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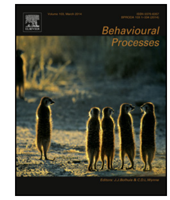

Choice and timing in pigeons under differing levels of food deprivation☆

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ABSTRACT

State-dependent valuation learning (SDVL) is a preference for stimuli associated with relative food deprivation over stimuli associated with relative satiety. Pigeons were exposed to experimental conditions designed to investigate SDVL and to test the hypothesis that obtained relative immediacy during training predicts choice during test probes. Energy states were manipulated using a procedure that has previously revealed SDVL in starlings and pigeons. In Experiment 1, pigeons preferred the stimulus associated with deprivation in the first choice probe session, but were indifferent in the second. Changes in choice were consistent with changes in obtained relative immediacy. In Experiment 2, training parameters were altered and SDVL did not occur. Obtained relative immediacy again predicted choice. Results of both experiments provide evidence that obtained relative immediacy may be an important contributing factor to the SDVL phenomenon.

1. State-dependent valuation learning and temporal control

State-dependent valuation learning (SDVL) is a preference for discriminative stimuli associated with the presentation of food under a state of relative food deprivation over discriminative stimuli associated with food presentation under a state of relative satiety (Marsh et al., 2004; Pompilio and Kacelnik, 2005; Pompilio et al., 2006; Vasconcelos and Urcuioli, 2008). Procedurally, organisms are presented with two discriminative stimuli in separate sessions. One stimulus is presented when the subject is food deprived (e.g., at 80% of its free-feeding bodyweight) and another stimulus is presented when the subject is fed prior to the experimental session. After multiple sessions of training under each food-deprivation state, subjects are exposed to choice trials in which the two discriminative stimuli are presented simultaneously. When SDVL occurs, a statistically significant majority of choice responses occur for the stimulus associated with food presentation under the relatively food-deprived state (e.g., Marsh et al., 2004; Vasconcelos and Urcuioli, 2008). One interpretation of these results is that food has more value when food deprivation is greater, so stimuli associated with food presented in a relatively food-deprived state have higher conditioned reinforcing value than stimuli associated with food presented after pre-feeding.

SDVL has been demonstrated in a variety of animals, including starlings (Marsh et al., 2004), banded tetras (Aw et al., 2009), and grasshoppers (Pompilio et al., 2006). However, it has proven transient in pigeons, which can make it difficult to measure using the traditional choice-probe preparation. Vasconcelos and Urcuioli (2008) reported results of two experiments with pigeon subjects. In one experiment, all four pigeons preferred the stimulus associated with deprivation in the first choice probe but one pigeon was indifferent in the second choice probe. The second experiment was a simultaneous discrimination experiment that involved four choice probes. Across six pigeons, there was no reliable preference for stimuli associated with deprivation or pre-feeding. Vasconcelos and Urcuioli's results indicate that SDVL in pigeons is either unreliable or transient, disappearing with training or exposure to both stimuli simultaneously under the same state. In addition, the behavioral process that produces the effect is not known.

Kacelnik and colleagues have conjectured that the value of a particular discriminative stimulus depends on the amount of "fitness gain" it has been associated with in the past (see Pompilio et al., 2006). For example, under greater food deprivation, food is more valuable because each calorie consumed results in a

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greater improvement in health or wellbeing. This relatively greater increase in fitness presumably produces the greater subjective value of the discriminative stimulus present at the time. The assumption is that preference for the discriminative stimulus emerges when pitted against discriminative stimuli associated with food under pre-fed conditions because when the latter stimuli were previously presented, less fitness was gained from the same amount of food. This evolutionary framework posits that some behavioral mechanism has resulted in the evolution of preferences for discriminative stimuli paired with food under relatively greater levels of food deprivation across multiple species.

One possible mechanism for SDVL is that preference for the stimulus associated with food under greater food deprivation is driven by procedural details that produce differences in time to food. Motivational variables such as food deprivation and reinforcer magnitude have been shown to affect timing processes in a peak procedure (Galtress and Kirkpatrick, 2009) and temporal bisection (McClure et al., 2009) task, and to affect start times, but not overall timing in a peak procedure (Ludvig et al., 2011). Similarly, in pigeons, preference for the stimulus associated with deprivation may be transient because as they gain additional exposure to the intervals, pigeons learn that the intervals signaled by the two stimuli are equivalent (Subramaniam, 2013).

In SDVL experiments, it is possible that there are differences in the perceived value of a stimulus associated with food delivery due to differences in obtained time to food delivery. Many SDVL procedures involve response-initiated fixed-interval (RIFI) schedules in which the interval that determines when a response will produce food does not begin timing until a response is registered. In these schedules, a longer latency to respond increases the obtained time to food. In spite of this additional contingency, response latencies are not shorter in RIFI schedules than in traditional fixed interval schedules (Fox and Kyonka, 2013). If response latency was systematically longer after pre-feeding than in deprived sessions, however, the time to food from stimulus onset would be longer as well. Therefore, preference for the stimulus associated with deprivation could be a preference for a stimulus associated with a shorter obtained time to food.

The objectives of the two experiments that follow were to determine the relations between food deprivation level, obtained time to food, temporal control of behavior, and choice in a SDVL experimental paradigm. If a difference in obtained or perceived time to food controls preference in choice probe sessions, the stimulus associated with greater food deprivation will be preferred when time to food is shorter under deprived training conditions than pre-fed training conditions. Differences in time to food, and therefore preference for the stimulus associated with deprivation, should disappear if first-response latency does not affect obtained time to food.

2. Experiment 1

Experiment 1 was an extension of Vasconcelos and Urcuioli's (2008) Experiment 1, which was based on Marsh et al.'s (2004) experiment with starlings. The primary objective was to compare obtained time to food in food deprived and pre-fed baseline sessions and to determine whether differences predict preference in choice probe sessions. Procedurally, Experiment 1 was kept as similar to the standard SDVL preparation (e.g., Vasconcelos and Urcuioli, 2008) as possible to ensure that procedural variations did not influence results. Based on prior pigeon experiments, SDVL was expected: a preference for the stimulus associated with relatively greater food deprivation. If the hypothesis that preference was driven by differences in time to food is correct, preference should be correlated with differences in time to food in the two baseline conditions. Specifically, obtained time to food should be shorter in the deprived condition than the pre-fed condition during the baseline conditions. If there is no difference in time to food during a baseline, there should be no preference for either stimulus during the choice probe that follows.

2.1. Method

2.1.1. Subjects

Four naïve White Carneau pigeons numbered 205–208. Prior to beginning the experiment and during pretraining, pigeons were maintained at 80% of their free-feeding weight plus or minus 15 g through appropriate post-session feedings. Pigeons were housed individually in a vivarium with a 12-h light:dark cycle with continuous free access to water and intermittent access to grit.

2.1.2. Apparatus

Four standard operant chambers (25.5 cm deep × 32 cm wide × 33.5 cm high) enclosed in a sound-attenuating boxes equipped with ventilation fans. Each chamber contained three response keys arranged 6 cm apart and 24 cm above the floor of the chamber. Response keys could be illuminated red, green or white. A food magazine (5.5 cm high × 6 cm wide) was located below the middle response key and 5.5 cm from the floor. A houselight was located at the top of the chamber on the wall opposite of the response keys. The houselight was illuminated during intertrial intervals (ITI) only. The food magazine was illuminated during reinforcement and contained mixed grain. A force of approximately 0.15 N was required to register a response on any key. All experimental events were controlled through a computer and MED-PC® interface located in an adjacent room.

2.1.3. Procedure

2.1.3.1. Pretraining. All pigeons were initially magazine trained and then trained to peck all three keys and colors using an autoshaping procedure. They were then exposed to response-initiated fixed-interval (RIFI) schedules. The schedule value was 1 s on the first day of pretraining and progressively increased to 6 s over five sessions. Each trial began with the illumination of a key light. The first peck to the key started the interval. Once the interval elapsed, the first peck produced food reinforcement. During this pretraining both red and green key lights were presented pseudorandomly (no more than twice in a row for any color on the same side), an equal number of times on both the left and the right keys. Training sessions lasted 20 trials. The houselight was off during stimulus and food presentations, but on during a 45 s fixed-time ITI.

2.1.3.2. Baseline 1. Pigeons were weighed 30 min prior to each session. If the pigeon was scheduled for a “pre-fed” session, it was fed 7% of its free-feeding weight. If it was scheduled for a “deprived” session, it waited 30 min. Pigeons experienced a total of 12 baseline sessions (6 pre-fed, 6 deprived), presented in pseudorandom order. To maintain a consistent difference in pigeons' weights in pre-fed versus deprived sessions, the same type of session occurred no more than two days in a row. An RIFI 6-s schedule operated in all baseline sessions. At the start of a trial, the left or right key was lighted red or green, depending on the pigeon's food deprivation state for that day. Keys were red in deprived baseline sessions and green in pre-fed baseline sessions for Pigeons 205 and 207; they were the opposite for Pigeons 206 and 208. A peck to the lighted key initiated the 6-s interval. The first peck at least 6 s after the interval was initiated resulted in food. The next trial was presented after a 45 s ITI. Sessions lasted for 20 trials or 60 min, which ever occurred first.