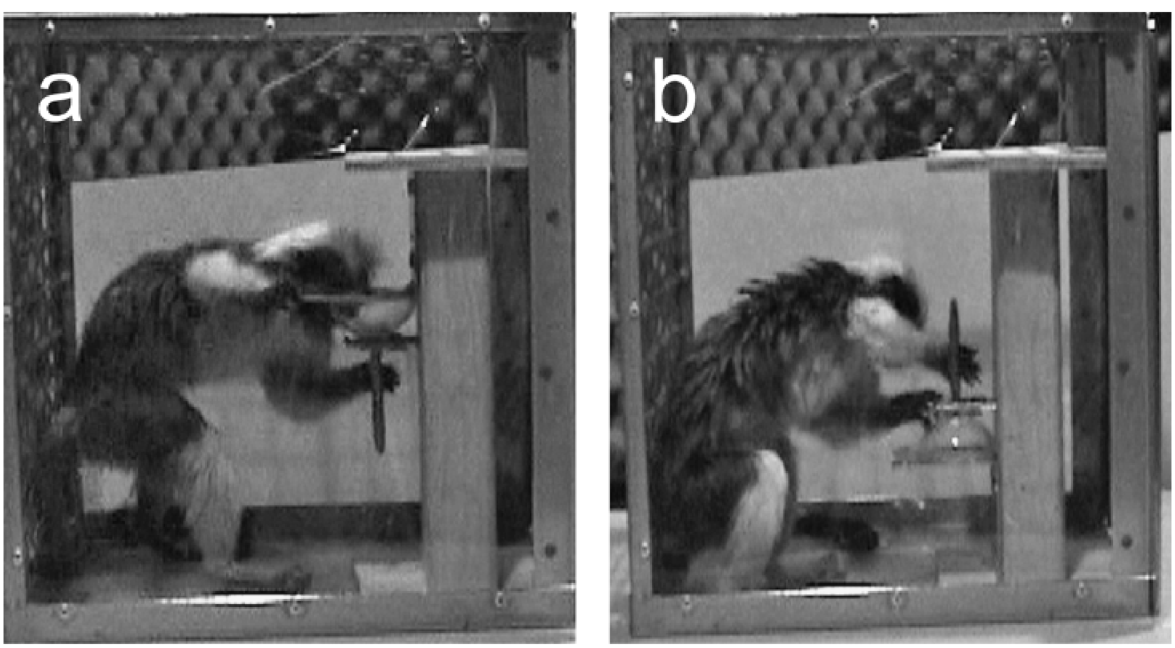

Fig. 1. A tamarin grasping the stem of a plastic champagne glass to pull the glass from the apparatus in order to extract a marshmallow stuck inside the glass. In (a), the monkey exhibits the thumb-up grasp orientation, and in (b), the monkey exhibits the thumb-down grasp orientation.

which is rarely if ever seen in tamarins. Indeed, before this experiment, we never saw it in our hundreds of hours of interaction with the monkeys in the colony from which our subjects were drawn. The thumb-down orientation would afford a more comfortable or more easily controlled final position when the cup was freed from the apparatus and was then held so the marshmallow could be taken from it with the other hand. Observing a thumb-down orientation when the cup was initially inverted would suggest that tamarins, like human adults (Rosenbaum et al., 2006) and 4-year-old children (Rosenbaum, 1994), anticipate future body states when they manipulate objects.

Method

Subjects

We tested 6 female and 3 male cotton-top tamarins (*Saguinus oedipus*). The monkeys were born at the New England Regional Primate Research Center in Southborough, Massachusetts, and were brought to Penn State in June 2005. The tamarins were housed in mated pairs in two colony rooms and had no previous experience with this type of experiment. Use and care of the tamarins conformed to the rules and regulations of the Institutional Animal Care and Use Committee at the Pennsylvania State University.

Stimuli and Apparatus

During the experiment, the tamarins were in a transport box (12 in. high × 9.25 in. wide × 12 in. deep) with two walls made of Plexiglas, one wall made of caging, and a front door made of Plexiglas with a hole cut out (1 in. high × 6 in. wide) so the tamarins could reach through it. The transport box was located in a soundproof chamber. Trials were recorded with a digital camcorder and were burned onto a DVD.

To accommodate the hand size and strength of the tamarins, we used plastic champagne glasses, modified by removing the base and extending the stem with wood and duct tape to create a more easily grasped handle. The cup was 2.25 in. tall (from the tip of the handle to the rim of the mouth), and the handle was 0.25 in. thick; the mouth of the cup was 2 in. in diameter, and the bowl was 1 in. deep. Half-pieces of miniature marshmallows (Kraft) were stuck to the bottom of the cup's interior.

During the second test phase, the cup was suspended from a wooden apparatus (see Fig. 1) that was 8.5 in. high and had a base measuring 5.5 in. × 4.5 in. The apparatus had a metal platform that was 2.75 in. wide × 2.5 in. deep. This platform was attached to a wooden post. One inch below the platform, there were two horizontal bars that were screwed into the wooden post 0.75 in. apart. The bars ran parallel to the center of the platform. When the cup was to be suspended in an upright orientation, the apparatus was placed such that the platform was above the bars. The upright cup was suspended on the two bars, with the handle of the cup located in the slit formed by the bars. The metal platform served as a cover for the cup opening so that the monkeys could not directly access the cup opening without pulling the cup out of the apparatus. When the cup was to be suspended in an inverted orientation, the apparatus was inverted such that the platform was closest to the ground, and the bars were above the platform. The space between the bars served as a slit for the cup handle, and the cup itself was supported on the metal platform, which again blocked access to the cup's opening. In both orientations, the metal bars blocked access to the cup from either side of the apparatus (access could be gained only by pulling the cup straight out via the handle).

Procedure

Because of tamarins' difficulty interacting with transparent containers (Santos et al., 1999), and because of possible difficulties associated with object containment (Hauser, Williams, Kralik, & Moskovitz, 2001), we familiarized the monkeys with the plastic cup and marshmallow in several stages. In all these familiarization stages, the monkeys could extract the marshmallow from the cup in any manner they chose. Each monkey was allowed to progress to the next familiarization stage when it was judged to have successfully performed the task in the current stage, as long as the extraction of the marshmallow from the cup was judged not to be accidental (e.g., inadvertent contact of the tail with the cup might dislodge the marshmallow). Each trial lasted up to 5 min. If the tamarin did not succeed in getting the marshmallow within that time, the same method of familiarization was repeated on a subsequent day. One familiarization trial was administered per day. Once the final stage of familiarization was passed, the formal testing procedure began.

In the first stage of familiarization, the experimenter inserted a marshmallow into the cup while the subject watched. The experimenter held the cup by the stem, with the opening facing the subject through the hole in the Plexiglas door. If the tamarin took the marshmallow from the cup, he or she was advanced to the second stage of familiarization, during which the experimenter inserted a marshmallow into the cup in view of the tamarin and then inserted the cup into the transport box, placing it on the floor with the opening (and therefore the marshmallow) facing the tamarin. There were no constraints on the manner in which the monkeys could then extract the marshmallow.

In the third familiarization stage, the cup with the marshmallow was placed on the floor of the transport box with the opening facing 90° away from the tamarin. Once this stage was passed successfully, the tamarin proceeded to the fourth stage, in which the cup was placed on the floor but with the opening of the cup 180° away from the tamarin, leaving the stem directly in front of the monkey. Once the tamarin completed this last stage of familiarization, he or she advanced to the test phase.

The test phase had two parts. In the first, the marshmallow was inserted into the cup, which was inverted and placed on the floor of the transport box next to the monkey. The monkey was not constrained in how he or she could obtain the marshmallow, but we restricted our analyses to trials in which the monkey used the handle of the cup. Each monkey received two test trials. Two coders watched a video of these test trials and scored the position of the subject's hand during the initial handle grasp, noting whether the hand was upright or inverted.

In the second and more scientifically critical part of the test phase, the cup was placed upright in the apparatus, with the stem in the slit formed by the two bars. After two successful trials (i.e., trials in which the monkey extracted the marshmallow by grasping the stem of the cup), the apparatus was inverted to test performance when the cup was in the downward orientation. This condition also consisted of two successful test trials. If the monkey managed to remove the cup without using the stem (e.g., grasped the rim of the mouth and slid it out), a trial was repeated.

Results and Discussion

All 9 monkeys passed all stages of familiarization. The average number of sessions needed to complete the four stages was 8.6. In the first part of the test phase, 5 of the 9 monkeys first grasped the stem with an inverted grasping orientation, 2 monkeys first grasped the stem with an upright orientation (both monkeys subsequently knocked over the cup and then used the other hand to grasp the cup with the thumb facing the bowl of the cup), and 2 monkeys used other methods to access the cup (1 monkey used its mouth and the other knocked it with its tail).

For the second part of the test phase, we analyzed the successful trials in each cup orientation (2 trials per monkey per orientation). Given the dichotomous nature of the dependent variable (thumb-up vs. thumb-down hand orientation), we performed a nonparametric analysis, using paired sign tests to compare performance across conditions. The monkeys grasped the stem with a thumb-up grasp on all 18 upright-cup trials (Fig. 2a). They grasped the stem with a thumb-down grasp in 15 out of 18 inverted-cup trials (Fig. 2a). The difference between the grasp orientations in the upright- and inverted-cup conditions was statistically significant (paired sign test, $p < .0001$).[1]

A possible concern in interpreting the results of this experiment is that the tamarins' hand orientations may have reflected needs for visual inspection rather than capacities for future planning. For example, the monkey shown in Figure 1 leaned down more when using the thumb-down orientation (Fig. 1b) than when using the thumb-up orientation (Fig. 1a). We chose this pair of images because the hand orientations and apparatus were easy to see in print, but in fact, although body postures varied during grasping, an analysis of the relation between body tilt and hand orientation for all the trials of all the monkeys failed to support the hypothesis that hand orientations were statistically related to body tilt.[2] These results suggest that the tamarins in this experiment adopted awkward or unusual grasping postures not just as a by-product of body tilt, but as a result of anticipation of future body states. To the extent that this conclusion is correct, this experiment provides the first demonstration of the end-state comfort effect in nonhuman animals.

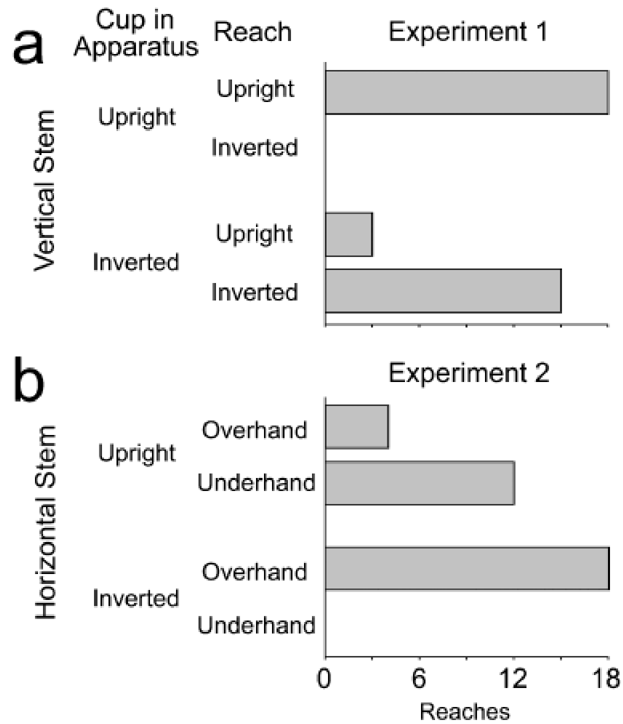

Fig. 2. Orientation of the tamarins' grasp as a function of whether the cup was upright or inverted. In Experiment 1 (a), the stem was vertically oriented, and in Experiment 2 (b), it was horizontally oriented.

EXPERIMENT 2

The second experiment was designed to provide a further check on our interpretation of the results of Experiment 1. We tested the hypothesis that the behavior observed in the second part of the test phase of Experiment 1 was due to simple behavioral associations, rather than sophisticated motor planning. The tamarins may have associated common (thumb-up) postures with upright cup orientations and uncommon (thumb-down) postures with inverted cup orientations. These simple associa-

[1]One monkey had a strong tendency to grab the cup by the bowl instead of the handle, so the cup had to be taped in more carefully for all trials. When restricted to the handle, the monkey used an upright grasp for the upright cup, but was unable to remove the cup successfully. Nonetheless, because the monkey used a distinct grasping posture, we included the data for this monkey in the analysis. The 1 monkey that grasped the handle with an upright posture in both inverted-cup trials was subsequently given more experience, whereupon, without any external reinforcement, the monkey switched to an inverted grasp.

[2]Two independent judges rated the tamarins' body tilt while grasping. For the upright-cup trials, all monkeys deployed a thumb-up grasping position regardless of whether they exhibited any body tilt. For the inverted-cup trials, there was also no difference in grasp type as a function of body tilt. In 8 of the 16 inverted-cup trials (the video for 2 trials was unavailable), the monkeys had discernible body tilt. In 7 of those trials, the monkeys deployed a thumb-down grasp. In 6 of the 8 trials that were judged to show no discernible body tilt, the monkeys deployed a thumb-down grasp. Thus, across trials, grasping behavior was unrelated to body tilt.

tions would have obviated planning via internal simulation, motor imagery, or other computational forecasting.

We tested this hypothesis by exploring the extent to which the tamarins' demonstration of the end-state comfort effect would generalize to a task involving a novel handle shape. We again gave tamarins the chance to extract a marshmallow from a cup that was suspended in the apparatus, but we replaced the vertical stem of the cup with a horizontally oriented U-shaped handle. This new handle, which the monkeys had never experienced before, altered what the tamarins were likely to do if they relied on planning rather than simple associations. If they relied on simple associations, they would be likely to grasp the U-shaped handle with the more common (palm-down) orientation when the cup was upright and with the less common (palm-up) orientation when the cup was inverted. However, if they relied on planning, they would be likely to grasp the U-shaped handle with the more common (palm-down) orientation when the cup was inverted and with the less common (palm-up) orientation when the cup was upright, as these grasping postures would allow for the easiest subsequent access to the marshmallow.

Method

The subjects were the same as in Experiment 1. The tests were conducted in the same transport box, using the same apparatus as in the second test condition in Experiment 1. The cup's stem was removed and replaced with a U-shaped handle that measured 0.75 in. high and 2 in. wide (the same width as the diameter of the cup opening). The apparatus was modified by adding flankers to the metal platform to prevent the monkeys from grabbing the vertical sides of the handle, making only the horizontal portion of the handle accessible. The procedure for this experiment was identical to the second part of the test phase of Experiment 1.

Results and Discussion

As Figure 2b shows, in all 18 trials of the inverted-cup condition, the monkeys grasped the handle using an overhand (palm-down) grasp. In the upright-cup condition, the monkeys grabbed the handle with an underhand (palm-up) grasp 12 times and with an overhand (palm-down) grasp 4 times. One monkey consistently used the rim to remove the cup in this condition, and these trials were therefore excluded from the analysis. It is also worth noting that only 1 monkey used an overhand grasp in both trials of the upright-cup condition. A paired sign test showed that the number of overhand and underhand grasps differed significantly between the upright-cup and inverted-cup conditions ($p < .001$). An analysis of the videos like the one reported in footnote 2 failed to support the hypothesis that there was any systematic relation between body tilt and hand orientation.

Thus, in the second experiment, most of the monkeys demonstrated behavior inconsistent with the association hypothesis. When the cup was inverted, all the monkeys used the common, palm-down grasp orientation, but when the cup was upright, most of the monkeys used the less common, more awkward, palm-up grasp. These results support the planning hypothesis and consequently bolster the conclusion that the manifestation of the end-state comfort effect in these animals reflected planning, rather than simple associations.

GENERAL DISCUSSION

The experiments reported here provide the first evidence we know of for the end-state comfort effect in nonhuman animals. In Experiment 1, we found that tamarins were more likely to grasp the stem of an upright cup with a common, upright grip than with an uncommon, inverted grip, and were more likely to grasp the stem of an inverted cup with an uncommon, inverted grip than with a common, upright grip. In Experiment 2, we found that the relation between postural frequency and cup orientation could be changed by putting a U-shaped handle on the cup. The observed behaviors demonstrate that tamarins can alter the way they grasp an object not just according to how the object appears, but also according to what they plan to do with the object.

The tamarins' performance indicates that they could exercise considerable inhibitory control. They refrained from doing what came most naturally (or was most common), in the service of what needed to be done later. Previous studies of reaching behaviors have also shown inhibitory control in cotton-top tamarins. In these studies, tamarins modified the direction of reaches or withheld reaches in order to obtain a food reward (Hauser et al., 2001; Hood, Hauser, Anderson, & Santos, 1999; Kralik, Hauser, & Zimlicki, 2002; Santos et al., 1999). The present work complements this earlier research.

Our investigation also has implications for the understanding of the cognitive substrates of tool use. Comparative work across different primate species has focused on one of the key abilities underlying tool use, namely, the ability to distinguish the functionally relevant properties of tools (Povinelli, 2000; Visalberghi & Limongelli, 1994). In this connection, it is interesting that although tamarins do not use tools in the wild, laboratory studies have shown that they can learn to identify at least a subset of functionally relevant features of objects and physically interact with those objects in ways that reflect appreciation of those features (Hauser, 1997; Hauser et al., 2002; Santos et al., 2005, 2006). Why, then, do tamarins not use tools in the wild?

Perhaps, as Santos et al. (2006) have suggested, tamarins do not use tools in the wild because they are unable to fully deploy their knowledge when confronted with real-world problems. Alternatively, as Johnson-Frey (2004) has suggested, it may be that a critical component of tool use is the ability to formulate motor plans that "extend beyond the immediate spatial constraints of the task and capture the demands of forthcoming actions" (Johnson-Frey, 2004, p. 72). Johnson-Frey (2003) has also suggested that this type of forecasting may be unique to humans. Our results indicate that tamarins do possess such forecasting abilities, albeit on a scale that is probably smaller than what Johnson-Frey had in mind. It may be that formulating relatively long-term motor plans is a necessary but not sufficient condition for tool use, and it may be that the end-state comfort effect reflects a cognitive ability that is just part of the scaffolding on which tool use depends. If this argument is accepted, our results may be taken to suggest that the reason tamarins do not use tools in the wild is not that they lack the ability to plan ahead, but rather that the scope of their planning is limited. Future studies can investigate the complexity of plans that tamarins can actually handle.

Finally, we note that our findings with respect to tamarins bear a noteworthy resemblance to the findings of Terrace and his colleagues with respect to macaques (Terrace, 2005; Terrace, Son, & Brannon, 2003). Terrace and his coworkers showed that macaques can learn abstract sequences. Our results show that tamarins can anticipate future actions, even though they cannot spontaneously use tools. Terrace's work and our study, like other ongoing research on the ontogeny and phylogeny of basic skills, show that many components are needed to allow for the assembly of higher skills. Whether such higher skills can emerge suddenly, in one fell swoop, seems doubtful in view of the incremental changes suggested by work such as Terrace's and the work reported here.

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