Evidence for future cognition in animals☆

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ABSTRACT

Evidence concerning the possibility of mental time travel into the future by animals was reviewed. Both experimental laboratory studies and field observations were considered. Paradigms for the study of future anticipation and planning included inhibition of consumption of current food contingent on future receipt of either a larger quantity or more preferred food, choice between quantities of food contingent on future pilfering or replenishment of food, carrying foods to different locations contingent on future access to those locations, and selection of tools for use to obtain food in the future. Studies of non-human primates, rats, black-capped chickadees, scrub-jays, and tayras were considered. It was concluded that current evidence favors future cognition in animals, and some theoretical issues concerning this ability were discussed.

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Since the late 1990s, the process of mental time travel (MTT) has become of considerable interest to psychologists. In general terms, MTT is a person's ability to travel backward and forward mentally from the present moment to remember specific past experiences stored in memory and to anticipate or plan future activities. Tulving (1972) originally defined episodic memory as retrieval of past episodes that contained information about *what* happened, *where* it happened, and *when* it happened (what–where–when or WWW memory). More recently, it has been pointed out that these criteria are not sufficient to define episodic memory (Zentall, Clement, Bhatt, & Allen, 2001; Zentall, Singer, & Stagner, 2008). For example, a person might learn and remember what, where, and when details of the war of 1812 from a history book without having any personal memory of it. Thus, Tulving added the criterion of *autonoetic consciousness*, the feeling that a memory was personally experienced (Tulving, 1985).

Tulving (1983) explicitly suggested that episodic memory was found only in humans and not in nonhuman animals (hereafter referred to as animals). Initial reviews of relevant literature on animal memory supported this position (Roberts, 2002; Suddendorf & Corballis, 1997). However, a spate of investigations have since been reported that indicate WWW memory could be shown in some animals. For instance, it was shown that species of food-storing birds could remember what, where and when a specific item of food had been stored or found (Clayton & Dickinson, 1998, 1999; Feeney, Roberts, & Sherry, 2009; Zinkivskay, Nazir, & Smulders, 2009) and that rats could remember what, where, and when a preferred food was found on a radial maze (Babb & Crystal, 2005, 2006a, 2006b; Naqshbandi, Feeney, McKenzie, & Roberts, 2007; Roberts, 2006). Because the experience of autonoetic consciousness could not be probed in animals, these demonstrations of WWW memory in animals were dubbed *episodic-like memory* (Clayton & Dickinson, 1998).

The finding of primary importance in demonstrations of WWW memory in animals was that they could remember when in past time an event had occurred. Considerable evidence already existed showing that a number of species could encode

and remember what and where preferred foods could be found. The use of semantic memory could largely account for these data. The finding that animals could remember when a food was cached or encountered led to the hypothesis that they might be using episodic memory and MTT. Birds made different choices depending on whether an event had occurred 4 hr or 5 days ago, and rats chose arms on a radial maze differently depending on whether preferred food had been found 30 min or 4 hr earlier. Roberts (2002) raised the possibility that animals in such experiments might have learned to use the strength of a memory trace to remember how-long-ago an event occurred instead of remembering when in past time it occurred. Roberts et al. (2008) tested this hypothesis and found that rats did remember experience with a preferred reward based on how-long-ago and not when that reward was encountered. More recent findings, however, indicate that both rats (Zhou & Crystal, 2009) and black-capped chickadees (Feeney, Roberts, & Sherry, 2011b) can remember when a preferred food was found if how-long-ago or memory strength cues are controlled. Thus, evidence of WWW memory in certain species of animals now seems firmly established.

The issue of MTT in animals has also given rise to the question of whether evidence for awareness of future time can be found in nonhuman species. Prospective MTT in people involves self-reflective consciousness (Terrace & Metcalfe, 2005) and mental self-projection (Buckner & Carroll, 2006). By viewing into the future, a person may see possible future events; anticipation of these events may lead to preparatory actions. A person may also project himself/herself into the future to see future activities (episodic future thinking; Atance & O'Neill, 2005), and this type of mental projection may lead to future planning behavior such as gathering tools to build a piece of furniture. It has been emphasized that future planning involves considerable flexibility or generativity, in that alternative plans may be formulated for different future contingencies. Suddendorf and Corballis (1997) have argued that the ability to anticipate and plan for the future was the driving force behind the evolution of MTT and episodic memory. Further, Corballis (2009, 2012) suggests that language may have developed largely for the formulation of future plans.

When future MTT in animals is considered within this framework of human future MTT ability, the possibility seems scant. We have virtually no evidence that animals formulate complex alternative plans for future behavior. However, Raby and Clayton (2009) have pointed out that directly comparing human with animal future oriented behavior may raise the bar too high and have a stultifying influence on comparative research. Much of the question of MTT in animals comes down to whether they have a concept or sense of time (Roberts, 2002). Considerable evidence indicates that many species of animals readily learn to use both time of day and elapsed time intervals as cues for significant events, such as food delivery. Although these temporal abilities can be explained by circadian timers and internal accumulators, it is possible that some appreciation of time as a bi-directional dimension that recedes into the past and opens into the future has grown out of these abilities. Some animals might anticipate different times of day (morning, noon, and night) or different days (today and tomorrow) or relative times in the future (soon versus distant). Thus, animals might not be bereft of all MTT capacity. For an alternative point of view, see Eacott and Easton's (2012) article in this volume. They argue that future thinking and episodic memory are based on representations of contexts that are not necessarily temporal and hence that a process of MTT may not be necessary.

Findings suggesting MTT into the future in animals have begun to accumulate, both from the field and from the laboratory. The validity of these findings as true evidence of MTT has been challenged, with alternative explanations offered for each case (Suddendorf & Corballis, 2007, 2008, 2010). One common criticism of laboratory studies is that they involve *only* associative learning. Labeling phenomena associative learning, however, neither explains them nor rules out future anticipation. In a well known article on "Pavlovian Conditioning: *It's Not What You Think It Is*", Rescorla (1988) pointed out that "Instead, conditioning is now described as the learning of relations among events so as to allow the organism to represent its environment" (p. 151). In many cases, the events to be associated may be separated in time. A prominent example is taste aversion conditioning, in which a novel taste becomes associated with illness experienced some hours later (Garcia, Ervin, & Koelling, 1966; Revusky & Bedarf, 1967). Other examples of operant learning with long intervals between a response and reward are found in the literature (Lett, 1973; Lieberman, Davidson & Thomas, 1985; Lieberman, McIntosh, & Thomas, 1979; Thomas, Lieberman, McIntosh, & Ronaldson, 1983). These findings challenge the old idea of a delay of reinforcement gradient that required temporal contiguity (Grice, 1942) or nextism (Gilbert, 2006) between response and consequence for association to occur. Thus, association may occur over an extended time interval and be one way in which an animal could anticipate an event distant in time.

The question which then arises is how events separated in time may become associated. The farther apart two events, A and B, are spaced in time, the more other events occur in the intervening time that might become associated with A or B. In some cases, these events may belong to a dedicated evolutionary motivational system that guarantees re-experiencing A will retrieve memory of B or that re-experiencing B will retrieve memory of A. Dickinson (2011) refers to this type of association as *mnemonic-associative theory*. Thus, within an internal gustatory-alimentary system (Garcia, Hankins, & Rusiniak, 1974), re-experiencing a novel taste may retrieve memory of subsequent illness. A scrub-jay searching a cache site retrieves a memory of caching a particular food at that site hours or days earlier. In other cases, however, it may not be obvious that two events belong to a dedicated system. For example, Naqshbandi and Roberts (2006) made the choice of different quantities of food determine when in future time access to water would be available. If an animal does have a sense of time over which a sequence of events occurs, it may be able to associate events A and B by noticing the correlation between them. Thus, if choice of A always leads later to consequence B but choice of X always leads later to consequence Y, an organism that can track events over time could learn to associate A with B and X with Y because these events follow one another more often than any other events.

Another issue that has arisen is whether bona fide future planning must involve different motivational incentives. Thus, people often shop for foods they currently have no hunger for but will use to prepare a meal at some future time. The Bischoff-Kohler hypothesis suggests that animals would never perform preparatory activities for the later consummation of a food for which they currently feel no hunger (Bischof-Kohler, 1985). Although findings now exist that challenge the Bischof-Kohler hypothesis, it is not clear why behaviors which prepare for later consumption of a reward now desired should not be examined as examples of future planning. For example, people who anticipate a tasty dessert restrain themselves from eating too much of the main course in order to have room in their stomachs for the dessert. This behavior appears to involve future planning and to be learned from previous encounters with meals that involve an ending dessert course in which different levels of consumption of the main course were associated with different degrees of enjoyment of the dessert. Similar behavior in animals would seem to suggest evidence of future planning.

In the remainder of this article, I will review some of the evidence that suggests future anticipation and planning in animals and relate this evidence to the theoretical issues I have raised. The evidence will be organized around different types of experiments that require different forms of behavior on an animal's part to show future-oriented cognition.

Modifying Consumption of One Food in Anticipation of Another

In an earlier often overlooked experiment, Flaherty and Checke (1982) trained four groups of rats to drink a 0.15% saccharin solution from a tube. Three of the groups were subsequently allowed to drink a 32% sucrose solution (a preferred solution), with the interval between access to saccharin and access to sucrose being 1, 5 or 30 min in different groups. In a control group, no sucrose was given after saccharin consumption. Over 11 days of testing, rats in the experimental groups came to suppress their intake of saccharin relative to the control group. The degree of suppression was greatest at 1 min and declined as the time interval between saccharin and sucrose increased to 5 and 30 min. This finding suggests that rats anticipated the delivery of sucrose at a future point in time and suppressed intake of saccharin accordingly. They presumably suppressed saccharine intake because the effort to consume saccharine was seen as unnecessary and/or the value of saccharine was degraded with the anticipation of more palatable and nutritive sucrose. The finding that degree of suppression was inversely related to length of the delay may mean that fewer rats could anticipate sucrose as the delay increased and/or that the incentive value of sucrose was discounted as the delay increased.

One concern with the Flaherty and Checke (1982) experiment is that suppression of consumption of one substance in anticipation of another might be limited to the case in which the first substance is non-nutritive (saccharin) and the second is nutritive (sucrose). This question was addressed in a recent experiment performed with black-capped chickadees by Feeney, Roberts, & Sherry (2011a). An experimental group of chickadees was initially given 5 min of access to a dish containing sunflower seeds. This dish was removed, and after a 5-min delay, a dish containing mealworms was provided. The control group was also given sunflower seeds but no subsequent access to mealworms. Although both of these foods are nutritive, chickadees strongly prefer mealworms to sunflower seeds. The average number of sunflower seeds consumed over 15 daily trials is shown for each group in Fig. 1 (panel a). By the final five days of testing, the curves have clearly separated, with the experimental group eating significantly fewer sunflower seeds than the control group. The interval between sunflower seeds and mealworms then was increased to 10 min for 10 trials (panel b) and then to 30 min for 10 trials (panel c). It can be seen that the suppression of sunflower seed consumption remained strong even at a 30-min delay.

Three things are striking about the results of the chickadee experiment. First, birds suppressed the intake of one nutritive food in order to consume a more preferred nutritive food later. Second, the suppression of sunflower seed eating was not weakened with a delay between foods of up to 30 min. Three, the data indicate that chickadees suppressed intake of a food they clearly were hungry for (as shown by the greater consumption of sunflower seeds by the control group) when a more preferred food was on the time horizon. These findings with chickadees, as well as the Flaherty and Checke (1982) rat findings, appear to be an animal analog of the human example discussed above. That is, people eat less of the main course in order to leave room for dessert.

An alternative interpretation of the findings shown in Fig. 1 is that chickadees in the experimental group remembered an association between mealworms and sunflower seeds and showed a negative contrast effect by lowered intake of sunflower seeds. A couple of things argue against this interpretation. First, there is evidence that birds may not show negative contrast effects (Papini, 1997). A second consideration is that negative contrast effects occur when a less preferred reward follows a more preferred reward. Thus, in the chickadee experiment, birds would have had to remember worms from the preceding day when they encountered sunflower seeds the next day. It seems more likely that birds anticipated worms after seeds over the far shorter delays of 5–30 min. Finally, negative contrast effects usually involve a sharp drop in intake of the less preferred reward, but birds continued to show a fairly constant intake of sunflower seeds over trials. It may be argued that the steady consumption of sunflower seeds by the experimental group also provides a problem for an anticipatory interpretation, because chickadees should have shown a decline in seeds consumed in anticipation of mealworms. Although mealworms are preferred to sunflower seeds, sunflower seeds are nutritive and readily consumed by chickadees. It may be that the experimental chickadees moderated but did not sharply decrease their intake of seeds because this level of seed consumption gave them a desired balance between seeds and worms (dinner and dessert).
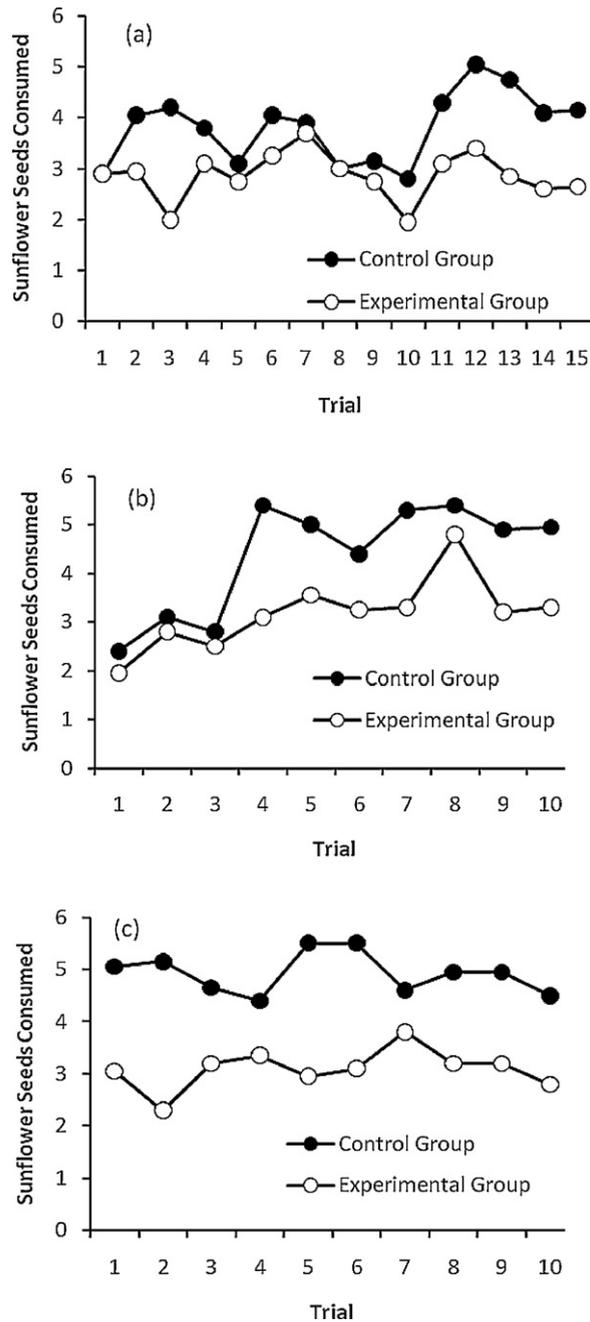
Fig. 1. Mean sunflower seeds consumed on daily trials by control birds and by experimental birds later given access to worms after 5 min (panel a), 10 min (panel b), or 30 min (panel c).

A related study has recently been reported by Wilson and Crystal (2012) and (also see Crystal, 2012). They argued that anticipation of an important future event draws on cognitive resources and thus may disrupt processing of a current task. Two groups of rats were trained to perform a temporal discrimination task in which one lever was pressed for reinforcement after a 2-s cue and another lever was pressed for reinforcement after an 8-s cue. Eventually, intermediate durations were presented on probe trials to generate a psychophysical curve. The important manipulation involved providing one group with a meal at the end of the 90-min testing session, while the control group received no meal. It was found that sensitivity to the test durations decreased in the later part of the test session in the meal group but not in the control group. That is, the psychophysical curve was flatter in the meal group than in the control group. Wilson and Crystal argued that the cognitive resources rats used to anticipate the meal at the end of the session interfered with their processing the temporal cues in the discrimination task.
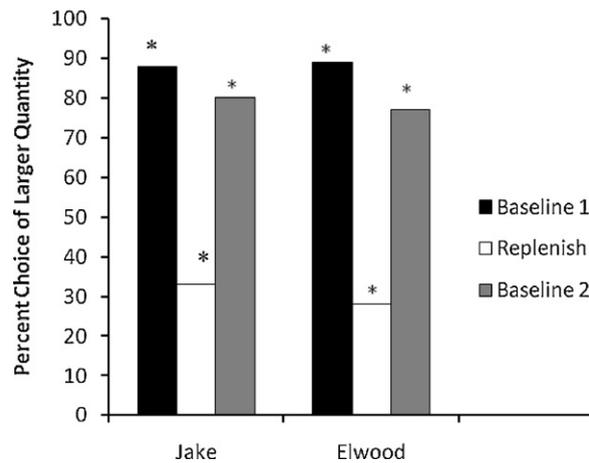
Fig. 2. Percentage of trials on which two squirrel monkeys, Jake and Elwood, chose the larger quantity of peanuts (four) baseline 1, replenishment, and baseline 2 phases. *Significantly different from 50%.

Choice Between Alternatives Yielding Different Future Outcomes

A substantial number of experiments has used this procedure. In what are referred to as self-control or temporal dis-counting studies, a subject is offered a choice between two responses, one of which leads to a small immediate reward and the other of which leads to a larger delayed reward. Temporal discounting models suggest that the momentary value of the larger reward is discounted as the delay increases (Green & Myerson, 2004). Thus an immediate smaller reward may have more value than a delayed larger reward. To the extent an animal can anticipate a larger delayed reward, such experiments may be seen to involve future thinking.

In studies with rats and pigeons, the larger reward is usually delayed for a few seconds and it is typically found that these animals prefer the small immediate reward (Mazur & Logue, 1978; Tobin, Chelonis, & Logue, 1993). A cynomolgous monkey, however, was shown to prefer the delayed larger reward (Tobin, Logue, Chelonis, Ackerman, & May, 1996), and more recent studies with apes indicate that they can tolerate substantial delays in variants of this task. Chimpanzees showed stronger preference than humans for a large reward delayed for 2 min than for a small reward given immediately after choice (Rosati, Stevens, Hare, & Hauser, 2007). Chimpanzees and an orangutan waited patiently for as long as 3 min for 20 pieces of chocolate to be put in a food bowl before consuming them, because delivery of chocolates stopped at the moment an ape began to consume them (Beran, 2002). Dufour, Pele, Sterck, and Thierry (2007) gave chimpanzees a small cookie that they could consume or trade in for a larger one after a time interval. Chimpanzees waited up to 8 min to trade cookies when the larger one was 40 times greater than the smaller one.

McKenzie, Cherman, Bird, Naqshbandi, and Roberts (2004) examined preference for different amounts of food in two squirrel monkeys when the chosen cache could be modified by the experimenter at a later point in time. In one study (Experiment 6), monkeys were offered a choice between trays containing 10 and 20 peanuts. Both monkeys chose the tray containing 20 peanuts on 80–90% of the trials. On 12 subsequent daily trials, a pilfering manipulation was introduced in which the experimenter returned 15 min after the monkey chose 20 peanuts (but not 10 peanuts) and removed the remaining peanuts in the tray. Because a monkey could consume only 6–8 peanuts in 15 min, more total peanuts could be earned on a trial during this phase by choosing the tray with 10 peanuts. However, doing so meant that the monkey had to suppress its initial tendency to choose the larger amount. The pilfering manipulation caused preference for 20 peanuts to drop to levels not significantly above the 50% chance level. When pilfering was discontinued, preference for 20 peanuts returned to 80–90%. That monkeys were anticipating the loss of peanuts after choosing the larger quantity was further suggested by the observation that on some trials when 20 peanuts had been chosen, monkeys removed peanuts from the food tray and attempted to hide them on the bottom of the cage before the experimenter returned to pilfer them.

In a further experiment, McKenzie et al. (2004; Experiment 7) used a replenishment procedure. Monkeys were given a choice between 2 and 4 peanuts during initial and final baseline phases and showed preference for 4 peanuts on 80–90% of the trials. During an experimental phase between the baseline phases, the experimenter returned 15 min after a monkey chose 2 peanuts (but not 4 peanuts) and replenished the food tray with 8 more peanuts. Thus, a monkey could obtain a total of 10 peanuts (2 + 8) by initially choosing the smaller quantity. The effect of this manipulation is seen in Fig. 2. Both monkeys showed a significant preference for the smaller amount of 2 peanuts over 4 peanuts during the replenish phase of the experiment.

Both of these experiments suggest that a consequence 15 min in the future significantly altered monkeys' choices. Although they were hungry for peanuts and strongly preferred the larger quantity, they actually chose the smaller quantity when it was in their long-term interest.
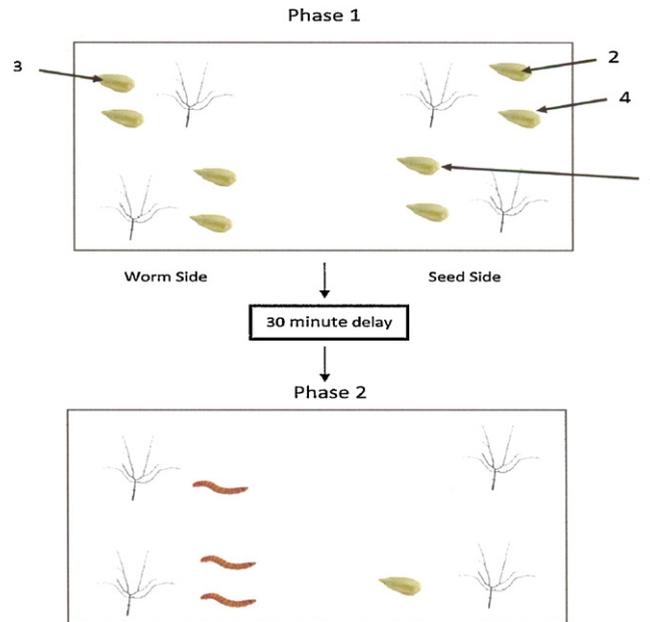
Fig. 3. Diagram shows four locations where a chickadee found a sunflower seed in Phase 1. In Phase 2, given 30 min later, seeds in locations not visited in Phase 1 are replaced with worms on the worm side and with fresh seeds on the seed side.

Other experiments that use different foods or different motivational states directly test the Bischof-Kohler hypothesis. Correia, Dickinson, and Clayton (2007; also see Roberts, 2007) used a pre-feeding procedure to examine future anticipation in western scrub-jays. Pre-feeding birds one food selectively reduces preference for that food when they are subsequently given an opportunity to consume or cache that food. Jays were pre-fed Food A and then allowed to cache Foods A and B. Before being allowed to recover their caches, the birds were pre-fed once again. Birds in group same were pre-fed Food A once again, but birds in group different were pre-fed Food B. Both groups then were allowed to forage for the foods they had cached after the initial pre-feeding. Both groups initially cached Food B more than Food A, as expected from their being pre-fed Food A. On subsequent trials, however, group different cached Food A more than Food B, while group same continued to cache more of Food B. It was suggested that group different anticipated their later preference for Food A, caused by pre-feeding Food B, and thus cached the Food for which they would have the greater need. Notice that birds in group different had to overcome their usual aversion to a pre-fed food in order to cache Food A, suggesting that anticipation of a future need caused them to act contrary to a current need.

In a somewhat similar experiment, Feeney et al. (2011a; Experiment 2) examined whether black-capped chickadees would selectively choose between spatial locations of one food in order to gain later access to a more preferred food. The design and procedure of this experiment are shown in Fig. 3. Birds were allowed to forage for food hidden in four artificial trees placed in an indoor aviary. Each tree contained four holes, and each hole was covered with a piece of string that had to be pulled out by a bird to gain access to its contents. The experiment consisted of two phases. In Phase 1, each tree had two sunflower seeds hidden in two of the four holes. One side of the aviary, containing two trees, was designated the worm side, and the other side, containing the other two trees, was designated the seed side. During Phase 1, a bird was allowed to forage until it collected four seeds from any of the trees. In the example shown in Fig. 3, the bird collected one seed from the worm side and three seeds from the seed side. After Phase 1, a bird returned to its home cage and then returned to the aviary 30 min later for Phase 2. Only sites (holes) that had not been visited in Phase 1 now contained food. The critical manipulation involved replacing sites not visited in Phase 1 with a preferred mealworm on the worm side, while unvisited sites on the seed side once again contained a sunflower seed. Thus, in order to obtain more mealworms in Phase 2, chickadees had to avoid taking sunflower seeds from the worm side in Phase 1.

Fig. 4 shows the results of this experiment for the first block of five daily trials and for the last block of five daily trials. Panel a shows the proportion of first choices of a hole on the worm side of the aviary in Phases 1 and 2, and panel b shows the percentage of total visits to holes on the worm side during Phases 1 and 2. It is clear that chickadees' preferences were modified from initial to final testing sessions. In the initial block of trials, they chose the worm side slightly less than 50% of the time in Phase 1. By the final sessions, however, choice of the worm side was significantly below 50% in Phase 1 and significantly above 50% in Phase 2. The findings imply that birds learned to anticipate the replacement of unvisited seed sites on the worm side in Phase 1 with mealworms in Phase 2. Birds thus avoided foraging for a food they hungered for (sunflower seeds) in one location in order to maximize their access to another favored food (mealworms) 30 min into the future. This finding is further impressive because it argues against a conditioned reinforcement interpretation of the data. Because preferred mealworms were only found and consumed on the worm side of the aviary, this side should have held
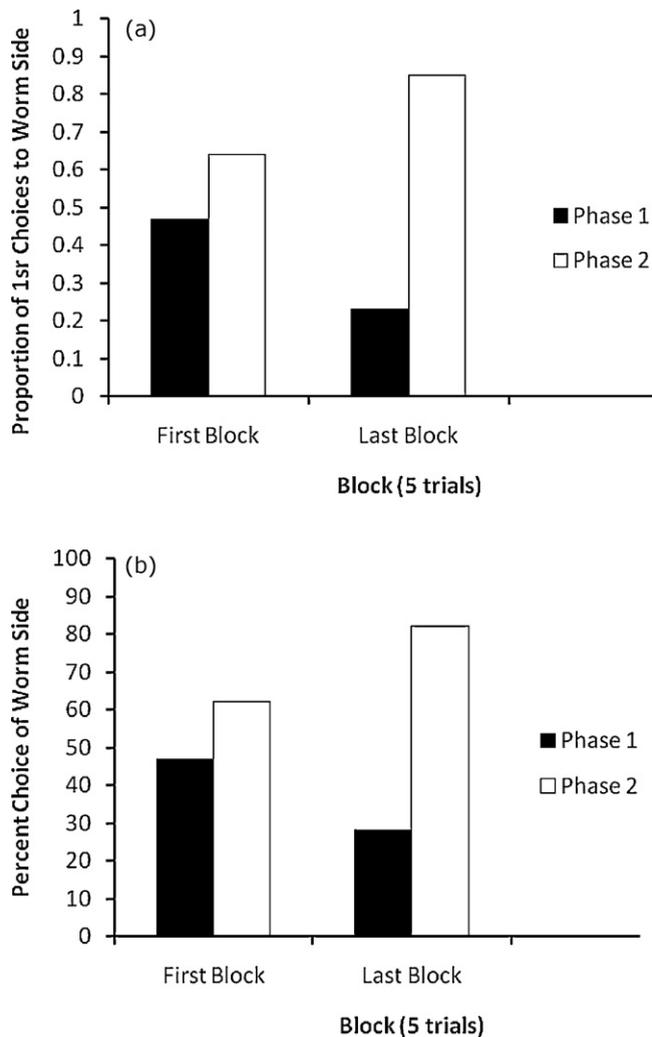
Fig. 4. Top panel (a) shows the proportion of trials on which the worm side was chosen first in Phases 1 and 2. Bottom panel (b) shows the percentage of total choices from the worm side in Phases 1 and 2.

more attraction for birds through its pairing with a preferred food (conditioned reinforcement). Yet, chickadees came to inhibit visits to trees on the worm side of the aviary in Phase 1.

The Correia et al. (2007) and Feeney et al. (2011a) experiments appear to challenge the Bischof-Kohler hypothesis because birds had to avoid caching or visiting sites containing one type of food in order to satisfy a future need for a more preferred food. Naqshbandi and Roberts (2006; Experiment 1) tested two squirrel monkeys to see if they could anticipate a qualitatively different drive state from the one currently experienced. In initial baseline sessions, it was established that both monkeys showed a strong preference for four dates (half pieces of date) over one date. Over 25 days of testing, an experimental procedure was introduced in which a monkey's water bottle was removed from its cage just before it was given a choice between one and four dates. Because water had been constantly available up to this point, the monkey was not thirsty. However, eating dates induced thirst, and time of return of the water bottle was contingent on the number of dates chosen. If only one date was chosen, the water bottle was returned after 30 min, but if four dates were chosen, the water bottle was not returned until 3 hr had passed. The results of these manipulations are shown in Fig. 5. Over 80% preference for four dates is shown for initial baseline (IB) trials, but this preference for the larger amount drops progressively over experimental sessions and reaches zero at the fourth block of trials. Preference for the larger quantity was re-established on the final baseline (FB) trials for one monkey (Jake); the other monkey fell ill and could not be tested. These findings suggest that the monkeys learned to anticipate the different consequences of choosing one and four dates and came to choose only one date when it led to sooner return of the water bottle. Because they were not thirsty for water at the time they made this choice, they had to anticipate different degrees of a motivational state (thirst) not currently experienced, contrary to predictions of the Bischoff-Kohler hypothesis.
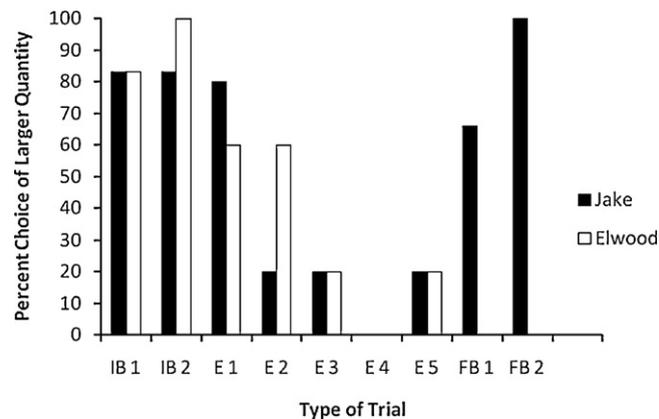
Fig. 5. Percentage of trials on which each squirrel monkey chose the larger number of dates plotted over blocks of six trials for the initial baseline (IB) and final baseline (FB) and over blocks of five trials for the experimental (E) phase. Elwood did not complete the final baseline trials.

An alternative account of this finding, not based on future anticipation, is that monkeys came to choose one date in the experimental phase because they were punished by greater thirst after choosing four dates. However, a control experiment (Naqshbandi & Roberts, 2006; Experiment 2) showed that Jake preferred four dates on 75% of trials when the water was not returned for 3 hr regardless of the number of dates chosen. It appears that sooner future return of the water bottle was necessary for monkeys to prefer choice of one date.

It should be mentioned that Paxton and Hampton (2009) were unable to find the results reported by Naqshbandi and Roberts (2006) when they tested rhesus monkeys. Although it is surprising that rhesus old world monkeys did not show the future anticipation behavior observed in squirrel new world monkeys, Paxton and Hampton (2009) pointed out that one account of this difference lies in the experimental history of the specific monkeys tested. The squirrel monkeys tested by Naqshbandi and Roberts were older (15–16 years) and had extensive prior training in cognition experiments and particularly in experiments involving choices that affected future outcomes (McKenzie et al., 2004). Paxton and Hampton's monkeys were 3–4 years old and had not had such extensive experience. It could be that the squirrel monkeys learned about future time and the effects of current behavior on future outcomes through this prior experimental training and thus were more prepared to learn how their current behavior would affect future outcomes than Paxton and Hampton's rhesus monkeys were.

Moving Food from One Location to Another

Studies or field observations in which animals actually move objects from one location to another more strongly imply future planning because the re-location of objects allows an animal to more easily take advantage of a future opportunity to satisfy a need.

One striking example of such behavior was re-caching of seeds by scrub-jays in apparent defence of their hoard (Emery & Clayton, 2001). Scrub-jays were allowed to cache worms either alone or in the presence of another scrub-jay. When given an opportunity to re-cache worms 3 hr later, those jays that had originally cached in the presence of another jay re-cached more worms to new sites than jays that had cached in private. This behavior occurred only in scrub-jays that had themselves previously pilfered food from other jays' caches. This finding implied that a jay felt that its cache was in danger only if it had itself previously stolen food from another jay's cache.

In a well-received pair of studies (Roberts, 2007; Shettleworth, 2007), Raby, Alexis, Dickinson, and Clayton (2007) reported evidence indicating that western scrub-jays carried out activities that constituted "planning for breakfast." Birds were trained and tested in an apparatus that contained a central compartment and two compartments on each side. In an initial experiment, birds were given a breakfast of pine seeds on one side on some days and nothing on the other side on other days. On a test day, the birds were pre-fed ground pine seeds in the evening and then allowed to cache whole pine seeds available in the central compartment. Scrub-jays selectively carried most of the pine seeds to the side where they had found no food on previous mornings. In a second experiment, jays were initially allowed to find pine seeds in one side compartment on some mornings and kibble in the other side compartment on other mornings. On an evening test, they were allowed to cache both pine seeds and kibble made available in the central compartment. Birds selectively cached most of the pine seeds on the side where kibble was given for breakfast and most of the kibble on the side where pine seeds were given for breakfast. The exciting implication of these experiments was that scrub-jays moved foods to appropriate locations where they normally were not found for breakfast. Thus, in Experiment 1, the jays could expect pine seeds on both sides for breakfast, and in Experiment 2, they could expect both pine seeds and kibble on both sides for breakfast.

In a criticism of the Correia et al. (2007) findings, Suddendorf and Corballis (2008) pointed out that scrub-jays pre-fed Food A different from the Food B they would be pre-fed later did not show an overall increase in caching food A. Instead,

they showed a decrease in caching Food B, leading to a relative increase in the caching of Food A. Thus, it was argued that jays may have learned only not to cache Food B and not to anticipate a need for Food A. Although this point was debated by Clayton et al. (2008), solid evidence against simple inhibitory learning has recently been provided by Cheke and Clayton (2012). Four Eurasian jays were studied in a three-stage experiment. In Stage 1, a bird was pre-fed Food A and then allowed to eat and cache Foods A and B in either of two trays, Tray 1 and Tray 2. As expected, birds ate and cached more of Food B than of Food A. In Stage 2, given 3 hr later, two birds were pre-fed Food A (same). The birds then were allowed to retrieve food items from only one of the two trays (Tray 1). Stage 3 occurred 24 hr later when the birds were pre-fed Food B (different) and then allowed to retrieve food items from Tray 2. Two other birds were pre-fed Food B (different) in Stage 2 and Food A (same in Stage 3), again with access to single trays in different locations after each stage. After a single three-stage trial of this procedure, three of the four birds showed differential caching of foods in the trays in Stage 1. Regardless of which food they were pre-fed in Stage 1, they cached more Food A items in the tray which they would subsequently have access to after being pre-fed Food B and more Food B items in the tray which they would subsequently have access to after being pre-fed Food A. It appears that jays planned for two separate needs by carrying foods to different locations (trays) where these foods would later be needed.

Examples of animals performing behaviors adaptive to seasonal change are typically dismissed as future planning because they appear to be instinctive or genetically hard-wired. Thus, squirrels burying nuts, bears hibernating, and birds flying south in the fall are not seen as intentional preparations for the onset of winter. Recent field observations of tayras, mustelids found in Costa Rica, provide evidence of long-term food caching that may involve foresight (Soley & Alvarado-Diaz, 2011). Tayras were observed foraging for bunches of plantains on forestry plantations. When ripe plantains were found, they were eaten immediately, but unripe plantains were not. It was observed that selected unripe plantains, only those in an advanced state of maturity, were taken away from the plantation to the surrounding forest and cached in trees. Tayras returned to these caches and consumed the plantains when they had ripened. The authors suggest that tayras may have a sense of future time over which initially unripe plantains will ripen. These observations are interesting to consider in light of the Bischof-Kohler hypothesis. In this case, it appears that animals cached a food they currently found unpalatable with the anticipation that it would become palatable in the future.

Planning with Tools

Perhaps the best evidence to date for the planned use of tools by animals appeared in research carried out with bonobos and orangutans by Mulcahy and Call (2006; also see Suddendorf, 2006). The apes learned to use tools to obtain a reward in two different problems. In one problem, a plastic tube had to be used to retrieve grapes from a cylinder, and in the other problem, a hook had to be used to obtain a bottle of grape juice. On test trials, an ape was allowed to see the problem (and reward) but was blocked from accessing it by a transparent Plexiglas barrier. Several tools were available outside the barrier, including the useful tool and several non-useful tools. A subject was allowed to select tools and carry them to a waiting room. After 1 hr, the subject returned to the test room and could bring any of the tools it had taken. The apes carried tools out of the test room on 70% of the trials and chose the useful tool for the problem shown significantly above chance probability. Two of the ten apes initially tested (one bonobo and one orangutan) were further tested with the delay between problem exposure and test extended overnight for 14 hr (Experiment 2). The orangutan chose the suitable tool on 11/12 trials, and the bonobo chose the suitable tool on 8/12 trials. On most of the trials, the apes also returned to the test apparatus with the appropriate tool to gain access to the reward. Even when not allowed to view the apparatus and reward before choosing tools (Experiment 3), two bonobos and two orangutans chose the suitable tool beyond chance expectancy. In a final control experiment, four naïve apes (two bonobos and two orangutans) learned to use the hook to obtain juice. When tested, however, they were rewarded for bringing back the hook after 1 hr, but no problem set-up was shown to the subjects before or after tool selection. In other words, the tool had no functional use during the tests. Under these conditions, the four apes chose the hook on only 7/64 trials, less than chance expectancy (25%). This control experiment argues against the idea that a tool was chosen only because it was associated with reward during initial learning of the problem.

In a somewhat similar series of experiments, Osvath and Osvath (2008) demonstrated tool selection for future use by two chimpanzees and an orangutan. In their initial experiment, these subjects were given one demonstration and one opportunity to use a hose to suck in a highly favored fruit soup. In subsequent tests given in a different setting, they chose between the hose and three other distractor objects. The ape then carried the object chosen back to the group enclosure, where it stayed for 70 min. It was then allowed to enter the reward room where it could use the hose, if it had selected the hose, to obtain fruit soup. During testing, one chimpanzee and the orangutan chose the hose on 14/14 trials, and the other chimpanzee chose the hose on 13/14 trials. It could be argued that the hose was chosen simply because it had become a conditioned reinforcer through its initial one-trial association with fruit soup. In a control experiment, apes were given two successive choice trials. On the first trial, they chose between the functional tool and three distractors, as in the initial experiment. On the second trial, they could choose between a copy of the functional tool, two distractors, and a favored fruit. On all 14 trials given to each subject, the apes chose the functional tool on the first trial and the fruit on the second trial. It appears that once the tool was obtained for its future use, a second tool held little value, although it should have been preferred if its selection was based on nothing but conditioned reinforcement value.

In a particularly convincing final experiment, Osvath and Osvath tested the apes on an initial choice between four new objects. Three objects were novel, but one of these novel objects could be used to suck in fruit soup (plastic pipe, hollow

aluminum frame, etc.), and the objects used were novel on each of 12 trials. The fourth object was always a bamboo stick previously associated with honey extraction. Thus the bamboo stick should have been favored as a conditioned reinforcer. On the majority of trials, all of the apes chose the novel tool that could be used to obtain fruit soup 70 min later. The orangutan chose it on 11/12 trials, one chimpanzee on 10/12 trials, and the other chimpanzee on 9/12 trials. Preference for a novel tool that could be used to obtain a favored food later in time was clearly shown over an object previously paired with food.

Another observation concerns a chimpanzee at a zoo in Sweden that had developed the habit of throwing stones at zoo visitors (Osvath, 2009). The chimpanzee was observed by caretakers fashioning missiles from concrete and carrying these and stones to caches located on the side of its island nearest the public observation area. Although the chimpanzee remained calm during its collection of ammunition before the zoo opened, it showed considerable arousal and stone throwing as crowds of people arrived for the day. Stones were not used in contexts other than throwing, and caching stone tools was not seen during the off-season when the zoo was closed. These observations suggest intentional planning for stone throwing at humans several hours into the future.

Although not involving tools, a relevant recent experiment was reported by Beran, Perdue, Bramlett, Menzel, and Evans (2012) in the current volume. A single chimpanzee (Panzee) was tested. Importantly, Panzee had been given language training previously and thus knew the meaning of a number of lexigrams. In the test procedure, Panzee was given a choice between two food items, one of which was preferred M&Ms and the other of which was one from over a dozen food or drink items. Panzee usually chose the M&Ms. Panzee was then taken to an outdoor enclosure and allowed to collect the M&Ms that were distributed about the enclosure. Also present in the outdoor enclosure were eight tokens turned face down so that the lexigram on each one could not be seen without turning the token over. The lexigrams on the tokens were names for different food items, including the food she did not choose earlier in the trial. If she took the token representing the food she had not chosen initially back to an experimenter in the inside enclosure, she was then given that food. On most trials, Panzee collected the M&Ms and then turned over the tokens until she came to the one that represented the alternative food. Panzee then took this item into the indoor enclosure to exchange for the remaining food item. Beran et al. suggest that Panzee's performance indicates both memory of the initial food choice episode and future planning to obtain the non-chosen food by retrieving and exchanging the appropriate token.

Although these experiments suggest the exciting possibility that apes may select tools in anticipation of their future use, criticism has focused on alternative learning processes and limitations to the extent an ape might be able to think of the future (Dufour & Sterck, 2008; Raby & Clayton, 2012; Roberts & Feeney, 2009a, 2009b; Shettleworth, 2010; Suddendorf & Corballis, 2008, 2010)

Some Theoretical Considerations

A first consideration is whether there is enough evidence to be convinced that future-oriented cognition can be found in animals. This author feels that there is, based on both field and laboratory reports that come from different species and different paradigms and procedures. In the current review, we found a number of examples. Rats, black-capped chickadees and apes inhibit consumption of a favored food when a more preferred food or quantity of food will become available in the future. Monkeys choose a smaller quantity of food over a normally favored larger quantity when this choice means an even larger quantity will be given in the future, or when an anticipated future need will be alleviated sooner. Scrub-jays re-cache foods that might be pilfered by other jays who observe their caching behavior. Jays also selectively carry foods to cache locations they anticipate access to in the future and to locations that will be accessible under appropriate hunger states in the future. Apes select appropriate tools needed for future retrieval of food, retain these tools, and carry them to a test site when given an opportunity to put them to use. Choice of even novel but appropriate tools is preferred over inappropriate objects previously associated with food reward. In field observations, tayras cached not-yet-ripe plantains in trees for later consumption when ripe, and a chimpanzee carefully stored caches of stones in an adventitious location for later use as missiles to throw at zoo visitors. Although a variety of lower-level mechanisms might be invoked in an attempt to explain these various observations, a more parsimonious view is that they represent future cognition or MTT in animals.

If we assume that future cognition is found in animals, a further theoretical question is "what is the nature of future anticipation and planning in animals?" There is virtually no evidence that animals have an ability to form several alternative future plans and choose among them, as people do. However, absence of evidence is not evidence of absence. Perhaps future experiments will be able to address this question of flexibility in animal future planning.

A more basic question is whether animals have a sense of future time as a dimension with a number of locations on it. The discovery of WWW memory in animals has been of major importance because it suggested that they could remember when events occurred at specific points in past time. A similar question can be asked about future time. Do animals anticipate that different events will occur at different points in future time? The alternative to this possibility is that animals might only have a representation of a generalized future in which events will happen. Such a non-temporally specific representation of the future would be more like semantic memory than like episodic future memory.

Some tests of this question are possible (Feeney & Roberts, 2012; Roberts & Feeney, 2009a, 2009b). Suppose that different events will occur at different points in future time, just as different events occurred at different past times in WWW or episodic-like memory experiments. In the Raby et al. (2007) planning for breakfast experiment, suppose that a scrub-jay is initially taught that food will be found in different locations in the morning and at noon. Thus, jays might be put in one side compartment and given pine seeds at 9 am on some days and put in the other side compartment and given no pine seeds at

9 am on other days. On still other training days, they would be put in the compartment that was empty at 9 am and given seeds at 12 pm, whereas placements in the compartment that has seeds at 9 am yields no seeds at 12 pm. When given an evening test, where will the scrub-jays cache pine seeds? If they have a sense of time and wish to have pine seeds available in both compartments for breakfast the next day, they should cache pine seeds in the compartment that was empty at 9 am and not the compartment that was empty at 12 pm.

Similar logic might be applied to the Osvath and Osvath (2008) procedure. Suppose apes are exposed to fruit soup, with no tube with which to drink it, at 10 am and to a jar of honey, with no stick to dig it out, at 2 pm for several days. At 8 am on a test day, the subjects are given a choice among tools that consist of a hose, a stick, and two other distractor objects and can only choose one object. If chimpanzees and orangutans can anticipate a future in which availability of fruit soup and honey occur at different times, one nearer the present time than the other, they should choose the hose. If they were given the same choice at 12 pm, however, they should choose the stick. Such experiments might begin to shed some light on whether animals can view different points in future time.

A final theoretical issue concerns the evolutionary implications of future MTT in animals. It has probably not escaped the reader's notice that most of the demonstrations of future anticipation and planning in animals involve either non-human primates or animals that cache and retrieve food, such as scrub-jays, black-capped chickadees, and tayras. Although rats are not scatter hoarders, they are central-place hoarders. The importance of this observation is that it leads to the hypothesis that evidence for future-oriented cognition in these non-primates might have been found because of evolutionary pressures that led to this ability. Animals that cache and later retrieve food from their caches may have to be particularly aware of the possible future fate of their caches. Thus, we might expect to find future-oriented cognition only in species of animals in which their survival depends on anticipation of future outcomes (Feeney & Roberts, 2012). The alternative is that future MTT is a general adaptive trait common to many species. This question of a general versus specialized trait encourages future research with a variety of species that would seem to have varying need for future anticipation and planning for their survival.

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