COGNITION

Ravens parallel great apes in flexible planning for tool-use and bartering

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The ability to flexibly plan for events outside of the current sensory scope is at the core of being human and is crucial to our everyday lives and society. Studies on apes have shaped a belief that this ability evolved within the hominid lineage. Corvids, however, have shown evidence of planning their food hoarding, although this has been suggested to reflect a specific caching adaptation rather than domain-general planning. Here, we show that ravens plan for events unrelated to caching—tool-use and bartering—with delays of up to 17 hours, exert self-control, and consider temporal distance to future events. Their performance parallels that seen in apes and suggests that planning evolved independently in corvids, which opens new avenues for the study of cognitive evolution.

Human planning is often characterized by decisions about future events that will unfold at other locations. The cognitive skill set that allows for planning outside the current sensory context operates across a range of domains, from planning a dinner party to making retirement plans. Such decisions require a host of cognitive skills, including mental representation of a temporally distant event, the ability to outcompete current sensorial input in favor of an unobservable goal, and understanding which current actions lead to the achievement of the delayed goal. Given these broader cognitive implications, whether any other animals can plan across different domains has remained one of the cardinal questions in animal behavioral sciences within the past decade.

Experiments have shown that great apes can plan across technical (tool use) and social (bartering) domains, incorporating self-control and time intervals up to at least one night (*1*–*4*). Because ape planning can relate to both tool use and bartering with humans, it is regarded as domain-flexible. Monkeys do not solve such tasks (*5*, *6*), which suggests that these skills evolved in the hominoid lineage.

Corvids are the only nonhominid animals that have experimentally demonstrated planning beyond the current moment. Scrub-jays plan for the type of food needed at a particular location in order to get next morning's breakfast (*7*) and, along with Eurasian jays, dissociate current satiation from future hunger (*8*, *9*). It is unlikely that such advanced skills were present in the last common ancestor of birds and mammals (320 million years ago) and instead must have evolved independently (*10*). This vast phylogenetic separation has provoked skepticism concerning whether corvid planning really is functionally similar to that of hominids. It has been contended that the—admittedly flexible—skills of corvids, which are habitual food cachers, may instead reflect adaptations confined to the food-caching domain (*4*, *11*–*13*). To reveal domain-general planning, animals should be tested in tasks for which they lack ecological or behavioral predispositions (*11*). Should corvids have the skill set to plan across domains, which so far is found only in hominids, it would be a remarkable finding in the charting of independently evolved complex cognition. It would imply that some underlying cognitive functions interact in analogous ways and that evolution can reiterate cognitive architectures that facilitate complex behaviors, either through parallelism or convergence.

In a series of four experiments, we investigated whether ravens (*Corvus corax*) plan domain-flexibly (*14*). Each experiment included two main conditions—a technical and a social one—for which ravens lack behavioral predispositions: tool-use and bartering with humans. Ravens are not habitual tool users, and bartering has never been observed in the wild. The experiments were mainly chosen because they replicate key experiments with primates (*1*–*4*, *14*, *15*). Specifically, we tested whether ravens can make decisions for an event 15 min into the future (experiment 1), and over longer intervals of 17 hours (experiment 2). We additionally tested whether ravens can exert self-control when making decisions for the future (experiment 3). Well-developed self-control is essential to planning because impulsivity keeps one stuck in the immediate context (*13*). The last experiment (experiment 4) did not replicate, but extended, what has been done in primate studies. It tested whether the ravens ascribed a higher value to a reward that was spatiotemporally closer than in experiment 3. Differences in self-control performance between various delays reveal temporal sensitivity and demonstrate that the decisions are made for nonarbitrary futures. We also analyzed the first trial performance in the two different conditions in experiment 1. In planning tasks, first trials are of consequence because they demonstrate what the animal does when facing the planning problem for the first time (*11*). In total, five captive and hand-raised adult ravens were tested (two males). Four individuals took part in each condition (tool or bartering); one male was too neophobic toward the tool apparatus, and one female was not trained in bartering (Table 1).

Experiment 1 investigated whether ravens could select, save, and later use either a tool or an exchangeable token that acquired functionality 15 min after being taken, at a different location from where it was selected. In the tool condition, subjects received five trials of learning on a tool's functionality (a stone of certain dimensions) on an apparatus containing a reward. They were subsequently given the opportunity to experience that other objects, which later served as distractors, did not open the apparatus. The following day, they were exposed to the baited apparatus,

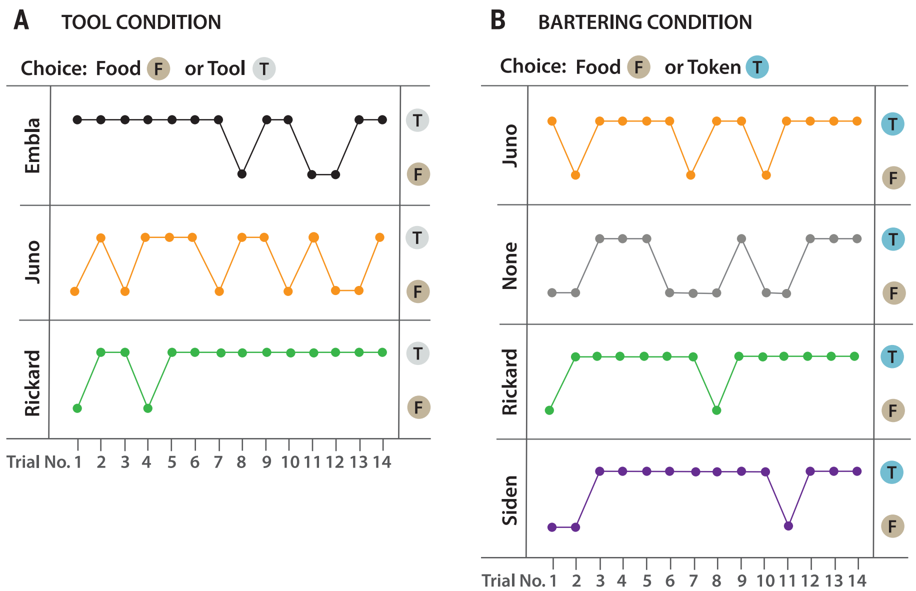

Fig. 1. Choices in experiment 3. (**A** and **B**) Selections across trials for each subject in the (A) tool condition and (B) bartering condition.

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which they could interact with, without a tool available in order to create a possible incentive for later planning. Thereafter, the apparatus was removed in the presence of the subject. One hour later, the ravens were offered, at a different location, a forced-choice selection from a tray containing the functional tool and three nonfunctional distractors. After their selection, a 15-min delay ensued before the apparatus was installed. The birds received 14 trials each. Only the first trial was preceded with a baited apparatus when the bird lacked a tool.

In the bartering condition, the birds were first given 35 trials of training on exchanging a specific token for an immediate food reward. To provide a planning incentive, the ravens were exposed to an experimenter asking for the token when they did not posses it. One hour later, a tray with the token and three distractors was offered at a different location by an experimenter with no history of bartering with the birds. The selection procedure differed from the tool condition because the ravens were given three trays in immediate succession (to be comparable with some studies on great apes) so that the subject could select, and later exchange, three tokens in one trial. After 15 min, the bartering experimenter showed up at a location not visible from the selection compartment. All subjects received 12 trials each.

In the tool condition, the subjects successfully selected and used the tool to solve the task in an average of 11 trials out of 14 (min, 8 trials; max, 12 trials), or 78.6%. In trial 9, one female invented a way to open the apparatus without the tool (and was therefore excluded from subsequent tool conditions in the rest of the study). When excluding her novel solution, the mean success rate was 86% for all subjects (min, 78.6%; max, 100%). In the bartering condition, the birds selected in total 143 tokens out of 144. On average, they exchanged 77.6% of the selected tokens (min, 58.3%; max, 86.1%). At least one token was exchanged in 91.6% of the trials (fig. S2).

Combining the results from the tool and bartering conditions yielded in total eight first trials with five subjects (two ravens took part in only one condition each). All subjects selected functional objects in their first trials. In six trials, the subjects used the items in the future task (75%). Four of the five birds succeeded in their very first task (of the two conditions) before they had experienced the delay in any task or experienced the consequences of their choices (table S1). These trials were the first time any subjects saved the items by caching them.

Experiment 2 extended the delay between item selection and use to 17 hours (overnight). It consisted of six trials per condition, and only one selection per trial was offered in the bartering condition. In the tool condition, the three ravens selected and used the tool in 88.8% of the cases (min, 5; max, 6). In the bartering condition, the mean success rate of the four ravens was 95.8% (min, 5; max, 6).

Experiment 3 tested planning in a self-control context to determine whether ravens can act with future events in mind by disregarding an immediate, valuable food reward in favor of an item that could give access to an even more valued reward occurring only after a 15-min delay. In both conditions (14 trials each), subjects were presented with a tray that included the distractor objects, the tool or token, and an immediate reward. In contrast to a control condition in which all ravens selected the immediate reward on 100% of trials when no tool or token was available (10 trials per subject), subjects selected the tool on average in 73.8% of the trials (min, 8; max, 12) and the token in an average of 73.2% of trials (min, 7; max, 12). When the subjects did not choose the functional object, they invariably took the immediate reward (Fig. 1).

Table 1. Overview of the results. Values indicate the number of trials in which the functional item was selected or used. The numbers in parentheses indicate the maximum possible number of successes. Each subject's individual performance in selecting the functional item was significant in all experiments (exact binomial test). N.A., not tested.

Experiment 1: 15-min delay

	Tool condition		Bartering condition	
Subject	**Selected**	**Used**	**Selected**	**Used**
Rickard (male)	14 (14)	12 (14)	36 (36)	29 (36)
Siden (male)	N.A.	N.A.	36 (36)	21 (36)
Juno (female)	14 (14)	12 (14)	36 (36)	31 (36)
None (female)	11 (14)	8 (11)	35 (36)	30 (35)
Embla (female)	11 (14)	11 (11)	N.A.	N.A.

Experiment 2: 17-hour delay

	Tool condition		Bartering condition	
Subject	**Selected**	**Used**	**Selected**	**Used**
Rickard (male)	6 (6)	6 (6)	6 (6)	6 (6)
Siden (male)	N.A.	N.A.	6 (6)	6 (6)
Juno (female)	5 (6)	5 (5)	6 (6)	5 (6)
None (female)	N.A.	N.A.	6 (6)	6 (6)
Embla (female)	6 (6)	5 (6)	N.A.	N.A.

Experiment 3: Self-control long delay

	Tool condition		Bartering condition	
Subject	**Selected**	**Used**	**Selected**	**Used**
Rickard (male)	12 (14)	12 (12)	12 (14)	10 (12)
Siden (male)	N.A.	N.A.	11 (14)	11 (11)
Juno (female)	8 (14)	7 (8)	11 (14)	10 (11)
None (female)	N.A.	N.A.	7 (14)	6 (7)
Embla (female)	11 (14)	11 (11)	N.A.	N.A.

Experiment 4: Self-control short delay

	Tool condition		Bartering condition	
Subject	**Selected**	**Used**	**Selected**	**Used**
Rickard (male)	14 (14)	14 (14)	14 (14)	14 (14)
Siden (male)	N.A.	N.A.	14 (14)	14 (14)
Juno (female)	14 (14)	14 (14)	14 (14)	14 (14)
None (female)	N.A.	N.A.	14 (14)	14 (14)
Embla (female)	14 (14)	14 (14)	N.A.	N.A.

Experiment 4 again presented the birds with bartering and tool-use tasks with the immediate reward available so as to determine whether they took the delay into account. That is, whether they would select the functional item more often when the reward was spatiotemporally closer than in experiment 3. If the item would carry an intrinsic value only, it should be selected equally often regardless of the delay. In both conditions (14 trials each), subjects walked past the reward opportunity (either the apparatus or the experimenter) to select an item from the tray from where they did not see the future reward. In both conditions, all subjects declined the immediate reward and instead selected and used the functional item in 100% of trials. This is a significant increase relative to experiment 3 on both group and individual levels (fig. S3). An overview of the results in all experiments is provided in Table 1.

This study suggests that ravens make decisions for futures outside their current sensory contexts, and that they are domain-general planners on par with apes. In the tool conditions, including self-control, the ravens were at least as proficient as tool-using apes (*1*, *2*, *15*). In the bartering conditions, the ravens outperformed orangutans, bonobos, and particularly chimpanzees (*3*, *4*, *15*). [Detailed comparisons are available in (*14*).] The first trial performances show that the ravens' behaviors were not a result of habit formation, and that they perform better than 4-year-old children in a comparable set-up (*16*).

Examining performance in different domains—unrelated to ecological predispositions—and on first trials is regarded as key for revealing planning, and previous studies on both great apes and corvids have been criticized for not meeting either or both of these criteria (*11*, *13*). This study also tested whether the birds made decisions for future events by inferring temporal distances to these events, which shows that the item is not selected because of an intrinsic value but because of its relation to a future. Previous studies have been questioned for not testing temporal sensitivity (*12*, *17*).

Ravens are avian dinosaurs that shared an ancestor with mammals around 320 million years ago. The conspicuous similarities in performance to great apes in tasks such as these opens up avenues for investigation into the evolutionary principles of cognition and shows what the brains of some birds are capable of.

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/357/6347/202/suppl/DC1
Materials and Methods
Figs. S1 to S3
Table S1
Reference (*18*)

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Making a plan

Until recently, planning for the future has generally been considered to be unique to humans. Studies in the past 10 years have suggested that apes and scrub jays are also able to make such plans. However, these studies—especially those in the birds —have been questioned. It has been argued that planning in foraging and natural tasks is not the same as planning in a more general way. Kabadayi *et al.* tested ravens with tasks designed to specifically assess their general planning abilities (see the Perspective by Boeckle and Clayton). Confirming their forward-planning abilities, the birds performed at least as well as apes and small children in this complex cognitive task.

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