



## Short report

## Reward magnitude and timing in pigeons

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## ABSTRACT

We investigated the interaction of motivation and timing by manipulating the expected reward magnitude during a peak procedure. Four pigeons were tested with three different reward magnitudes, operationalized as duration of food access. Each stimulus predicted a different reward magnitude on a 5 s fixed-interval schedule. Trials with different reward magnitudes were randomly intermingled in a session. Most pigeons responded less often and started responding later on peak trials when a smaller reward was expected, but showed no differences in response termination or peak times. Reward magnitude was independently corroborated through unreinforced choice trials, when pigeons chose between the three stimuli presented simultaneously. These results contribute to a growing body of evidence that the expected reward magnitude influences the decision to start anticipatory responding in tasks where the reward becomes available after a fixed interval, but does not alter peak times, nor the decision to stop responding on peak trials.

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Early theories of timing supposed that motivational factors, such as reward magnitude or satiety, should have no influence on timing (e.g., Gibbon, 1977). Initial data supported this position (Roberts, 1981; Hatten and Shull, 1983), but more recent results have revealed that motivational manipulations do alter responding on timing procedures (e.g., Balci et al., 2010a,b; Galtres and Kirkpatrick, 2009, 2010; Ludvig et al., 2007; McClure et al., 2009). For example, decreased reward magnitude (Galtres and Kirkpatrick, 2009; Grace and Nevin, 2000; Ludvig et al., 2007), pre-feeding (Plowright et al., 2000), and increasing satiety during a session (Balci et al., 2010b) all increase the time to initiate responding in the peak procedure, while having more muted effects on the remainder of the response curve. The studies with reward magnitude have mostly involved changing reward magnitude for an extended period, across multiple sessions (e.g., Galtres and Kirkpatrick, 2009; Ludvig et al., 2007), thereby producing differences in the overall reward rates across conditions. Here, we evaluate dynamic changes in timed responding on the peak procedure by intermingling three different reward magnitudes in a session.

The peak procedure is the most prominent method for evaluating timing in animals (Roberts, 1981). There are two types of

trials in a peak procedure. On rewarded trials, pigeons are reinforced for the first response emitted after a fixed amount of time has elapsed since stimulus onset. On peak trials, no reward is available and the stimulus remains present considerably longer than on rewarded trials. Typically, average response rates on peak trials increase until around the time the reward is usually available and decrease afterward. Individual peak trials can be approximated as a three-state process, where an initial pause is followed by a burst of responding, followed by another pause (Church et al., 1994; Gallistel et al., 2004a). This molecular approach allows for independent estimates of the time to start and stop responding on individual trials.

In this paper, we extended the recent results on the interaction of motivation and timing by using three reward magnitudes within a session of the peak procedure in pigeons. Stimuli were different colours for the three different reward magnitudes. This design allowed us to change the local expectation of reward without altering the overall reward rate. As a result, there should not be any overall changes in attention or arousal that could differentially affect the levels of expected reward magnitude. In addition, we incorporated choice trials that allowed for independent corroboration that the reward magnitudes led to different preferences. Finally, we explored performance on a shorter (5 s) fixed interval than earlier studies. Based on previous results (e.g., Ludvig et al., 2007; Galtres and Kirkpatrick, 2009), we hypothesized that smaller reward magnitudes would lead to later start times on peak trials, with limited changes later in the trial.

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## 1. Methods

### 1.1. Subjects

Four adult pigeons (*Columba livia*), two Silver Kings and two Racers, were obtained from local suppliers (numbered P5, P18, P35, and P299). Pigeons were housed in standard cages and given unlimited access to water and grit. The light cycle was 12:12, and all testing occurred during the light portion of the cycle. Pigeons were maintained at 85–90% of ad libitum body weight by post-session feeding in their home cage. Sessions were run 6 days a week. All pigeons had prior experience with operant conditioning tasks, but not with the stimuli used, nor with similar timing procedures.

### 1.2. Apparatus

Testing occurred in custom-made operant chambers. The chambers were 44 cm high, 32 cm deep, and 74 cm wide (inside dimensions). At the front, there was a Carroll Touch infrared touch fame (Elo Touch Systems, Inc., Menlo Park, CA) to record pecks, which was mounted in front of a 15 in. LCD monitor that displayed all stimuli. On either side of the touchscreen/monitor, there were solenoid-type bird feeders that, when raised, provided access to pigeon feed, which was delivered randomly through one of the feeders on a trial. Photocells in the feeder trough detected the presence of the pigeon's head and allowed precise control of the duration of feeder access. Stimuli were presented and data recorded by computers running in adjoining room. A fan provided masking noise and adequate ventilation.

### 1.3. Procedure

**Phase 1: Pre-training.** Pigeons were initially autoshaped to peck at the three different colour stimuli (red, green, and yellow) and two additional stimuli (black-and-white dotted and striped patterns) by rewarding the first response on that stimulus, or, in the absence of responding, after 60 s. On each trial, only one stimulus was present, and there were up to 60 trials per session. All stimuli were 3.8 cm × 3.8 cm squares (113 × 113 pixels), and the stimulus appeared in the center of the screen. The red stimulus was rewarded with .5 s of grain access, yellow with 1.5 s, and green with 4.5 s of access, except for pigeon P5, who had these reward durations reduced by 40%, following session 22 of pre-training, because it repeatedly failed to eat in the latter half of sessions.

Once the pigeons responded reliably to all the stimuli, they were exposed to an FI 5 s schedule with each of the 3 colour stimuli. On this schedule, the first peck on the stimulus after 5 s was followed by a reward of the appropriate duration (i.e., magnitude). Occasional (20%) FI trials were followed immediately by a “choice” probe before the reward, during which the two different (non-colour) stimuli appeared on the sides of the initial stimulus, and the reward duration was determined by that choice. For the final 12 sessions of this phase, these choice trials were eliminated, and unreinforced equidistant choice trials were interspersed among the FI trials instead. On these equidistant probes, all 3 colour stimuli were simultaneously presented in locations surrounding the usual stimulus location. Location was counterbalanced across choice trials. The first peck to any of the 3 stimuli was recorded as the choice, the stimuli disappeared, and no reinforcement was given. This pre-training phase lasted from 67 to 70 sessions.

**Phase 2: Peak testing.** Pigeons received 35–45 sessions of peak testing, and only data from the final 10 sessions for each pigeon were analyzed to ensure that stable responding had been reached. Sessions of peak testing consisted of 60 trials. The first 6 trials always consisted of 2 FI trials with each of the 3 stimuli. The remaining 54 trials consisted of an additional 8 FI and 6 peak trials with

each of the 3 stimuli, and 12 of the equidistant, unreinforced choice probes, all randomly intermixed. Peak trials were not reinforced and lasted from 20 to 40 s (uniformly distributed). Inter-trial intervals of 30 to 50 s, uniformly distributed, separated all trials. Pigeon P299 became ill in its final (36th) test session—data from this test session have been discarded. Data from the penultimate session for pigeon P18 were lost due to a hardware failure and are not included in the analysis.

**Data analysis.** To estimate start and stop times on individual trials, we used a relative-likelihood change-point algorithm that finds statistically reliable changes in response rates (for details, see Gallistel et al., 2004a; Balci et al., 2009). In short, the approach assumes that inter-response times (IRTs) are exponentially distributed. The algorithm works by examining each successive IRT on a trial and, for each data point, computing the relative likelihood that all IRTs up to and including that data point come from the same distribution or from two different distributions. A user-specified decision criterion (the Bayes factor) determines the sensitivity of the change-point algorithm for finding transitions; we used a Bayes factor of 10, which adequately characterized the current dataset. Stricter criteria did not qualitatively change our results. Start times were defined as the first positive change point in a trial, and stop times were defined as the first negative change point.

Pair-wise comparisons of start, stop, peak (midpoint of start and stop), and wait times (time to first response) across different reward magnitude conditions were conducted for individual pigeons using a Mann–Whitney *U*-test. We followed up these analyses with single-subject permutation tests with 10,000 iterations per test, using the difference between the medians. Choice proportions were compared by chi-squared tests for each subject, followed by pairwise comparisons using one-tailed binomial tests. The Holm–Bonferroni method (with alpha of .05) was used to correct for multiple comparisons.

## 2. Results

Fig. 1 shows the average normalized response rates on peak trials. For all 4 pigeons, responding increased earlier in the trial for the largest reward magnitude. These differences were not as consistent later in the trial, where responding tailed off for the larger reward magnitude more quickly (P18), more slowly (P5, P35), or at around the same rate (P299), depending on the pigeon. There was some tendency towards a bimodal response distribution with a sharp early peak, followed by a lower, later peak (most notable for P18 and P35).

To quantify these observations, we extracted start and stop times for each trial from the single-trial analyses. Fig. 2A–C depict the start, stop, and wait times for the different reward magnitude for each pigeon. For three subjects (P5, P18, P299), start and wait times were significantly delayed during the low-reward stimulus as compared to both the medium-reward and high-reward stimuli (all  $ps < .02$ ). For the fourth pigeon, the lower magnitude did not reliably affect start or wait times (though the pattern in Fig. 1 resembles the other pigeons), but did produce earlier stop times than the two larger magnitudes (both  $ps < .03$ ). For all pigeons, there were no reliable differences in peak times (not shown) nor between the two larger reward magnitudes on any of the measures (all  $ps > .05$ ).

The choice proportions further suggest that pigeons were indeed sensitive to the reward magnitudes as predicted by the different stimuli. Fig. 2D depicts how all four pigeons chose the stimulus that cued the largest reward magnitude more frequently than the stimulus that cued the smallest reward magnitude (all  $ps < .05$ ). There was not, however, a graded preference curve as the medium reward magnitude was always chosen in equal proportion with either the higher (3 pigeons) or lower (pigeon P18) reward magnitude.

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