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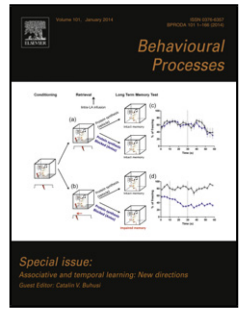

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Choice and Timing in Pigeons under Differing Levels of Food Deprivation

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Highlights

- Preferring stimuli associated with food deprivation is a state-dependent learning effect.
- Evidence for this effect is less robust in pigeons than in other animals.
- Food deprivation altered pigeons' obtained time to food delivery.
- When time to food was constrained to be similar, pigeons were indifferent.
- Obtained relative immediacy may be an important factor in state-dependent learning.

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.

Keywords: foraging, relative immediacy, state-dependent learning, temporal discrimination, timing, pigeons, key peck

Choice and Timing in Pigeons under Differing Levels of Food Deprivation

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; Vaconcelos 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 the state-dependent learning effect in pigeons is either unreliable or transient, disappearing with training or exposure to both stimuli simultaneous 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 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 behavioural 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 state-dependent learning 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 state-dependent learning 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-hr 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 X 32 cm wide X 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 X 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 inter-trial intervals (ITI) only. The food magazine was illuminated during reinforcement and contained mixed grain. A force of approximately .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 5 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 pseudo-randomly (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 intertrial interval (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 minutes, which ever occurred first.

2.1.3.3 Choice 1

A single 20-trial choice session immediately (the next day) followed the last baseline session. During choice sessions, pre-fed and deprived stimuli (red and green key colors) were presented simultaneously on the left and right response keys. Whether the pre-fed stimulus was on the left and the deprived was on the right, or vice versa, was determined pseudorandomly on each trial. A key color could not appear on the same side for more than two consecutive trials. During the first choice session Pigeons 205 and 207 were pre-fed and Pigeons 206 and 208 were deprived. A single peck to either side key extinguished the other key and initiated the 6-s interval to food, after which the first peck resulted in reinforcement.

2.1.3.4 Baseline 2

After the first choice session, all pigeons were exposed to a second baseline condition. Conditions were the same as in Baseline 1.

2.1.3.5 Choice 2

A second 20-trial choice session immediately (the next day) followed the last session in Baseline 2. Conditions were the same as in Choice 1, except that Pigeons 205 and 207 were deprived and Pigeons 206 and 208 were pre-fed (opposite of the first choice session).

2.2. Results

The top panel of Figure 1 shows mean latency to the first response (the response that initiated the interval in the RIFI schedules) calculated separately for deprived and pre-fed sessions of Baselines 1 and 2. Latencies that were greater than 166% (10 s or greater) of the programmed RIFI interval were excluded from analysis to reduce skewing of means by outliers. Response latencies were entered into a repeated-measures analysis of variance (ANOVA) with deprivation level (deprived or pre-fed) and baseline (1 or 2) as factors. Response latencies were significantly shorter in deprived sessions than in pre-fed sessions $F(1,3) = 16.67$, $p = 0.03$, $\eta_p^2 = 0.85$. Neither the main effect of baseline condition nor the deprivation level X baseline interaction were statistically significant (both Fs < 1): the difference in latency to the first peck observed in Baseline 1 was maintained in Baseline 2.

The bottom panel of Figure 1 shows mean time to food from trial onset (signaled by the illumination of the key light) during Baselines 1 and 2. In RIFI schedules, latency to respond affects the amount of time that elapses before food is delivered at the beginning of a trial and at the end, once the RIFI has elapsed. Therefore, observed differences in latency to the first response do not guarantee the same differences will be observed in obtained time to food. Times to food were entered into a repeated-measures ANOVA with deprivation level and baseline as factors. As with response latency, time to food was significantly shorter in deprived sessions than in pre-fed sessions $F(1,3) = 16.92$, $p = 0.03$, $\eta_p^2 = 0.85$, and there were no other statistically significant effects. The absence of a statistically significant interaction ($F(1,3) = 5.90$, $p = 0.09$) indicates that the difference in time to food observed in Baseline 1 was maintained in Baseline 2. If choice in probe sessions was solely determined by obtained time to food in baseline, group mean response allocation should have favored the deprived stimulus in both Choice Sessions.

Figure 2 shows choice for the deprived-state stimulus for each pigeon during Choice Sessions 1 and 2. Pigeons chose the deprived stimulus 65% and 46.25% for Choice Sessions 1 and 2, respectively. A paired-samples *t* test indicated preference for the deprived stimulus was significantly higher during Choice Session 1 than it was during Choice Session 2, $t(3) = 5.00$, $p = 0.02$, $d = 2.57$. To determine whether choice in either session was statistically significantly greater or less than indifference, separate single-sample *t* tests were conducted comparing percent choice in Choice Sessions 1 and 2 to a null hypothesis of indifference (50% choice for each stimulus). Deprived-stimulus choice in Choice Session 1 was significantly greater than indifference, $t(3) = 4.24$, $p = 0.02$, $d = 2.12$. However, deprived-stimulus choice was not significantly greater or less than indifference in Choice Session 2, $t(3) = 1.0$, $p = 0.39$. Consistent with predictions based on group mean obtained time to food, group mean response allocation favored the stimulus associated with deprivation in Choice Session 1. In contrast to predictions based on group mean obtained time to food, group mean response allocation was indifferent in Choice Session 2.

The top left graph in Figure 3 shows relative immediacy from each baseline for each pigeon. Immediacy is the reciprocal of a temporal interval, in this case obtained time to food. The relative immediacy shown in Figure 3 is the ratio of immediacy in deprived sessions to immediacy in pre-fed sessions: (1/time to $food_{deprived}$)/ (1/time to $food_{pre\text{-}fed}$). In both baselines, immediacy ratios were greater than 1 for all pigeons: time to food was more immediate, or shorter, in deprived sessions. However, from Baseline 1 to Baseline 2, immediacy ratios decreased for all pigeons. Although the deprivation level X baseline interaction was not statistically significant, the disparity in obtained time to food decreased for all pigeons. Deprived and pre-fed obtained times to food were more similar in Baseline 2 than they had been in Baseline 1. If choice in probe sessions was determined by obtained time to food in baseline, this decrease in disparity generates the prediction that preference for the deprived stimulus should be less extreme in Choice Session 2 than Choice Session 1 for all pigeons. Moreover, the decrease in preference should be positively correlated with the decrease in disparity. The bottom left graph in Figure 3 shows the percentage choice for the stimulus associated with deprivation from each choice session for each pigeon. Consistent with predictions based on individual-subject relative immediacy, all pigeons chose the stimulus associated with deprivation less often in Choice Session 2 than in Choice Session 1.

To evaluate the prediction that larger decreases in time-to-food disparity were correlated with larger decreases in choice for the deprived stimulus, slopes from the top and bottom left-hand graphs in Figure 3 were compared for each pigeon. All slopes in both graphs were less than 1. Choice for the deprived stimulus decreased over time, with a mean slope of 0.71 (SD = 0.11). Disparity in choice also decreased from Baseline 1 to Baseline 2 with a mean slope of 0.85 (SD = 0.09). We predicted that larger decreases in disparity would produce larger decreases in preference, yielding a positive correlation between slopes. The graph on the right of Figure 3 shows preference slopes plotted as a function of relative immediacy slopes. Consistent with predictions, the slopes were significantly positively correlated, $r = 0.96$, $N = 4$, $p = 0.04$. Greater changes in relative immediacy were in fact correlated with greater changes in choice.

2.3. Discussion

Preference for the stimulus associated with food under relatively greater food deprivation was observed during Choice Session 1 and is consistent with previous research (Pompilio and Kacelnik, 2005; Pompilio et al., 2006; Vasconcelos and Urcuioli, 2008). The shift to indifference observed during Choice Session 2 is partially consistent with the simultaneous discrimination results and indifference for one of four pigeons that Vasconcelos and Urcuioli reported during a second choice session of their Experiment 1. In the present experiment, obtained time to food was shorter for deprived than pre-fed sessions during both baselines. Differences in obtained time to food were smaller in Baseline 2 for all pigeons, and the relative changes in choice and relative immediacy were positively correlated. This positive correlation suggests that SDVL may be driven by differences in obtained time to food. Although the absolute difference between obtained time to food was relatively small between deprived and pre-fed conditions, there is evidence that pigeons can discriminate such differences quickly (Rice et al., 2013).

Vasconcelos and Urcuioli (2008) hypothesized that the decrease in preference for one pigeon in their Experiment 1 was caused by the "promotion of indifference" (p. 14) in the first choice session. A similar shift to indifference was observed for all four pigeons in Experiment 1 here. Consistent with their hypothesis, preference for the deprived stimulus in Choice Session 1 was less extreme than has been reported in other experiments using the same procedure. Vasconcelos and Urcuioli also non-differentially reinforced 50% of choice probe trials, which may also account for the slightly different results. It seems unlikely, though, that one 20-trial choice session in which the red and green key-light stimuli were initially presented concurrently would undo the initial effect and two weeks of subsequent training. Either the effect is much less robust in pigeons than has been reported in other species, or variables other than relative food deprivation during baseline training are affecting preference during choice sessions.

The differences in obtained time to food from trial onset observed under different levels of food deprivation provide a potential mechanism for the state-dependent learning effect. In RIFI schedules, the latency to the first response in each trial increases the time until the fixed interval is initiated. The latency to respond after an interval has elapsed increases the time until food is collected. Both increase time to food. Differences in response rate or pattern produced systematic differences in time to food from trial onset under pre-fed and deprived states during Baseline 1 that were maintained, though smaller in magnitude, during Baseline 2. Thus, it is possible that pigeons preferred the deprived stimulus during Baseline 1 because it was the stimulus associated with more immediate reinforcement. Obtained time to food was more similar in deprived and pre-fed sessions of Baseline 2. Since different deprivation levels were necessarily presented in different sessions, it is possible that the smaller difference in obtained time to food in Baseline 2 was less discriminable, which would explain the shift to indifference observed in Choice Session 2.

The theory that SDVL is caused by obtained differences in relative immediacy can explain the results of Experiment 1, but several questions remain. Why does SDVL disappear with training for pigeons, but persist for other species? A comparative analysis is beyond the scope of this paper, but it is possible that the change in obtained time to food is preserved or disappears more slowly in other species. Pompilio and Kacelnik (2005) reported that starlings preferred the deprived stimulus even when the programmed RIFI was longer in deprived than pre-fed sessions—up to 1.75 times as long. However, they did not report obtained time to food or interfood intervals. Obtained mean interfood intervals in RIFI schedules ranging from very close to the programmed interval to more than double the programmed interval have been reported (Fox and Kyonka, 2013), so it is possible that increasing the programmed interval by a factor of 1.75 did not have as dramatic an effect on obtained time to food.

Experiment 1 was not designed to determine what produced longer first-response latencies in the pre-fed baselines. Traditionally, motivational variables such as food deprivation and reward magnitude were thought to affect response rate but not temporal discrimination (Roberts, 1981; Shull et al., 2001). However, experimental manipulations designed to increase motivation behaviorally or pharmacologically can produce changes in temporal discrimination and induce relatively early high-state responding in interval schedules (e.g., Galtress and Kirkpatrick, 2009; McClure et al., 2009; Balci et al., 2010a, 2010b; Ludvig et al., 2011).

3. EXPERIMENT 2

Experiment 2 was conducted to test the hypothesis that contrasting food deprivation states in the manner described in Experiment 1 initially produced differences in motivation that initially caused differences in obtained time to food in the two conditions. In Experiment 2, fixed interval (FI) schedules were used instead of RIFI schedules to ensure that first response latency did not increase obtained time to food during a trial. Peak trials were inserted during baseline sessions to obtain measures of temporal control.

During a peak procedure a portion of trials are “no-food” or “peak” trials: Instead of delivering food for the first peck after an FI has elapsed, the trial continues for at least twice as long as the typical interval and food is never delivered (e.g., under a FI 15-s schedule in procedure described below, no-food trials lasted 45 s). Measures of temporal discrimination, including start times and stop times (Cheng and Westwood, 1993; Church et al., 1994) can be derived from responding on individual no-food trials before and after the time of typical food delivery. If preference for the stimulus associated with food under relatively greater food deprivation occurs because motivation to respond is higher in that state, response rates should be higher overall and start times should be earlier in peak trials of deprived sessions compared to pre-fed sessions, even though obtained time to food is expected to be similar throughout training.

3.1. Method

3.1.1. Subjects

Four naïve White Carneau pigeons numbered 401-404. 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-hr light:dark cycle with continuous free access to water and grit.

3.1.2. Apparatus

As in Experiment 1, except that due to changes in WVU Laboratory Animal Resources dietary recommendations, the food delivered in pre-feeding, during sessions and in post-session feedings was Purina Nurtrigrain pigeon pellets instead of mixed grain.

3.1.3. Procedure

3.1.3.1 Pretraining

All pigeons were initially magazine trained and then trained to peck all three keys and colors using an autoshaping procedure. They were then trained on an FI schedule that was leaned from 1 s to 15 s over a 5 session period. During this training both red and green key colors were presented pseudorandomly (no more than twice in a row for any color on the same side), but 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 the 5-s variable-time (VT) ITI.

3.1.3.2 Baseline 1

As in Experiment 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.

Two types of trials were included during baseline training: food and no-food trials. At the start of a food trial the left or right key was lighted red or green. Keys were red in deprived baseline sessions and green in pre-fed baseline sessions for Pigeons 401 and 403; key color assignments were the opposite for Pigeons 402 and 404.The first peck at least 15 s after trial onset resulted in food. The next trial began after a VT 5-s ITI.

One out of every 5 trials was a no-food trial. The temporal location of the no-food trial was determined pseudorandomly within blocks of 5 trials. The beginning of a no-food trial was the same as a food trial, but no-food trials lasted 45 s instead of 15 s and did not result in food delivery. After a no-food trial, the key light was extinguished and the ITI and subsequent trial followed. The location of the peak trial within each 5-trial block was randomly determined, imposing the constraint that no more than 2 peak trials could occur consecutively. Sessions lasted for 25 trials or 60 minutes, whichever occurred first. To summarize, during baseline conditions a red and green key-color was associated with reinforcement under pre-fed and deprived conditions, respectively (counterbalanced), and during a session 20 trials ended in food delivery and 5 trials were no-food trials that lasted 45 s.

3.1.3.3 Choice 1

A 20-trial choice session immediately (the next day) followed the last baseline session. During choice sessions, pre-fed and deprived stimuli (red and green key colors) were presented simultaneously on the left and right response keys. Whether the pre-fed stimulus was on the left and the deprived was on the right, or vice versa, was determined pseudorandomly on each trial. The first key peck to either key extinguished the alternate key. The first peck to the selected key at least 15 s after trial onset resulted in reinforcement. If the first peck to either key was after 15 s had elapsed, it resulted in both keys extinguishing and reinforcement. During choice sessions all trials ended in food delivery. During the first choice session Pigeons 402 and 404 were pre-fed and Pigeons 401 and 403 were deprived.

3.1.3.4 Baseline 2

After the first choice session, all pigeons were exposed to a second baseline condition. Conditions were the same as in Baseline 1.

3.1.3.5 Choice 2

A second 20-trial choice session immediately (the next day) followed the last session in Baseline 2. Conditions were the same as in Choice 1, except Pigeons 402 and 404 were deprived and Pigeons 401 and 403 were pre-fed (opposite of the first choice session).

3.2. Results

In Experiment 2, FI schedules were used in order to reduce the differential effects of first-response latency on obtained time to food observed in Experiment 1. Longer first-response latencies in the pre-fed conditions in Experiment 1 produced statistically significantly longer delays to food than in deprived conditions. Figure 4 shows the mean time to food from trial onset during Baselines 1 and 2 in Experiment 2, excluding no-food trials. Time to food was entered into a repeated-measures ANOVA with deprivation level and baseline as factors. There were no statistically significant effects (all Ps > .06). Time to food was statistically equivalent in the two food-deprivation states and did not change across baseline conditions. If relative immediacy during baseline controlled choice, there should be no preference for either stimulus in either choice session because time to food was not significantly different across baselines or levels of deprivation.

No-food trials were included to measure temporal control of behavior. Responding on individual no-food trials typically conforms to a low-high-low pattern (Church et al., 1994). On any given no-food trial, responding usually starts at a low rate, increases to a high rate at some inflection point or "start time," continues in this high state until after the time of typical food delivery and then decreases to a low rate at a second inflection point or "stop time." The midpoint of the start time and stop time is referred to as the "middle time" and is considered an alternative measure to the time of peak response rate observed in response rate gradients (Church et al., 1994). To calculate start, stop and middle times an index (*A)* was maximized using the following equation for responding in each no-food trial for all pigeons:

$$A = d_{L1}(r - r_{L1}) + d_H(r_H - r) + d_{L2}(r - r_{L2}), \qquad (1)$$

where r was the mean response rate across the entire trial, r_{L1}, r_H and r_{L2} were the response rates during the first low, the high and the second low periods, respectively, and d_{L1}, d_H and d_{L2} were the respective durations of those states. The time of the transition from the first low state to the high state was considered the start time and the time of the transition from the high state to the second low state was considered the stop time. Trials in which the start time was after 15 s (the time of typical food delivery) or the stop time was before 15 s, or trials for which the stop time was determined to be the last response recorded on the trial and that response occurred during the final second of the trial (i.e. no clear stop was determined), were excluded.

Figure 5 shows mean durations of high states for each pigeon in each condition. High states began and ended at the individual-subject mean start time and mean stop time calculated from all no-food trials of all deprived or pre-fed sessions from a baseline. Start, middle and stop times were entered into separate repeated-measures ANOVA with deprivation level and baseline as factors. Although there were no differences in first-response latencies, mean start times were statistically significantly lower in deprived conditions, $F(1,3) = 76.45$, $p = 0.003$, $\eta_p^2 = .96$. Consistent with response latencies obtained in Experiment 1, high-state responding started earlier in deprived than pre-fed sessions. There were no other statistically significant effects (all other Fs < 2.62, all Ps > .20). During Baseline 1, the group mean middle time from deprived sessions ($X + SE$ = 19.49 + 0.80 s) was later than the middle time from pre-fed sessions ($X + SE$ = 18.32 +0.88 s). During Baseline 2, group mean middle times were nearly equivalent in deprived ($X + SE$ = 19.92 + 1.62 s) and pre-fed ($X + SE$ = 19.73 + 1.49 s) sessions. Although responding started earlier in the deprived sessions, temporal control of behavior measured using middle and stop times was equivalent in deprived and pre-fed sessions of both baselines.

Figure 6 shows choice for the deprived state stimulus for each pigeon in Choice Session 1 and Choice Session 2 in Experiment 2. The mean percent preference across pigeons for the deprived stimulus was 45% and 42.5 % for Choice Sessions 1 and 2, respectively. A paired-samples t test revealed that preference for the deprived stimulus was not significantly different in Choice Session 1 from preference in Choice Session 2, $t(3) = -0.92$, $p = 0.88$. Separate single-sample t tests compared percent choice in Choice Sessions 1 and 2 to a null hypothesis of indifference (50% choice for each stimulus). Deprived-stimulus choice was not significantly different from indifference in Choice Session 1 $t(3) = 0.59$, $P = 0.59$ or Choice Session 2, $t(3) = 1.0$, $p = 0.39$. Consistent with predictions based on obtained time to food and temporal control of behavior, there was no difference in choice in either choice session.

Although there were no differences in obtained time to food at different baselines or levels of deprivation, if obtained relative immediacy was a factor in the mechanism responsible for the state-dependent learning effect, changes in disparity from Baseline 1 to Baseline 2 should be positively correlated with changes in choice for the deprived stimulus from Choice Session 1 to Choice Session 2. To assess this possibility, slopes reflecting rates of change in choice and immediacy were calculated as in Experiment 1. The top left panel of Figure 7 shows relative immediacy for each baseline. The bottom left panel of Figure 7 shows choice for the deprived stimulus from each choice session. Across pigeons, mean slopes for choice and immediacy were respectively 1.18 ($SD = 0.88$) and 0.89 ($SD = 0.20$). For both measures, disparity increased for some pigeons and decreased for others from Baseline 1 to Baseline 2, but neither increased or decreased consistently across pigeons. The graph on the right of Figure 7 shows preference slopes plotted as a function of relative immediacy slopes. Slopes were positively correlated, but the correlation was not significantly different from 0, $r = 0.57$, $N = 4$, $p = 0.43$.

3.3. Discussion

Experiment 2 did not replicate previous research reporting the state-dependent learning effect: when simultaneously presented with stimuli associated with relative food deprivation and with pre-feeding, pigeons chose both stimuli about equally often. Neither obtained time to food nor temporal control of behavior (based on middle and stop times) were affected by relative food deprivation state in baselines. However, because obtained time to food during deprived and pre-fed baseline conditions were not statistically different, the indifference observed in choice sessions neither supports nor disconfirms the theory that obtained relative immediacy determines response allocation during choice probes in SDVL experiments.

Comparing changes in obtained relative immediacy with changes in choice session response allocation permitted an additional test of the relative immediacy hypothesis. Even though no changes were statistically significant at the group level, greater changes in obtained relative immediacy for individual subjects were positively correlated with changes in choice. Although ordinally consistent with the results of Experiment 1, changes in obtained relative immediacy were not significant predictors of changes in choice, perhaps owing to a range restriction effect caused by the stricter temporal control in the FI (compared to the RIFI) procedure.

Start times were earlier in deprived sessions, but there was no difference in temporal control under deprived and pre-fed conditions in Experiment 2. Results of some interval timing experiments have demonstrated that motivation-related variables can affect timing (Galtress and Kirkpatrick, 2009; McClure et al., 2009; Balci et al., 2010a, 2010b), the present data support previous findings that suggest relative food deprivation state may not affect temporal control of behavior (e.g., Galtress et al., 2012). The results are also consistent with research finding that manipulating variables related to motivation can disrupt performance on tasks used to measure temporal control of behavior, but produce no consistent effect on timing behavior (e.g., Ward and Odum, 2006), and research finding that manipulating food deprivation shortens start times, but does not affect overall temporal control of behavior (e.g., Ludvig et al., 2011).

It should be noted though that the present results are based on relatively limited exposure to experimental contingencies compared to other timing research. The duration of exposure to experimental conditions was limited to replicate previous research investigating the state-dependent learning phenomenon and to test for preference between the stimuli associated with each food deprivation condition. It is possible that differences in temporal control between the two food-deprivation conditions presently would appear with more exposure to the contingencies.

4. GENERAL DISCUSSION

Taken together, the results of Experiments 1 and 2 are generally consistent with previous research and support the hypothesis that obtained relative immediacy affects choice in this SDVL paradigm. Shorter latencies to first responses in deprived sessions of Experiment 1 are consistent with earlier start times in deprived sessions of Experiment 2. In the first baselines of both experiments, pigeons started to respond earlier in trials during deprived sessions than during pre-fed sessions. Consistent with predictions of the relative immediacy hypothesis, choice was positively correlated with obtained relative immediacies in both experiments.

In Experiment 1 there was a significant positive correlation between changes in obtained relative immediacy and changes in choice. In Experiment 2 the correlation was ordinally consistent but non-significant. A positive correlation between obtained changes in relative immediacy and obtained changes in choice is necessary to support the theory that obtained differences in relative immediacy determine choice for the stimulus associated with deprivation in state-dependent learning experiments. The functional relation between relative immediacy and choice is well-established in concurrent-chain schedules of reinforcement (e.g., Fantino, 1969), even when the differences in delays to food was relatively small and changed frequently

(Kyonka and Grace, 2010). However, the results of Experiments 1 and 2 do not conclusively show that relative immediacy does indeed control choice in this procedure. To parse the separate and combined effects of differences in relative immediacy and energy state would require parametric manipulation of both factors. Parametric manipulations may not be feasible with pigeons, because SDVL seems to occur only transiently. It may not be possible to capture the trajectory of SDVL effects in a procedure that requires many days between choice probes.

The most parsimonious explanation for why relative immediacy during baseline training predicts choice in state-dependent learning experiments may be that organisms prefer the richer of two options when presented with a choice between them (Herrnstein, 1961). If the training parameters are such that under deprived conditions food is coming more often, be it because of the behavior of the organism or programmed contingencies, then a stimulus associated with that richer rate of food delivery will be preferred over a stimulus associated with a leaner rate of food delivery. Experiments 1 and 2 provide evidence that obtained relative immediacy does predict and may functionally determine choice in SDVL experiments.

The results of Experiment 1 are also consistent with the Sequential Choice Model (SCM) (Shapiro et al., 2008; Kacelnik et al., 2011). SCM predicts that the subjective value of any single option is best determined by the latency to respond to that option when it is presented alone. Consistent with SCM, in Experiment 1 when the latency to respond was shorter in the presence of the stimulus associated with food deprivation, preference for that option was observed in choice probe 1; when the disparity in latencies to respond was reduced in the presence of the two discriminative stimuli, no preference was observed in choice probe 2. The results of Experiment 2, however, initially appear partially inconsistent with SCM. Pigeons started pecking sooner in deprived than prefed conditions. Hence, SCM predicts the deprived stimulus has greater value and a preference should exist for it over the prefed stimulus. This was not the case in Experiment 2 choice probes. In previous research evaluating SCM, latencies to respond directly influenced overall time to food. Longer latencies to respond meant longer overall delays to food. The notion that longer overall delays to food affect the value of a discriminative stimulus, is consistent with results from both Experiments 1 and 2. As suggested above, this overall delay to food may be the most relevant variable in determining the value of a discriminative stimulus, not just latency to respond to it. However, when latency to respond influences overall delays to food, SCM predicts it should be a highly predictive variable determining value and choice (Kacelnik et al., 2011; Shapiro et al., 2008).

In general, preference for stimuli associated with food during or following relatively aversive circumstances seem to rely on specific experimental parameters during training. For example, the "work-ethic" effect (Clement et al., 2000; Kacelnik and Marsh, 2002)— a preference for discriminative stimuli associated with food on a "high-effort" task (e.g., multiple key pecks required to obtain food) over discriminative stimuli associated with food on a "low-effort" task (e.g., a single key peck is required to obtain food)—has proven difficult to replicate (Arantes and Grace, 2008; Aw et al., 2011; Vasconcelos et al., 2007; but see Zentall and Singer, 2007). Also, SDVL, which has been the focus of the present research, has been replicated in multiple species, but only under very specific training conditions with pigeons. Both our FI peak-trial training procedure and Vasconcelos and Urcuioli's (2008) simultaneous discrimination training yielded indifference during choice sessions (see review, Meindl, 2012). The effect may be less robust in pigeons than in other avian (starlings; Pompilio and Kacelnik, 2005) and non-avian (grasshoppers; Pompilio et al., 2006) species, but that notion is based on limited data. Together, these findings raise interesting questions about what mechanism controls the reported preference for stimuli associated with food under conditions of relatively greater aversiveness. It appears that these phenomenon are inextricably linked with the training parameters that produce them—an indication that it may not be solely the contrasting states of relative food deprivation or relative work required to obtain reinforcement, but, at least in part, some other aspect of the experimental design and training procedure (see also, Aw et al., 2011).

The present results suggest that obtained relative immediacy during training sessions may be an important contributing factor and should be experimentally controlled in SDVL experiments. Obtained relative immediacy can differ widely in RIFI schedules depending on the subject's latency to respond at the beginning of a trial and response rate at the end of the interval (Fox and Kyonka, 2013); therefore, reponse-independent (i.e., fixed time) schedules may be useful for investigating SDVL. At the very least, obtained relative immediacies should be reported and taken into consideration in explanations of SDVL results.

The theory that choice in SDVL experiments is controlled by obtained relative immediacy does not oppose the fitness gain hypothesis (Pompilio et al., 2006). If the utility of food determines the point in a trial when a subject begins to respond at a high rate, greater fitness gains would result in shorter time to food in RIFI schedules. Greater fitness gained would, ultimately, result in a preference for the deprived stimulus, but energy state would function to alter patterns of responding in baselines, rather than determining choice directly. Hence, the fitness gained and relative-immediacy hypotheses are compatible and complementary. Relative immediacy provides a potential explanation for the mechanism that underlies the fitness gained hypothesis.

In conclusion, results from Experiments 1 and 2 support Vasconcelos and Urcuioli's (2008) conclusion that while SDVL is replicable in pigeons, it may be constrained to specific training parameters. Based on the present results, these training parameters may produce relatively shorter delays to food under deprived than pre-fed conditions. Although more research is needed to disentangle effects of energy states from relative immediacy, obtained relative immediacy under differential deprivation conditions may be an important contributing factor to the SDVL phenomenon.

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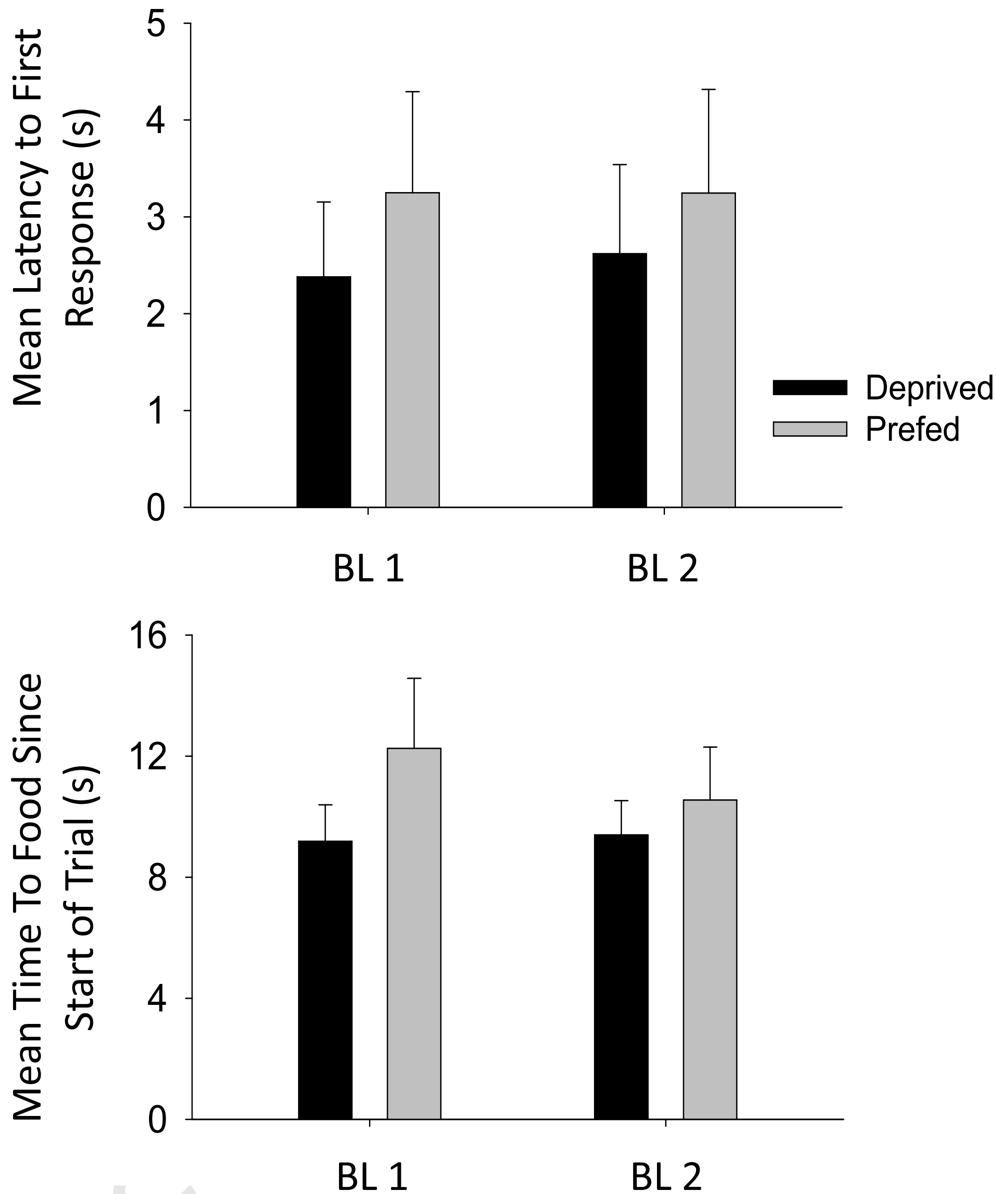

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2 *Figure 1.* Mean latency to the first response and mean time to food from start of trial in deprived

3 and pre-fed states during Baseline (BL) 1 and Baseline 2 in Experiment 1.

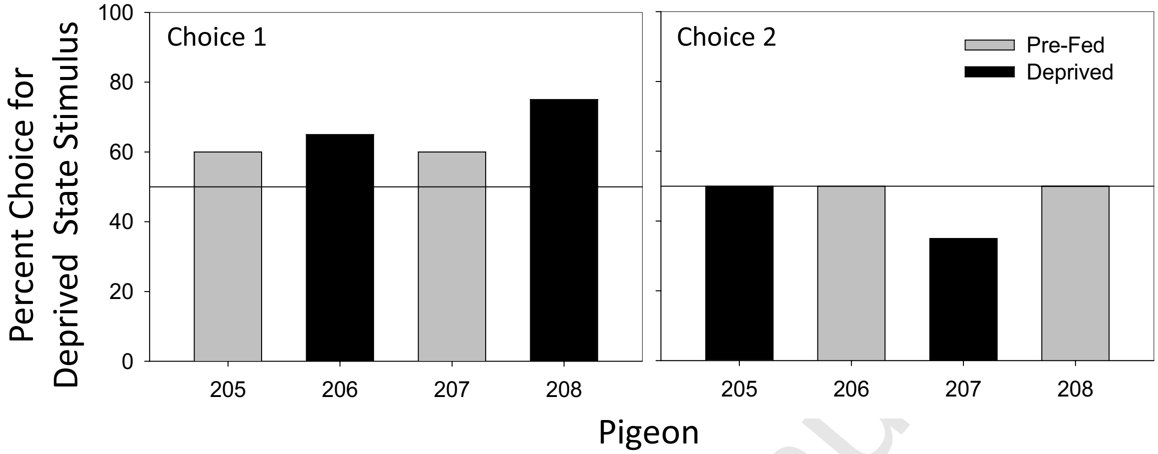

Figure 2. Percent choice for the stimulus associated with food under relatively greater food deprivation for all pigeons in Experiment 1 for Choice 1 (left) and Choice 2 (right). Black and gray bars represent choice under deprived and pre-fed conditions, respectively. Horizontal lines indicate indifference.

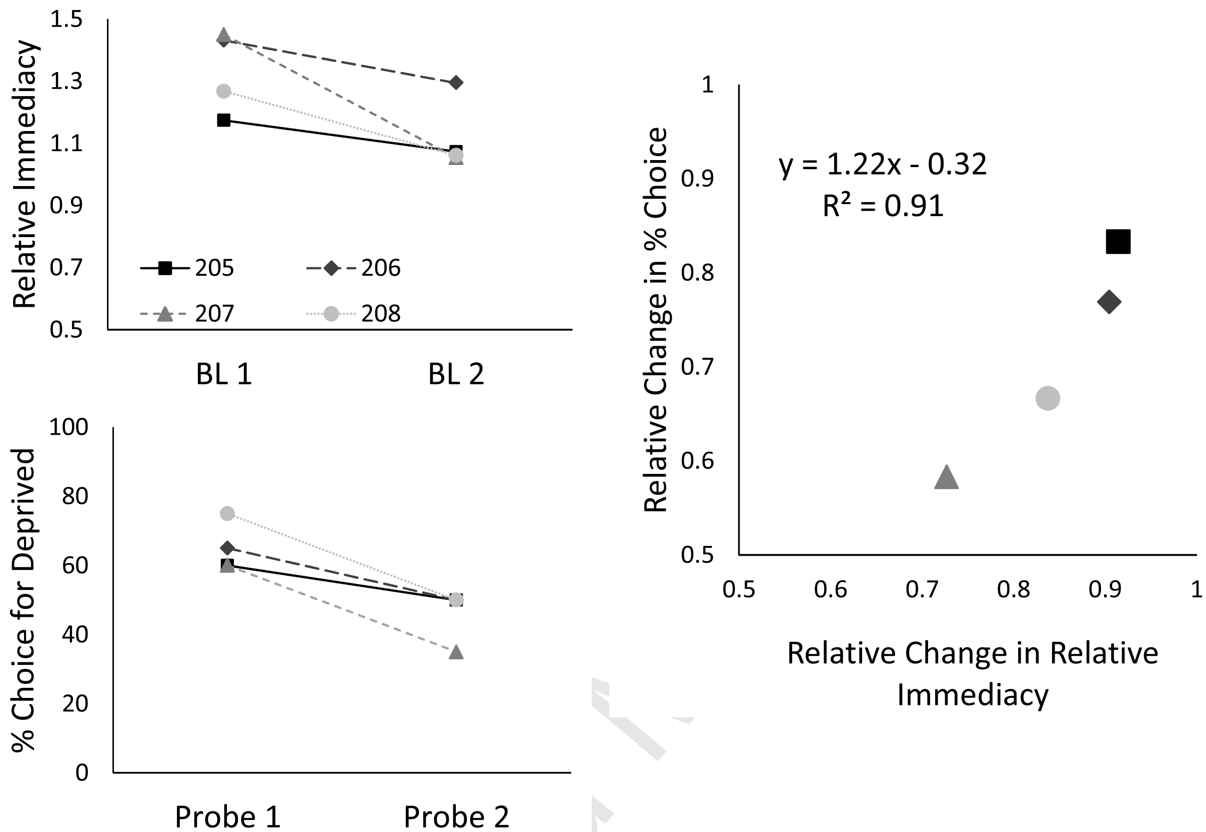

Figure 3. Relative change in choice for the deprived stimulus was correlated with relative change in relative immediacy. The top left graph shows relative immediacy (deprived sessions/pre-fed sessions) from each baseline (BL) for each pigeon. The bottom left graph shows choice for the stimulus associated with deprivation from each choice session (Probe) for each pigeon. The graph on the right shows the ratio of deprived stimulus choice in Choice Session 2: deprived stimulus choice in Choice Session 1 as a function of the immediacy ratio from Baseline 2: immediacy ratio from Baseline 1 (i.e., the slopes of the lines in the top left graph are on the x-axis and the slopes of the lines in the bottom left graph are on the y-axis). The equation for the line of best fit and proportion of variance accounted for (R^2) are shown. The same symbols

represent the different individual Pigeons (205-208) in all three graphs.

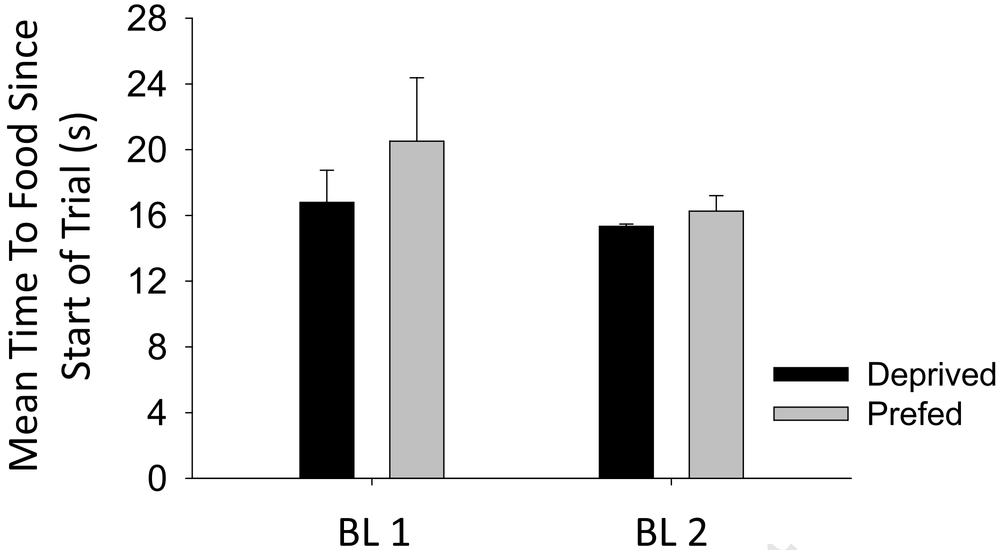

Figure 4. Mean time to food from start of trial in deprived and pre-fed states during Baseline (BL) 1 and BL 2 in Experiment 2.

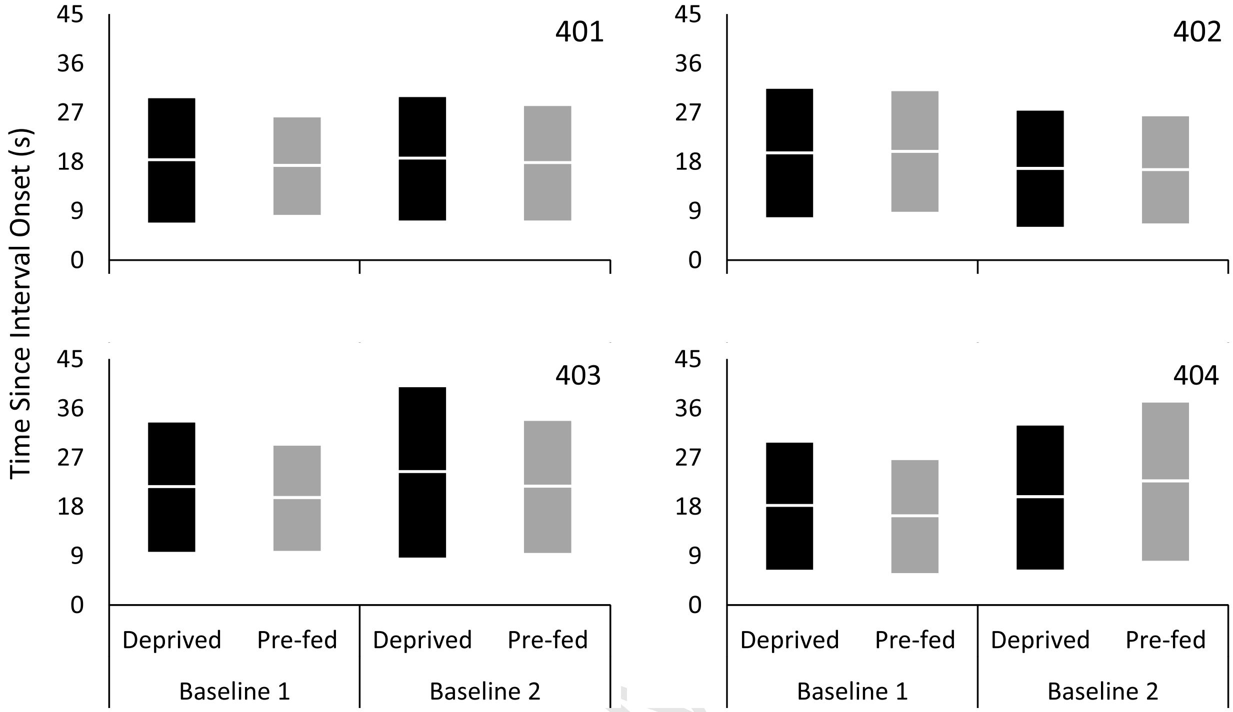

Figure 5. Times of high-rate responding on no-food trials in Experiment 2 during Baseline 1 and Baseline 2. The bottom, the white line bisecting the center, and the top of each bar represent the mean start time, middle time, and stop time, respectively. Each graph shows high-state durations for an individual pigeon identified by number in the upper right corner.

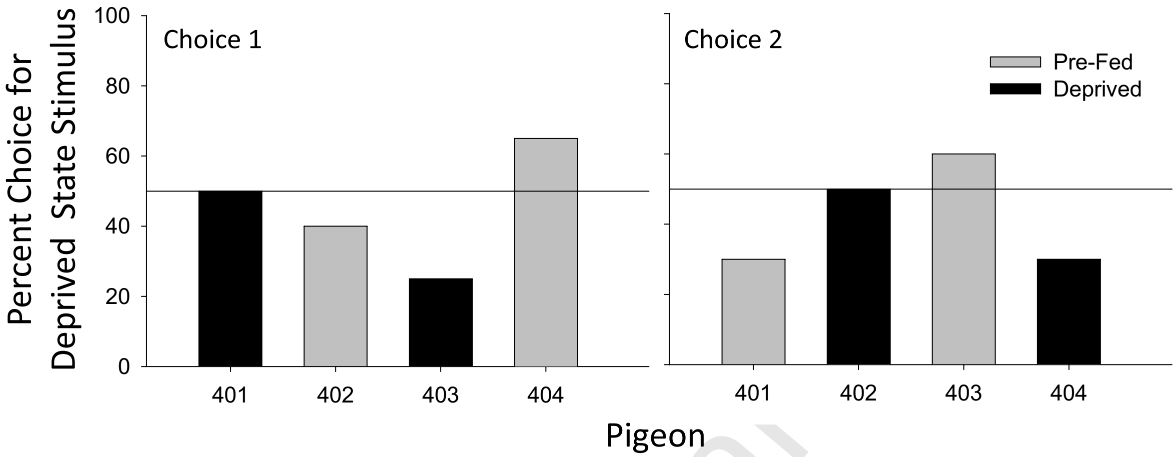

Figure 6. Percent choice for the stimulus associated with food under relatively greater food deprivation for all pigeons in Experiment 2 for Choice 1 (left) and Choice 2 (right). Black and gray bars represent choice under deprived and pre-fed conditions, respectively. Horizontal lines indicate indifference.

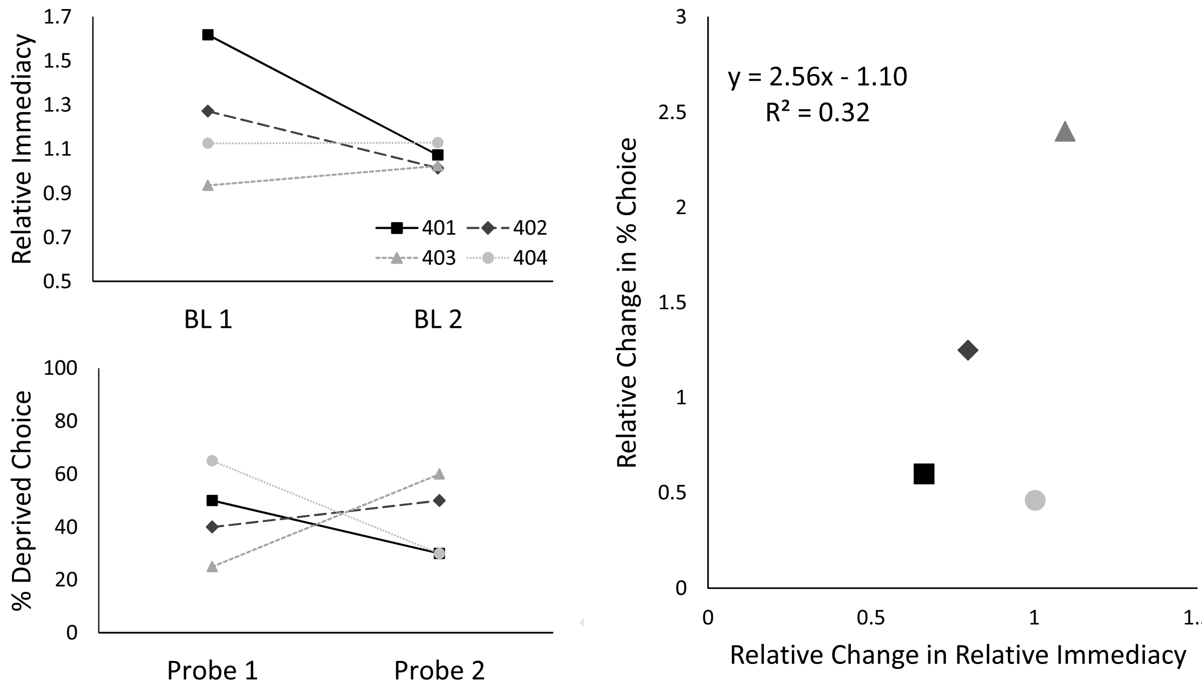

Figure 7. For individual pigeons, relative change in choice for the deprived stimulus was not significantly correlated with relative change in relative immediacy. The top left graph shows obtained relative immediacy (deprived sessions/pre-fed sessions) from each baseline (BL) for each pigeon. The bottom left graph shows choice for the stimulus associated with deprivation from each choice session (Probe) for each pigeon. The graph on the right shows the ratio of deprived stimulus choice in Choice Session 2: deprived stimulus choice in Choice Session 1 as a function of the immediacy ratio from Baseline 2: immediacy ratio from Baseline 1. The equation for the lines of best fit and proportion of variance accounted for (R^2) are shown. The same symbols represent the different individual Pigeons (401-404) in all graphs.