



An operant analog of food caching in the pigeon (*Columba livia*)

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Abstract

Although pigeons do not naturally cache and recover food items as found in members of the corvid and parid families, an operant analog of food caching and recovery in pigeons was studied in four experiments. Pigeons were trained to peck a caching key that added a fixed increment of time to the final duration of reinforcement obtained by pecking a payoff key. The same key served as the caching and payoff keys in Experiment 1, but separate caching and payoff keys were used in Experiments 2–4. In Experiments 2–3, each peck on a left red caching key added 0.5 s of reinforcement earned by pecking a right white payoff key. In Experiment 4, red or green caching keys appeared on different trials, with 0.5 s of reinforcement earned for pecking the red key and 1.0 s of reinforcement earned for pecking the green key. Pigeons showed an increased number of pecks on the caching key over ten sessions in Experiments 1–3 and more pecks on the green caching key than on the red caching key in Experiment 4.

Keywords Caching · Pigeon · Reinforcement duration · Food recovery · Payoff

Introduction

One of the most important discoveries in the fields of behavioral ecology and comparative cognition has been the finding that certain species of birds cache food in different locations and later retrieve it using spatial memory. Birds in the Corvid family, Clark's nutcrackers and scrub jays, cache food in different locations and recover it over extended periods of time in both natural and laboratory settings (Balda & Turek, 1984; Clayton & Dickinson, 1998, 1999; Kamil et al., 1994; Kamil & Balda, 1983, 1990; Olson et al., 1995; Tomback, 1980; Vander Wall, 1982). Memory for cached food by birds in the Parid family, tits and chickadees, has been extensively studied by David Sherry and his colleagues (Sherry, 1987, 1992; Shettleworth, 1983, 1990). Among their findings is the discovery that memory for stored-food sites in black-capped chickadees is long term, lasting as long as 28 days (Hitchcock & Sherry, 1990). Further studies of black-capped chickadees revealed that birds learn to avoid caching food at sites where caches had previously been stolen (Hampton & Sherry, 1994), that although birds cache out of sight of other birds, cache pilfering is rare (Hitchcock & Sherry, 1995), that

birds remember cache locations using distal and not proximal cues (Herz et al., 1994), and that birds show what-where-when memory (Feeney et al., 2009).

Of particular importance has been Sherry's investigations of the role of the avian hippocampus in spatial memory for food sites. Sherry and Vaccarino (1989) aspirated a structure homologous to the mammalian hippocampus in black-capped chickadees and found that their spatial memory for stored-food sites was reduced to chance. Knowledge of the evolutionary role of the hippocampus was further revealed in an extensive study by Sherry and Vaccarino (1989). The volume of the hippocampal complex and telencephalon was found to be larger in three families of passerines that store and retrieve food (chickadees, nuthatches, and jays and crows) than in ten non-food-storing families and subfamilies of passerines.

An interesting issue that arises concerning food caching and retrieval is *intentionality*. Are birds simply driven to cache food items in different locations with no intention of retrieving them at a later time, or are food items purposefully cached with a plan to later retrieve them (Roberts, 2002, 2012)? Studies of scrub jays (Raby, Alexis, Dickinson, & Clayton, 2007) and black-capped chickadees (Feeney, Roberts, & Sherry, 2011) suggest that these birds may anticipate the recovery of cached food items, but others have questioned the validity of this conclusion (Martin, Martin, Roberts, & Sherry, 2021; Suddendorf & Corballis, 2008; Shettleworth, 2007).

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The experiments reported here are a clear departure from the summarized research on corvids and parids. There is no evidence that pigeons or other members of the Columbidae family store and recover food items. However, this research asks the question of whether a pigeon might be able to learn to cache food that it would be able to consume a short time later. Pigeons in these experiments were not required to remember the spatial locations of food items. Rather, these experiments used a three-key operant chamber in which pecks on a target key would deliver reward from a food hopper. However, the size (temporal length) of the food reinforcement was dependent upon the number of pecks made on the target key (Experiment 1) or on another caching key (Experiments 2–4). Each peck made on the key cached an additional fixed duration of reinforcement time. There is some precedent for these experiments. Killeen et al. (1981) performed a central-place foraging experiment with rats by training them to press one lever to accumulate food pellets that could then be accessed by responding on a second lever. The question raised by these experiments was whether pigeons can learn such a contingency and thus cache increasingly larger amounts of food reinforcement.

The task used in these experiments is much shorter than those required of animals that cache in the wild and requires a pigeon to use both short-term working memory and reference memory. For pigeons to learn the relationship between pecking the caching key and the payoff for pecking the payoff key, they must retain working memory for quantity of pecks made on the caching key. Over repeated trials of high or low food-duration availability for high or low numbers of pecks on the caching key, reference memory for the relationship between caching and payoff should be acquired, leading to more efficient caching behavior.

Experiment 1

When placed in a darkened operant chamber, a pigeon would periodically see an illuminated key. The first peck on this key after an interval of 10 s could deliver food reinforcement from a central hopper. Although this description sounds like a traditional fixed interval (FI) schedule, an additional contingency was introduced. For the peck after 10 s to deliver reinforcement, at least one peck had to be made on the key before the 10 s elapsed. Furthermore, each peck on the key added 0.5 s of time that the food hopper would remain available. For example, if a pigeon pecked the key eight times during the 10 s, the first peck after 10 s delivered 4 s of access to the food hopper. Thus, each peck cached food access time that could be cashed in by a peck after 10 s.

Subjects

Four adult White King pigeons (*Columba livia*) were used. These birds had previously been used in experiments on midsession reversal and memory systems interaction. Birds were maintained at 90% of their free-feeding weight throughout the experiment, with constant access to water and health grit. They were individually housed in individual cages in a room kept environmentally controlled at 22 °C. Fluorescent lights were turned on at 7:00 a.m. and off at 7:00 p.m. each day. Testing was performed between 9 a.m. and 4 p.m. for 5 days each week.

Apparatus

A sound-attenuating operant chamber measuring 31 × 35.5 cm (floor) × 35.3 cm (height) was used. The front wall of the chamber held three pecking keys, 2.5 cm in diameter and level with the pigeon's head, in a row, spaced 8 cm apart. Projectors behind each key projected filtered light, presenting different colors or patterns on the keys. Grain reinforcement was delivered by an electromechanical hopper through a 6 × 6 cm opening in the front wall located near the floor, directly below the center key. Presentation of stimuli, reinforcement, and recording of responses were carried out by a microcomputer interfaced to the operant chamber.

Procedure

A pigeon was placed in the darkened operant chamber. When the experimental program began, the right key was illuminated with white light. After 10 s, the first peck on the key could lead to delivery of food reinforcement from the central food hopper. If the key had not been pecked during the 10 s, then no food was delivered. However, each peck on the white key during the 10 s added 0.5 s to the length of time the food hopper remained available when the key was pecked at the end of 10 s. The first peck after 10 s raised and illuminated the food hopper for the duration of time cached by pecking and turned off the white key. After food delivery, an intertrial interval of 10 s elapsed in darkness, followed by the onset of the white key for the next trial. Each session lasted for 20 trials, and pigeons were trained for ten sessions.

Results and discussion

The mean pecks per trial made by pigeons over ten sessions are shown in Fig. 1. The figure shows that the rate of pecking increased from a little over six pecks per trial on session 1 to 15–17 pecks per trial on sessions 3–10. A one-way ANOVA revealed that the rise in the peck rate over sessions was statistically significant, $F(9, 27) = 4.73$, $p < .01$, $\eta_p^2 = .61$. Thus,

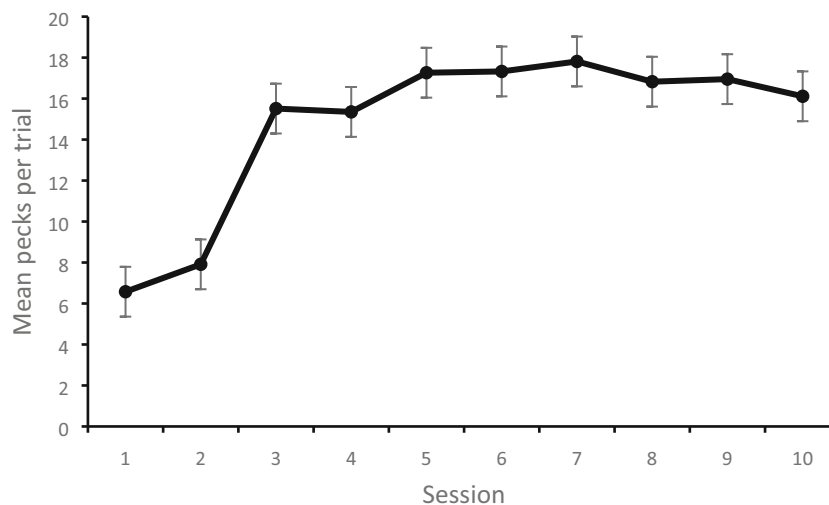


Fig. 1 Pigeons' rate of pecking a white key in Experiment 1 increased over ten sessions when each peck added 0.5 s of access to grain reinforcement. Error bars are SEM

pigeons learned to peck the white key at a high rate to deliver an extended temporal cache of reinforcement.

Experiment 2

Although pigeons showed a significant increase in peck rate in Experiment 1, it may be argued that greater reinforcement time had simply reinforced more frequent key pecking. In other

words, pigeons had not learned the relationship between frequency of key pecking and duration of reinforcement. In order to pursue this question further, Experiment 2 was carried out to separate the caching response from the reinforced or payoff response. On each trial in Experiment 2, pigeons initially saw only the left key illuminated with a red light for 10 s. The

white right key then came on after 10 s, and the red key was turned off. For each peck made on the red key during the initial 10 s, the pigeon received 0.5 s of reinforcement when the right white key was pecked.

Procedure

The same four pigeons and apparatus used in Experiment 1 were used in Experiment 2. Pigeons received 20 trials per daily session over ten sessions, with trials separated by a 10-s intertrial interval. Each trial began with the onset of red light on the left key. After 10 s, the red light was turned off and the right key was illuminated with white light. Each peck made on the red key over 10 s added 0.5 s of time to the duration of reinforcement delivery. The first peck made on the white key delivered the reinforcement accumulated by pecks on the red key. If a pigeon did not peck the red key for 10 s, pecking the white key ended the trial without reinforcement.

Results and discussion

Mean pecks per session are shown for ten sessions in Fig. 2. Pigeons' rate of pecking again increased over sessions. Pigeons began pecking the red key about four times in session 1 but increased their rate of pecking to 12–14 pecks over the final sessions. An ANOVA showed that the increase in peck rate over sessions was statistically significant, $F(9, 27) = 4.63$, $p < .01$, $\eta_p^2 = .61$.

The findings of Experiment 2 indicate that pigeons learned to make increasingly more pecks on the red caching key during its 10-s duration. During these 10 s, a pigeon could only peck or not

peck the caching key. That is, it could not strike the white payoff key until 10 s had gone by. The question addressed by the next experiment is how pigeons deal with a situation in which they can choose to cache or cash in at any time during a trial.

Experiment 3

Experiments 1 and 2 placed a limit on the length of time a pigeon could cache reinforcement time. Experiment 3 explored a more open form of caching and retrieval that perhaps more closely resembles natural caching in animals. On each trial, both the left red key and right white key were illuminated simultaneously. As in Experiment 2, each peck on the red key added 0.5 s of time to the duration of reinforcement. However, access to the red key was not time limited. A pigeon could peck the red key repeatedly to store reinforcement time, and the red key only went off when the pigeon had pecked the white key five times (FR 5). Thus, a pigeon could store unlimited reinforcement time by pecking the red key but could strike the white payoff key at any time during the trial. A

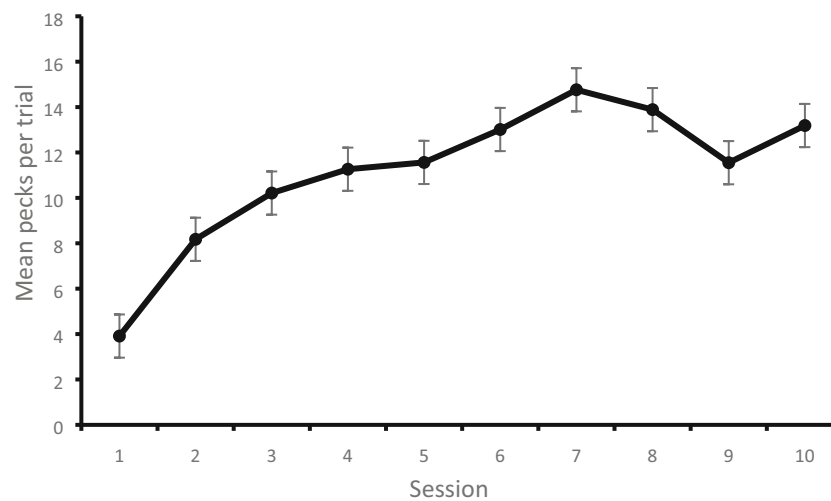


Fig. 2 Pigeons showed a significant increase in rate of pecking the red caching key over ten sessions of testing in Experiment 2. Error bars are SEM

pigeon could peck the red and white keys alternately, but pecks on the white key continued to accumulate toward the FR 5 during a trial. Thus, the effort required to receive the payoff was raised from FR 1 in Experiment 2 to FR 5 in Experiment 3.

Procedure

The same pigeons and apparatus used in the first two experiments were used in Experiment 3. Each pigeon was tested for ten daily sessions with 20 trials per session. Each trial began with the simultaneous onset of the red left key and the white right key. Five pecks on the white key always terminated the trial with or without reinforcement. Each peck on the red key added 0.5 s to the duration of time the food hopper was available for reinforcement. There was no limit on the time the red key was available or on the number of pecks that could be made on the red key. However, completing the FR 5 on the white key without pecking the red key darkened the chamber without reinforcement. Trials were separated by 10 s between the end of reinforcement and the onset of the side keys.

Results and discussion

Figure 3 shows the mean frequency of pecking on the red key as sessions progressed. It can be seen that the number of pecks increased over sessions, and this increase was statistically significant, $F(9, 27) = 5.67, p < .01, \eta_p^2 = .65$. Although the number of pecks on the red key increased over sessions, it is interesting to note that mean pecks on the red key in this experiment were substantially lower than those made on the white key in Experiment 1 or on the red key in Experiment 2. This observation shows that pigeons were often drawn to the white key before making substantial pecks on the red key.

Experiment 4

Pecks made to cache reinforcement time in Experiments 1–3 always added 0.5 s of time. Because each peck added a small addition to food-access time, a pigeon had to make considerable pecks on the caching key to earn a sizeable duration payoff. In Experiment 4, two different caching keys were presented on different trials. Pecks on one key, the standard red key, added 0.5 s of reinforcement as in Experiments 2 and 3. Pecks on the other key, a green key, added 1.0 s of reinforcement. Thus, each peck on the green key added twice as much reinforcement time as pecks on the red key. The question of interest was whether pigeons would discriminate between the red and green keys by making more pecks on one caching key than on the other. The keys differ in work versus payoff. Pigeons might peck the green key less than the red key because they can obtain the same reinforcement duration previously earned on the red key by pecking the green key half as

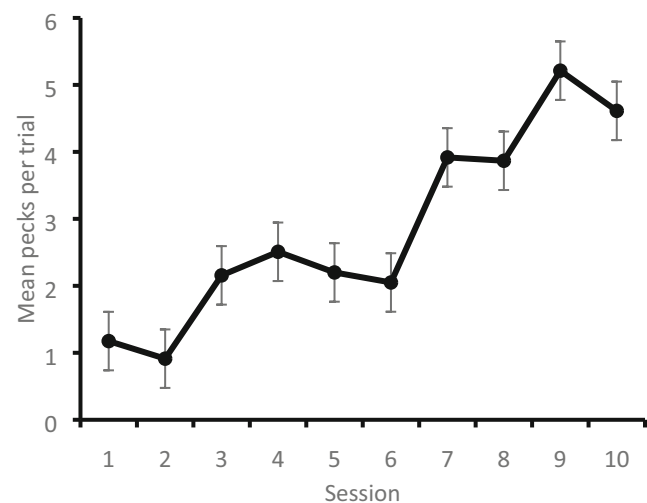


Fig. 3 Figure 3 shows the significant increase in mean pecks made on the red key before pecking the white key in Experiment 3. Error bars are SEM

often. The other possibility is that pigeons will peck the green key more than the red key because each peck earns twice as much reinforcement time.

Procedure

The same pigeons and apparatus used in Experiments 1–3 were used in Experiment 4. Pigeons again received daily sessions of 20 trials. The procedure was similar to that used in Experiment 3. Each trial began with the onset of a left caching key and a right white payoff key. On half the trials, in random order, the caching key was red and on the other half of the trials, the caching key was green. Pigeons could make unlimited pecks on the caching key on each trial, and cashed in the reinforcement time accumulated by completing an FR 5 schedule on the white key. On trials that presented the red caching key, each peck added 0.5 s to the duration of reinforcement received after pecking the white key. On trials that presented the green caching key, each peck added 1.0 s to the duration of reinforcement received after pecking the white key. The intertrial interval was 10 s, and the experiment lasted for ten sessions.

Results and discussion

Figure 4 shows the mean number of pecks made on each key over ten sessions. Although pigeons pecked both keys equally on the first session, pecking on the 0.5-s red key declined over sessions while pecking on the 1.0-s green key remained at a higher level. A key \times session ANOVA revealed a significant effect of key, $F(1, 27) = 12.71, p < .01, \eta_p^2 = .32$, but non-significant effects of session, $F(9, 27) = 1.16, p > .05$, and the key \times session interaction, $F(3, 27) = 1.01, p > .05$.

The findings of Experiment 4 suggest that pigeons quickly learned to peck more frequently on the green key than on the red key. The low rate of pecking on the red key showed that pigeons were not attempting to earn the same amount of reinforcement time on this key as they obtained for pecking the green key. In fact, rate of pecking on the red key dropped to a lower rate than obtained in the final sessions of Experiment 3. Although pecks on either the red or the green key only paid off after completion of an FR5 schedule on the white key, pigeons' more frequent pecks on the green key than on the red key suggest that they learned something about the relationship between each key and the payoff in reinforcement time duration. They may not have learned that each peck on the green key added 1.0 s of reinforcement time but pecks on the red key added only 0.5 s of reinforcement time. However, if they learned that pecks on the green key led to generally more reinforcement time than pecks on the red key, this information may have generated a preference for pecking the green key.

General discussion

Although several species of corvids and parids cache food items and later recover them using spatial memory both in natural habitats and in laboratory settings (Clayton & Dickinson, 1998, 1999; Feeney et al., 2009; Herz et al., 1994; Hitchcock & Sherry, 1990, 1995; Kamil & Balda, 1983, 1990), no evidence of food caching has been found in members of the columbidae family.

Nevertheless, four experiments were reported here that examined a possible operant analog of food caching in pigeons. The question examined was whether pigeons could learn that each peck on a key in an operant chamber added a unit of time to the duration of food reinforcement given at the end of a trial.

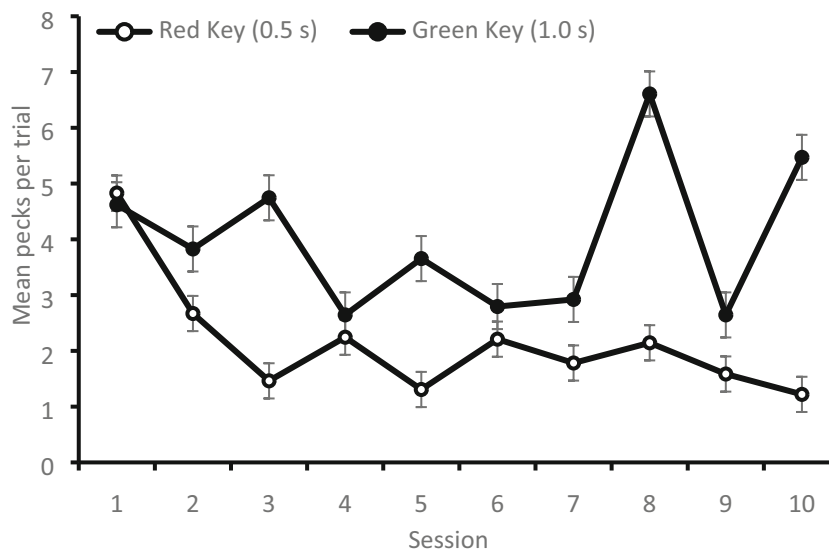


Fig. 4 Mean pecks per session made on the red (0.5 s) key and on the green (1.0 s) key over ten sessions. Error bars are SEM

In fact, a previous set of experiments with rats showed that rats learned to press one lever to accumulate food pellets that could then be accessed by pressing another lever (Killeen et al., 1981).

These experiments showed largely that pigeons learned to peck a “caching key” in order to earn reinforcement when they pecked a “payoff key.” The number of pecks on a right white key increased over sessions in Experiment 1 when each peck added 0.5 s of time to the duration of grain reinforcement. When a second caching red key was added on the left in Experiments 2 and 3, pigeons learned to increasingly peck this key for larger reinforcements delivered for pecking the white payoff key. Pigeons showed an increased number of pecks on the red key both when access to the red key was limited to 10 s (Experiment 2) and when access to the red key was unlimited (Experiment 3). In Experiment 4, pigeons pecked more frequently on a green key that cached 1.0 s of reinforcement for each peck than on a red key that cached only 0.5 s of reinforcement for each peck.

In Experiments 1 and 2, pigeons were allowed access to the caching key for 10 s before responding to cash in the reward duration earned. The pattern of responding on the caching key is of interest. Did pigeons show the typical scallop pattern of responding seen on fixed-interval schedules? A second-by-second record of pigeons responding on the caching key within trials in these experiments showed that the rate of responding accelerated during the first 4–5 s and then leveled off for the remainder of the 10-s interval. Thus, pigeons did not show an initial low rate of responding with acceleration only at the end of the 10 s. This observation reinforces the conclusion that pigeons learned the relationship between responding on the caching key and length of food access for response to the payoff key.

Caching found in corvids and parids appears to be an evolved form of preparation for a future need, with spatial memory for cached food dependent upon an enlarged hippocampus (Sherry et al., 1989; Sherry & Vaccarino, 1989). The experiments reported here suggest that pigeons learned to increasingly make pecks on one key to receive a longer temporal reinforcement payoff by pecking another key. Although pigeons may not have understood that each peck on the caching key added a fixed increment of reinforcement time, they appear to have learned a general rule about frequency of pecking and the ultimate payoff. Pigeons learned or formed reference memory for the relationship between working memory for caching responses made on one key and the temporal amount of food payoff earned on another key. Thus, a bird that does not naturally cache and retrieve food can learn an operant analog of caching. This finding raises the interesting question of whether food caching and retrieval in animals that appear to have evolved this ability involves a learning component and how learning interacts with evolved behavior.

However, an examination of trial to trial pecking behavior within sessions suggests a complex relationship between responses on the caching and payoff keys. In Experiments 3 and 4, pigeons had unlimited time to peck the caching key on each trial but also could peck the white payoff key at any time during a trial. On many trials, pigeon omitted responses on the caching key and immediately pecked the white payoff key, thus earning no reinforcement. In Experiment 3, pigeons pecked the caching key on 42.5% of the trials and went directly to the payoff key on the other 57.5% of the trials. In Experiment 4, pigeons pecked the red caching key on 52.8% of the trials when it appeared and pecked the green caching key on 64.2% of the trials when it appeared.

Thus, pigeons showed a pattern of alternating between zero pecks on the caching key and a sometimes high frequency of pecks on the caching key before pecking the payoff key. This pattern suggests that pigeons developed a conflict between the caching and payoff keys. After a number of pecks on the caching key, pigeons received an extended duration of access to the feeder. Because this access to the feeder followed pecks on the payoff key, pigeons were immediately drawn to the payoff key on subsequent trials. However, when pecks on the payoff key then yielded no reinforcement, pigeons returned to the caching key on the following trials. This pattern of responding might loosely be described as one of repeated reinforcement of pecking on the payoff key (when the caching key had been pecked) followed by extinction of immediate pecking on the payoff key (and alternative pecking on the caching key) when no reinforcement had been given for pecking on the payoff key.

In conclusion, these experiments suggest that an operant analog of food caching and recovery was established in pigeons but that the processes involved are likely very different from those responsible for food caching and retrieval in corvids and parids. Pigeons did learn about the relationship between frequency of pecking on the caching key and the duration of reinforcement delivered by pecking the payoff key, as shown by the increase in frequency of pecking the caching key over sessions in Experiments 1–3. However, the learned relationship between caching key pecks and duration of reinforcement was tempered by a conflicting tendency to peck directly on the payoff key that delivered immediate reinforcement. Thus, a conflict developed between pecking the caching key and pecking the payoff key. A procedure that somehow eliminated this conflict might show more consistent pecking of the caching key across trials within sessions.

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