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Apes Save Tools for Future Use

Nicholas J. Mulcahy and Josep Call*

Planning for future needs, not just current ones, is one of the most formidable human cognitive achievements. Whether this skill is a uniquely human adaptation is a controversial issue. In a study we conducted, bonobos and orangutans selected, transported, and saved appropriate tools above baseline levels to use them 1 hour later (experiment 1). Experiment 2 extended these results to a 14-hour delay between collecting and using the tools. Experiment 3 showed that seeing the apparatus during tool selection was not necessary to succeed. These findings suggest that the precursor skills for planning for the future evolved in great apes before 14 million years ago, when all extant great ape species shared a common ancestor.

Tulving (*J*) recounts an Estonian tale of a girl who dreamed about attending a party but was unable to eat her favorite dessert because there were no spoons available. Facing the possibility of attending the party again, she took a spoon to bed. Crucially, the girl took the spoon not because she currently needed it, but because she would need it in the future. Tulving used this example to illustrate the putatively unique human ability to think about the past and plan for the future (2–4) and proposed that an analogous “spoon” test could be used to test for future planning in nonhuman animals. Future planning is cognitively demanding because it imposes a long delay between performing an action and getting rewarded for it: a skill that humans use when preparing a suitcase before a trip or by making a cake to celebrate someone’s birthday. Although various animals can plan and execute multiple actions toward a goal (5, 6), they may achieve this without taking into account future needs, just current ones (3, 4, 7). Thus, when chimpanzees transport stones to use them to crack open nuts, or New Caledonian crows make hook-shaped tools to fish for insects, they do so in an attempt to satisfy their current hunger state, not some future one.

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To date, the only evidence suggesting future planning in animals is the cache protection strategy of scrub jays (8). These birds transport food from old sites and re-cache it in new ones to avoid losing their caches to conspecifics that observed the initial location of the cache sites, thus saving the items for future consumption. Some researchers argue that future planning may have evolved independently in various taxa (9), whereas others argue that the non-human data do not truly capture the essence and complexity of human mental time travel (1, 4). For instance, it is unknown whether animals would also transport and save non-edible items that would enable them to get food at a later time, an ability that may have played a crucial role in human evolution (10–12). Would extant apes also transport tools that they do not currently need, anticipating that they will need them in the future? This would be an important addition to the complex behavior displayed by scrub jays, because what is saved is not the food itself but a means to get the food, which is one step removed from the goal itself. The tool has no value in itself; it has value only in relation to the food.

We investigated future planning in bonobos and orangutans, because they represent our closest and most distant great ape relatives, respectively. This allowed us to make inferences about the possible time of emergence of the precursor skills for future planning in this group.

If both species showed this skill, this would suggest that it may have evolved before 14 million years ago (Ma), when all apes shared a common ancestor (13); whereas if only bonobos showed it, it may have evolved within the past 14 My. Its absence in both species would suggest that future planning is a human adaptation that appeared within the past 7 My.

We tested five bonobos and five orangutans (table S1). First, subjects learned to use a tool to get a reward from an apparatus in the test room (14). Then, we placed two suitable and six unsuitable tools in the test room but blocked subjects’ access to the baited apparatus. After 5 min, subjects were ushered outside the test room into the waiting room, and the caretaker removed all objects left in the test room while subjects watched. One hour later, subjects were allowed to return to the test room and were given access to the apparatus. Thus, to solve the problem, subjects had to select a suitable tool from the test room, bring it into the waiting room, keep it there for 1 hour, and bring it back into the test room upon their return (fig. S1). The trial ended after the subject retrieved the reward or 5 min had elapsed.

Subjects solved the problem an average of seven times (SEM = 1.8), with all subjects succeeding at least once within the first seven trials (Table 1). Subjects performed the key behavior of transporting tools out of the test room in 70% of the trials, targeting suitable tools significantly more often than would be expected by chance ($t_5 = 2.59$, $P = 0.049$) (expected = 25%, observed = 40.9%). Moreover, they returned to the test room 77.5% of the suitable tools but only 32.6.5% of the unsuitable tools ($t_5 = 2.73$, $P = 0.041$) (Fig. 1). Two orangutans (Dokana and Toba) on one and three occasions, respectively, brought back an inappropriate tool but broke off some small piece from it with which they still obtained the reward. Even if those trials are excluded from the analyses, subjects still initially targeted suitable tools ($t_5 = 3.09$, $P = 0.027$) and brought them back more often than

Table 1. Number and order of correct trials for each subject for each experiment. NT, not tested.

Subjects	Experiment 1		Experiment 2		Experiment 3		Experiment 4	
	Correct trials (<i>n</i>)	Trial no.	Correct trials (<i>n</i>)	Trial no.	Correct trials (<i>n</i>)	Trial no.	Correct trials (<i>n</i>)	Trial no.
Bonobos								
Kuno	7/16	7, 8, 10, 13–16	8/12	2–6, 9–11	7/16	5, 7, 8, 10, 11, 13, 15	NT	
Joey	2/16	1, 13	NT		NT		NT	
Limbuko	5/16	7, 10, 11, 13, 16	NT		6/16	5–7, 13, 14, 16	NT	
Yasa	NT		NT		NT		0/16	
Ulindi	NT		NT		NT		0/16	
Orangutans								
Walter	6/16	4–8, 14	NT		NT		NT	
Toba	7/16	1, 3, 6, 10–13	NT		6/16	1, 4, 6, 7, 12, 13	NT	
Dokana	15/16	1, 3–16	7/12	2, 4–6, 9, 11, 12	7/16	6–9, 11, 14, 16	NT	
Dunja	NT		NT		NT		2/16	2, 16
Pini	NT		NT		NT		5/16	1, 13–16

unsuitable tools ($t_5 = 2.77$, $P = 0.04$). Tool transport did not occur simply because subjects were already holding the tool when the door was opened after the delay period. Indeed, the opposite was true. On average, subjects were already holding the tool in only 8.2% (SEM = 5.3) of the successful trials when the door opened to return to the test room (this figure was 26.5% for the tools taken out of the test room). If those trials are excluded, subjects still solved the task on an average of 4.7 trials (out of 16).

In experiment 2, we increased the delay between tool retrieval and reward retrieval to 14 hours. We brought the subject into the test room, then sent her to the sleeping room (which served as waiting room) for the night, and brought her back to the test room in the morning. The sleeping room was not contiguous to the test room but located one floor above it. We tested one orangutan and one bonobo. Neither ape took any tools in the first trial. The orangutan took suitable tools in all 11 remaining trials (binomial test: $P = 0.01$, one-tailed), which she brought back and used in 7 trials to get the reward. The bonobo took suitable tools in 8 of the remaining 11 trials (binomial test: $P < 0.001$, one-tailed), which he always brought back to the testing room to get the reward.

In experiment 3, two bonobos and two orangutans had to use a hook to get an out-of-reach juice bottle suspended from a string (fig. S1). After subjects had learned to use the hook appropriately, they were presented with the hook and three unsuitable tools in the absence of the apparatus (or the reward). Five minutes later, subjects were ushered outside of the test room and brought back 1 hour later. Once subjects were inside the test room, the apparatus was installed and subjects could get the reward if they had returned with the hook. This experiment addressed two outstanding issues. It tested whether subjects would select the suitable tool in the absence of the apparatus or the reward. It controlled for the possibility that subjects took

the tool in previous experiments to reduce their current hunger state, because the hook had been associated only with liquid procurement. Moreover, because water was available ad libitum, it is unlikely that subjects took the hook to reduce their thirst. Subjects' performance was comparable to that in experiment 1. Subjects solved the task on an average of 6.5 trials (SEM = 0.3), succeeding at least once within the first six trials, and transporting suitable tools more often than would be expected by chance ($t_3 = 2.69$, $P = 0.037$ one-tailed) (expected = 25%, observed = 41.5%). Moreover, they returned more suitable than unsuitable tools (79.6% versus 47.2%), but the difference was not statistically significant ($t_3 = 2.25$, $P = 0.055$, one-tailed) (Fig. 1).

Experiment 4 established the baseline probability of transporting tools in the absence of a future task but using identical reinforcement contingencies as in experiment 3. Two bonobos and two orangutans received the same treatment as in experiment 3, except that no apparatus was set up upon their return to the test room although they were rewarded if they brought the suitable tool back. Subjects solved the task significantly less often (mean = 1.8, SEM = 1.2) than did those in experiment 3 ($t_6 = 3.91$, $P = 0.008$). In fact, only two of the four subjects brought back the suitable tool at all, and they behaved differently from other successful subjects because after their first successful trial, they failed the next 11 and 14 trials, respectively (Table 1). Subjects in experiment 4 also solved the task significantly less often than those in experiment 1 ($t_8 = 2.81$, $P = 0.023$), thus ruling out the possible confounding effects of practice, because both groups of subjects were naïve when their respective experiments began.

Apes selected, transported, and saved a suitable tool not because they currently needed it but because they would need it in the future. These data taken all together cannot be easily

explained by invoking traditional operant learning, because there was at least a 1-hour delay between the response (tool selection and transport) and the reinforcement. Typically, instrumental conditioning fails to occur if the response-reinforcement interval is greater than a few seconds in the absence of conditioned reinforcers (3, 15, 16), as evidenced by the poor performance of the subjects in experiment 4 as compared to other experiments. Arguably, the suitable tool could have acted as a conditioned reinforcer. However, this still does not explain the difference between experiment 4 and the other three experiments (fig. S2), which is even more remarkable because subjects were reinforced for returning with the tool in all experiments. Perhaps subjects did not transport the tool in experiment 4 because they had not been reinforced to do so. However, subjects in experiment 1 faced the same situation, and all of them transported the tool before any reinforcement had occurred.

Our results also differ from the phenomenon of taste aversion, whereby an animal learns within one trial to avoid the ingestion of a substance after becoming sick 1 hour later (17), because taste aversion involves learning to avoid a stimulus, not acquiring an instrumental response. Moreover, taste aversion shows a high degree of stimulus specificity because it develops when gustatory stimuli are paired with digestive sickness but not when gustatory stimuli are paired with other modalities of aversive stimuli. It is highly unlikely that a similar form of specialized learning also exists for tool transportation.

Another alternative is that our results represent an unlearned biological predisposition. Many species appear to plan for the future when they build nests to lay their eggs or hoard food for the winter (18). However, unlike tool transportation, these other activities have obvious fitness consequences (channeled by strong physiological and genetic determinants) that have favored their selection in all the individuals of a species. In contrast, tool transportation, even tool use, has not been documented in most wild populations of bonobos or orangutans (19, 20). More important, apes do not store food or objects in their natural habitats because those are generally available throughout the year. It is therefore unlikely that saving and transporting tools are unlearned biological predispositions.

Because traditional learning mechanisms or certain biological predispositions appear insufficient to explain our current results, we propose that they represent a genuine case of future planning. Subjects executed a response (tool transport) that had not been reinforced during training, in the absence of the apparatus or the reward, that produced no consequences or reduced any present needs but was crucial to meet future ones. The presence of future planning in both bonobos and orangutans

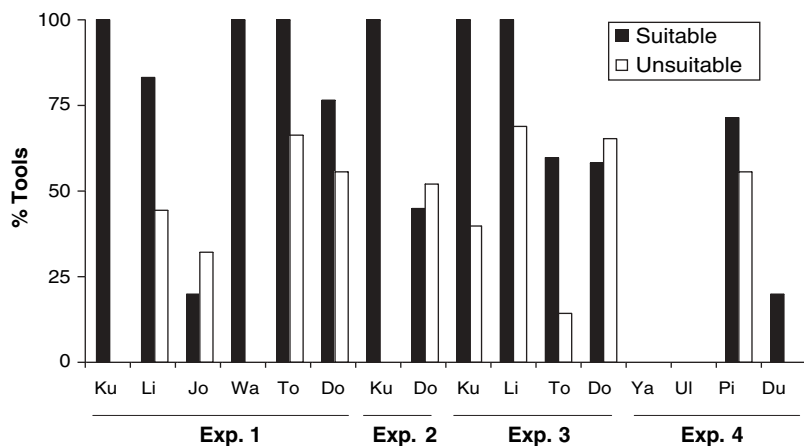


Fig. 1. Percentage of suitable and unsuitable tools transported into the test room by each subject after the delay period in each experiment. Subject name abbreviations are as follows: Ku, Kuno; Li, Limbuko; Jo, Joey; Wa, Walter; To, Toba; Do, Dokana; Ya, Yasa; Ul, Ulindi; Pi, Pini; Du, Dunja.

suggests that its precursors may have evolved before 14 Ma in the great apes. Together with recent evidence from scrub jays (8, 9, 21), our results suggest that future planning is not a uniquely human ability, thus contradicting the notion that it emerged in hominids only within the past 2.5 to 1.6 million years (10, 11, 22). Indeed, its presence in distantly related taxa such as corvids and apes reinforces the hypothesis that these taxa may have undergone convergent cognitive evolution (23). Future studies should investigate whether apes, like corvids, will not only transport tools for future use but also protect them from conspecifics that may steal them.

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Supporting Online Material

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Materials and Methods

Figs. S1 and S2

Table S1

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CO/FT Regulatory Module Controls Timing of Flowering and Seasonal Growth Cessation in Trees

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Forest trees display a perennial growth behavior characterized by a multiple-year delay in flowering and, in temperate regions, an annual cycling between growth and dormancy. We show here that the *CO/FT* regulatory module, which controls flowering time in response to variations in daylength in annual plants, controls flowering in aspen trees. Unexpectedly, however, it also controls the short-day–induced growth cessation and bud set occurring in the fall. This regulatory mechanism can explain the ecogenetic variation in a highly adaptive trait: the critical daylength for growth cessation displayed by aspen trees sampled across a latitudinal gradient spanning northern Europe.

Trees have extended juvenile phases that can last for decades before the first flower is formed. Trees can also cycle between periods of growth and dormancy. In temperate regions, this involves a short-day–induced growth cessation and bud set in the fall, after which the tree enters a dormant state characterized by an enhanced cold tolerance. Tree populations (provenances) from northern latitudes typically display growth cessation at a longer critical daylength, leading to earlier bud set during fall compared with southern populations (1). This is a high-

ly adaptive trait because it ensures that bud set and dormancy have been induced well before the risk of frost damage. This response is under strong genetic control and is maintained when trees are moved between latitudes (2, 3). The molecular mechanism that controls growth cessation at different critical daylengths is not known; neither is the mechanism controlling the multiple-year delay in flowering.

In the annual plant *Arabidopsis*, the genes *CONSTANS (CO)* and *FLOWERING LOCUS T (FT)* are necessary for the daylength regulation of flowering, inducing flowering as a response to long days (4). *CO* displays a diurnal regulation in which the mRNA accumulation peaks at the end of the day in long days and during the night in short days (5). Furthermore, the *CO* protein is extremely labile in darkness, leading to an accumulation of *CO* protein only in long days (6). *CO* then induces transcription of the gene *FT* in the leaf, and the *FT* mRNA moves from leaf to

shoot apex (7, 8), where the translated *FT* protein induces the formation of flowers (8, 9). The *FT* mRNA fulfills many of the criteria characterizing the elusive flower-inducing molecule “florigen” described in the 1930s (7).

To determine whether a tree *FT* ortholog is also involved in the regulation of flowering time in trees, a process that is not obviously regulated by daylength because of their long juvenile phase, or whether it is involved in the daylength regulation of perennial growth and dormancy, we have investigated the role of the *FT* ortholog in *Populus* trees (poplars, aspens, and cottonwoods).

We isolated the *Populus trichocarpa FT* ortholog, which we call *PtFT1* (fig. S1) and showed that its function in inducing early flowering is conserved in transgenic *Arabidopsis* (fig. S2) (10). *Populus trichocarpa* is difficult to transform, but all *Populus* species are closely related, and the sequence identity between homologous genes in different *Populus* species is often 99% (11). Male *Populus tremula x tremuloides* transformed with *35S::PtFT1* initiated flowerlike structures directly from the Agrobacterium-infected stem segments within 4 weeks (Fig. 1, A and B), compared with the normal flowering time of 8 to 20 years (12). This shows that *PtFT1* is a powerful inducer of flowering in *Populus*. Weaker expressing lines could be regenerated and planted in the greenhouse. These trees produced inflorescences (catkins) (Fig. 1, C to E, H, and I; and fig. S3, A to C) containing phenotypically normal male flowers (Fig. 1, F and J) with an apparently normal pollen development (Fig. 1, G and K). We also generated early-flowering female *Populus tremula* with normal inflorescence development (fig. S3D). This is the first report of juvenile transgenic trees producing inflorescences. In contrast, early-flowering *Populus* ectopically expressing

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