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Pigeons' memory for empty and filled time intervals signaled by light

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Abstract

In Experiment 1, pigeons were trained in a within-subjects design to discriminate durations of a filled interval (2 and 8 s of light), and durations of an empty interval (2 and 8 s bound by two 500-ms light markers). Filled intervals required a response to one set of comparisons (e.g., blue vs yellow), whereas empty intervals required a response to a different set of comparisons (e.g., red vs green). Delay testing and sample stimulus omission both resulted in a choose-short bias on filled interval trials, and a choose-long bias on empty interval trials. In Experiment 2, the results of mixed-choice probe tests ruled out an explanation of these response biases in terms of asymmetrical coding and default responding. In Experiment 3, the results of varying the duration of the second marker on empty interval trials ruled out a reliance on timing and summing the duration of the markers themselves. In Experiment 4, the sample durations were changed to 0.5 and 2 s in order to minimize the possibility that the birds were counting the markers, but a choose-long effect on empty interval trials was still evident. The signal detection model of memory biases described by Gaitan and Wixted (2000) was considered to have some strength in providing a parsimonious explanation for the current within-subject findings.

1. Introduction

Studies of memory for event duration in pigeons typically employ a symbolic matching-to-sample task in which the pigeon is required to peck one comparison

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stimulus (e.g., red) on trials initiated by a 2-s sample stimulus and to peck a different comparison stimulus (e.g., green) on trials initiated by an 8-s sample stimulus. Once the task has been acquired, the delay interval between the end of the sample stimulus and the presentation of the comparison stimuli is manipulated. The typical finding is that at delays longer than baseline training, pigeons respond with high accuracy on trials initiated by the short sample, while accuracy of responding on trials initiated by the long sample drops to well below 50% correct (Fetterman, 1995; Gaitan & Wixted, 2000; Grant, 1993; Grant & Kelly, 1996, 1998; Grant & Spetch, 1991, 1993, 1994; Kelly & Spetch, 2000; Kraemer, Mazmanian, & Roberts, 1985; Santi, Bridson, & Ducharme, 1993; Santi, Ducharme, & Bridson, 1992; Sherburne, Zentall, & Kaiser, 1998; Spetch, 1987; Spetch & Rusak, 1989, 1992; Spetch & Wilkie, 1983). This result has been called the choose-short effect, because pigeons show a bias to peck the comparison stimulus correct for the short duration sample as the delay interval is extended beyond that used in training. The choose-short effect has played an important role in contributing to an understanding of memory coding in animals (see Grant, Spetch, & Kelly, 1997, for a review).

Recent findings indicate that the choose-short effect does not occur when memory for empty time intervals is studied in pigeons. Santi, Ross, Coppa, and Coyle (1999) trained pigeons with a 0-s delayed symbolic matching-to-sample task to discriminate the duration (2 or 8 s) of an empty interval separated by two 500-ms tone markers, or two 500-ms light markers. Both types of markers were presented randomly within the same session. Delay testing resulted in a small choose-short effect at the 1-s delay, but a large choose-long effect at both the 3- and 9-s delay regardless of whether the trials were initiated by the tone markers or the light markers. Santi et al. (1999) suggested several possible explanations for the pattern of response biases observed during delay testing with empty intervals. A number of these explanations could account for the occurrence of a choose-long effect, but they could not account for the choose-short effect at the 1-s delay. In order to explain both the choose-short effect at 1-s delay and the choose-long effect at the 3- and 9-s delays, Santi et al. (1999) suggested that the pigeons were timing from the presentation of the first marker to the presentation of the comparison stimuli on some proportion of the trials, but on the remaining trials they timed from the second marker to the onset of the comparisons. Thus, the choose-short bias at the 1-s delay was viewed as the result of the pigeon's response being based on the time since the second marker on some proportion of the trials. On these trials, a timed duration of 1 s from the second marker to the onset of comparison stimuli would be more similar to that established for the short empty interval than the long empty interval during training. A simple quantitative model was tested in which the data from marker omission testing in one experiment was used to predict the delay test data reported in other experiments. The model fit the tone marker data well but did not provide as good a fit for the light marker data.

In the study by Santi et al. (1999), the same physical event served as the first and the second marker. This may have contributed to a tendency to initiate the timing of a new interval upon presentation of the second marker. Recently, Grant

(2001) examined memory for empty time intervals in pigeons with a procedure that reduced or eliminated the tendency for the second marker to initiate timing of a new interval. This was accomplished by using different colored keylights as the first and second markers on each trial. In one group, the first (start) marker was always a red keylight and the second (stop) marker was always a green keylight. In another group, although different colored keylights were presented as the first and second markers, the markers could be either red or green. Following training with variable delays, Grant (2001) obtained a choose-long effect at extended delays in both groups. Thus, the choose-long effect which occurs when memory for empty intervals is tested at extended delays occurs even when the first and second markers are predictably different. It should be noted that the timing of a new interval following the second marker was not required to explain the choose-long effect at extended delays in Santi et al. (1999), it was only needed to account for the choose-short effect which occurred at the 1-s delay. The choose-long effect at extended delays could have occurred if the birds had simply timed from the first marker to the onset of the comparison stimuli. Grant (2001) attempted to minimize this possibility by training with variable delays that ranged from 1 to 3 s.

The results of Santi et al. (1999) and Grant (2001) differ from those typically obtained when memory for filled intervals is tested. This suggests that pigeons process filled and empty intervals differently. The present experiments were designed to further investigate the differences in memory performance produced by filled interval and empty interval procedures.

2. Experiment 1

Additional evidence that pigeons process filled and empty intervals differently would be obtained if it could be demonstrated that the different memory biases continue to be observed even when pigeons are trained to time both types of intervals within the same experimental session. In Experiment 1, pigeons were trained in a within-subjects design to discriminate durations of a filled interval (2 and 8 s of light), and durations of an empty interval (2- and 8-s bound by two 500-ms light markers). Filled intervals required a response to one set of comparisons (e.g., blue vs yellow), whereas empty intervals required a response to a different set of comparisons (e.g., red vs green). In this within-subject study, it is possible that the strategy for processing empty intervals might alter the strategy for processing filled intervals or vice versa. For example, pigeons might adopt a strategy of timing from the start of a sample to the onset of comparisons on both filled and empty interval trials. If this occurred, then during delay testing, a choose-long bias should be observed for both filled and empty intervals. On the other hand, pigeons might continue to process filled and empty intervals differently even when they are encountered within the same experimental session. In this case, it would be expected that a choose-short bias would be obtained for filled interval trials, while a choose-long bias would be obtained for empty interval trials.

2.1. Method

2.1.1. Subjects

Nine White Carneaux pigeons, maintained at approximately 80% of their free feeding weights, and housed individually with constant access to grit and water, served as subjects throughout the experiment. The colony room was kept at a constant temperature of 22 °C and was illuminated on a 12:12 cycle by fluorescent light turned on at 6:00 a.m. each day. Testing was conducted 5 days a week between 9:00 a.m. and 3:00 p.m. When necessary, supplementary feedings of Purina Pigeon Chow occurred after the experimental sessions and on days when the birds were not run to maintain their 80% weight. All of the birds had prior experience in psychophysical timing experiments that involved a symbolic delayed matching-to-sample task with empty and filled time intervals.

2.1.2. Apparatus

Three touchscreen-testing stations located in individual test rooms were used. Each test station consisted of a clear Plexiglas cage (30 cm wide × 40 cm deep × 36 cm high) with a large opening cut into the one end wall, which was constructed of stainless steel. On both the left and the right sidewalls of the cage, adjacent to the end with the large opening, was a 5.7 × 5 cm opening that provided access to a hopper filled with mixed grain (Coulbourn Model E14-10). A color SuperVGA monitor (Mitsubishi SD4311C) with an attached touch frame (Carrol Touch, Frame 8100-9583-01, Card 8200-3224-01) was placed against the opening in the stainless steel wall. An IBM-compatible microcomputer located in each of the individual rooms controlled the stimulus displays, recorded peck location, and operated the feeders.

2.1.3. Procedure

Baseline training. Prior to this experiment, the birds had been trained to discriminate various target training durations of filled and empty intervals within-subject (1 vs 4 s, 2 vs 8 s, and 4 vs 16 s) with psychophysical testing conducted after training at each set of durations. For the present study, the birds were retrained to discriminate between short (2 s) and long (8 s) durations of filled and empty intervals of light. The visual stimulus consisted of the presentation of a homogeneous white square, 3.3 × 3.3 cm, in the central area of the monitor (approximately 12 cm from the left and right bezel, as measured to the nearest edge). On filled interval trials, the white square was presented for either 2 or 8 s. On empty interval trials, the white square was presented for 500 ms at the beginning and at the end of a 2- or 8-s unfilled interval. Comparison stimuli were presented in two rectangular response areas, each measuring approximately 3.4 cm × 3.2 cm (width × height), one on the left and one on the right side of the monitor (approximately 15.6 cm apart, as measured from their inside edges). Position of the color comparison stimuli was counterbalanced over trials. For five of the birds, red and green comparisons were presented after empty intervals and blue and yellow comparisons were presented after filled intervals. For four birds, blue and yellow comparisons were presented after empty intervals and red and green comparisons were presented after filled intervals. The comparison stimulus that was designated correct following the short and the long duration signal was also balanced across birds. One of the eight different combinations of comparison stimuli designated as correct following the short and long signals was randomly assigned to each bird. For example, one of the eight combinations was as follows: green was correct following the short empty interval, red was correct following the long empty interval, yellow was correct following the short filled interval, and blue was correct following the long filled interval. Because there were nine birds, two of the birds received the same combination. The relationship between the type of interval (filled or empty), duration of the interval (short or long), and corresponding correct comparison stimulus (red, green, blue, and yellow) was consistent with the previous training of each bird, and it remained constant throughout this experiment.

For all the birds, a single response to one of the two comparison stimuli turned them off and, if correct, provided 4-s access to mixed grain at either the left or the right hopper opening. Location of grain access was randomly determined on these trials. Incorrect responses to the comparison stimuli produced a 4-s blackout, followed immediately by representation of the same interval duration and comparison stimulus configuration. A correct response on a correction trial produced 4-s access to mixed grain, although only the choice response on the initial (noncorrection) trial was used to calculate matching accuracy. Within each block of eight trials, all combinations of the four sample stimuli (two interval types $\times$ two signal durations) and the two comparison stimulus configurations occurred once. The order of presentation was randomized individually for each bird. Baseline training was given for 12 sessions with 160 trials per session. The duration of the intertrial interval randomly varied within sessions (4, 8, 16, or 32 s). Throughout all of the experiments reported in this paper, there was no illumination present during the intertrial interval.

Delay testing. Delay testing was conducted for 15 sessions of 144 trials each. Within each session, 24 trials for each of the four sample stimuli (empty 2 and 8 s and filled 2 and 8 s) occurred at the 0-s baseline delay, and 4 trials for each sample occurred at each of the other delays (1, 3, and 9 s). This distribution of delays (66.6% baseline delay and 33.3% other delays) was used so that the reference memory for time samples and their association with the comparison stimuli established during 0-s baseline delay training would remain stable during testing (Spetch & Wilkie, 1983). Delay intervals were spent in darkness. During delay testing, the correction procedure remained in effect only for 0-s delay trials. All other parameters remained the same as those described for training.

Sample-omission testing. Following delay testing, the birds received three sessions of baseline training, which were identical to those that preceded delay testing. Following these sessions, the pigeons received five sessions in which 128 of the 160 trials were baseline trials identical to those that preceded delay testing. On the remaining 32 trials, the visual stimulus (white square) that marked or signaled the sample duration on empty and filled interval trials was not presented. However, the ITI (4, 8, 16, or 32 s) which preceded sample-omission trials was randomly increased by 2 or 8 s. One sample-omission trial occurred randomly within each block of 5 trials. On these test trials, a response either to the left or to the right response area was randomly followed by 4-s access to mixed grain with a probability of .50. All of the other parameters during testing were identical to those explained for baseline training. In all the statistical analyses reported in this experiment, the rejection region was $p < .05$.

2.2. Results and discussion

2.2.1. Delay testing

On the last two days of baseline training, prior to delay testing, accuracy was very high on both empty and filled interval trials (90.1% correct on empty interval trials and 91.3% correct on filled interval trials). The mean percentage of correct responding during delay test sessions is shown in Fig. 1. The data for trials in which filled intervals were presented are shown in the top of the figure. For filled intervals, accuracy was very similar following short- or long-sample durations at the shorter delay intervals, but at the longest delay of 9 s accuracy was greater following the short

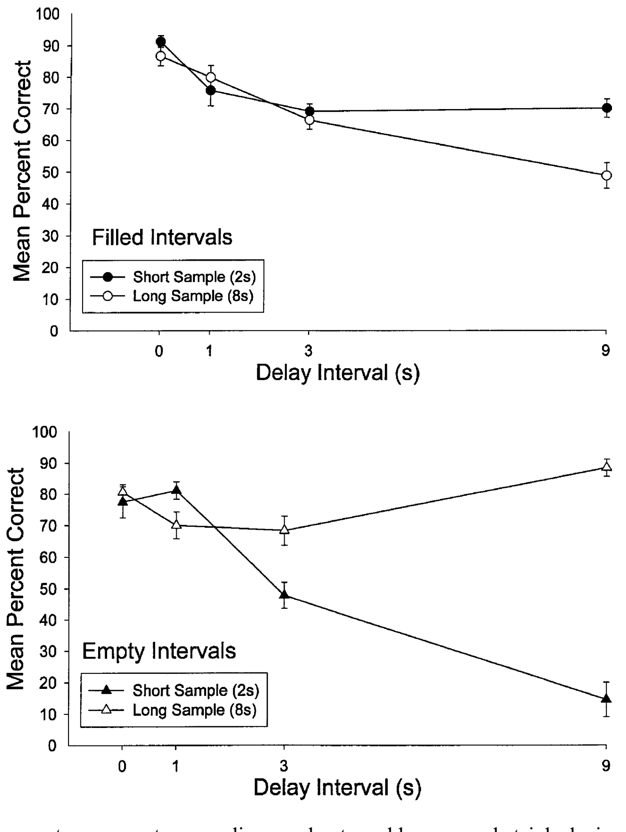

Fig. 1. The mean percentage correct responding on short- and long-sample trials during delay test sessions in Experiment 1. The data for filled intervals are shown in the top panel and the data for empty intervals in the bottom panel. Error bars represent the standard error of the mean.

sample than the long sample. For filled intervals, significant effects of delay interval [$F(3,24) = 48.84$] and a sample duration × delay interval interaction [$F(3,24) = 7.61$] were obtained. At delay intervals of 0, 1, and 3 s, there was no difference in accuracy between short-sample and long-sample trials. However, at the 9-s delay, accuracy was significantly greater on the short-sample trials than on long-sample trials [$F(1,8) = 12.89$].

The data for trials in which empty intervals were presented are shown in the bottom of the figure. Overall, accuracy decreased much more on short-sample trials than on long-sample trials as the delay interval increased. For empty intervals, significant effects of sample duration [$F(1,8) = 9.09$], delay interval [$F(3,24) = 64.93$], and a sample duration × delay interval interaction [$F(3,24) = 22.06$] were obtained. At delay intervals of 0, 1, and 3 s, there was no difference in accuracy between short-sample and long-sample trials. However, at the 9-s delay, accuracy was significantly greater on the long-sample trials than on short-sample trials [$F(1,8) = 12.89$].

2.2.2. Sample-omission testing

The mean percent choice of the comparison alternative correct for the long-sample duration (i.e., a long response) is shown in Fig. 2 as a function of the type of interval (filled or empty) and the sample trial type (no-sample, short-sample, or long-sample). As expected, when the long-sample duration was presented, the comparison alternative correct for long was very frequently selected following filled and empty intervals. Similarly, when the short-sample duration was presented, the long comparison alternative was selected very infrequently following both filled and empty intervals. However, on no-sample trials, the long comparison alternative was selected approximately 23% of the time when the comparisons for filled intervals

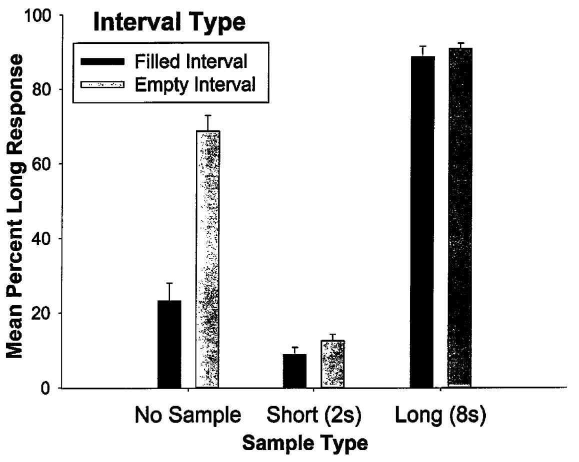

Fig. 2. The mean percentage of responses to the comparison associated with the long-sample duration on no-sample, short-sample, and long-sample trials for empty and filled intervals during sample-omission testing in Experiment 1. Error bars represent the standard error of the mean.

were presented, but it was selected approximately 69% of the time when the comparisons for empty intervals were presented. An analysis of variance indicated significant effects of interval type [$F(1,8) = 29.36$], sample type [$F(2,16) = 264.66$], and an interval type × sample type interaction [$F(2,16) = 42.73$]. When either the long sample or the short sample was presented, there was no significant difference in the percentage of long responding for filled and empty intervals. However, on no-sample trials, the percentage of long responding was significantly greater when the comparisons for empty intervals were presented than when the comparisons for filled intervals were presented [$F(1,8) = 41.83$]. In addition, a single-sample t test confirmed that the percentage of long responses was significantly greater than chance on no-sample trials for empty intervals [$t(8) = 4.48$], while it was significantly below chance on no-sample trials for filled intervals [$t(8) = -5.59$].

These results indicate that pigeons continue to process filled and empty intervals differently even when both are encountered within the same experimental session. At a long delay interval, there was a choose-short bias on trials in which the sample duration had been filled and there is a choose-long bias on trials in which the sample duration had been empty. The same difference in response bias occurred on trials in which the sample was omitted and the comparison stimuli for empty intervals or for filled intervals were presented.

The similarity of response biases at long delays to that observed when the sample is omitted suggests that pigeons could be using a default rule and asymmetrically coding the samples. According to this hypothesis, on trials involving filled intervals, the pigeons only code the long sample in working memory and they respond to the short-associated comparison only when there is no code active in working memory. This would explain both the choose-short effect at long delay intervals as well as the bias to respond to the short-associated comparison when the sample is omitted. Grant and Spetch (1994) have already undertaken tests of this hypothesis with respect to the memory biases obtained for filled intervals and they obtained evidence inconsistent with the asymmetrical coding and default responding hypothesis. Experiment 2 extended the logic of the Grant and Spetch (1994) test methodology to the current study in order to assess the role of asymmetrical coding and default responding in the choose-long effect obtained with empty intervals.

3. Experiment 2

According to the asymmetrical coding and default responding hypothesis, on trials in which a filled interval is presented, pigeons only code the long filled interval in working memory and they respond to the short-associated comparison only when there is no code active in working memory. On trials in which an empty interval is presented, pigeons only code the short empty interval in working memory, and respond to the long-associated empty interval comparison only when there is no code active in working memory. In order to assess the role of asymmetrical coding and default responding, a mixed-choice probe testing procedure was used. On one type of mixed-choice trial, both the empty-long-sample duration and the filled-short-sample duration were followed by a choice between the comparison alternatives correct for the long-empty and the short-filled samples. According to the asymmetrical coding hypothesis, on these trials, neither sample would be coded in working memory, and the birds would be presented with a choice between the two "default" responses. Consequently performance would be expected to be at chance on these trials. On the remaining mixed-choice probes, both the empty-long-sample duration and the filled-short-sample duration were followed by a choice between the comparison alternatives correct for short-empty and the long-filled samples. Again according to the asymmetrical coding and default responding model, neither sample is coded in working memory, and there would be no basis on which to respond to the comparison stimuli.

3.1. Method

3.1.1. Subjects and apparatus

The subjects and apparatus used in Experiment 1 were also used in Experiment 2.

3.1.2. Procedure

Following the testing conducted in Experiment 1, the birds were given three sessions of baseline training consisting of 160 trials as previously described. Following these sessions, the pigeons received five sessions in which 128 of the 160 trials were baseline trials identical to those that preceded delay testing. On the remaining 32 trials, mixed comparison probe trials were presented following either the empty-long-sample duration (8 s) or the filled-short-sample duration (2 s). On mixed-choice probe trials, both the empty-long sample and filled-short sample were followed by a choice between the comparison alternatives correct for the filled-short samples and the empty-long samples (16 trials), or between the comparison alternatives correct for the filled-long samples and the empty-short samples (16 trials). One mixed-choice probe trial occurred randomly within each block of 5 trials. On test trials, a response either to the left or to the right response area was reinforced by access to mixed grain for 4 s with a probability of .5, regardless of the color comparison chosen. All other parameters remained the same as those described for training.

3.2. Results and discussion

The mean percent choice of the comparison stimulus associated with empty intervals is shown in Fig. 3. When given the empty-long sample and a choice between the comparison stimuli associated with default responding (i.e., filled-short and empty-long), pigeons selected the comparison stimulus that was correct for the empty-long interval significantly above chance [$t(8) = 5.00$]. When given the filled-short sample and a choice between the comparison stimuli associated with default responding (i.e., filled-short and empty-long), pigeons selected the comparison stimulus that was correct for the empty-long interval significantly below chance [$t(8) = -10.07$]. If asymmetrical sample coding and default responding had occurred, then accuracy on these trials should have been at chance (50%). Clearly, both the empty-long and the filled-

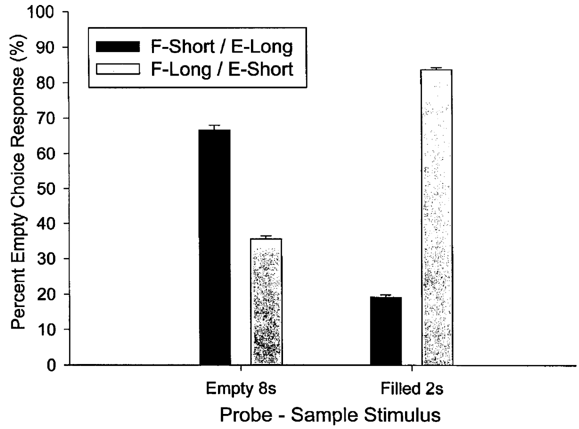

Fig. 3. The mean percentage of responses to the comparison associated with empty intervals on mixed-choice probe trials in Experiment 2. Error bars represent the standard error of the mean.

short samples exerted control over choice responding. Another indication of this control comes from trials in which the empty-long and the filled-short samples were followed by a choice between the comparison stimuli associated with presumably coded samples (i.e., filled-long and empty-short). On trials in which the empty-long sample was presented, the birds tended to choose the comparison associated with the filled-long sample rather than the comparison associated with empty-short sample. Choice of the empty-short associated comparison was significantly below chance on these trials [$t(8) = -2.91$]. On trials that involved the presentation of the short-filled sample, the birds tended to choose the comparison associated with the empty-short sample rather than the comparison associated with filled-long sample. Choice of the empty-short associated comparison was significantly above chance on these trials [$t(8) = 7.24$]. Overall, these results strongly suggest that each of the four sample stimuli exerted control over choice responding. The response biases that occur when memory for empty and filled intervals is tested does not appear to be the result of asymmetrical sample coding and default responding.

4. Experiment 3

Experiment 3 was conducted to determine if the choose-long bias on empty interval trials was occurring as a result of the pigeons simply timing and summing the total duration of the two light markers which occurred on empty interval trials. If pigeons were timing the two markers, the subjective duration of the first marker would be expected to foreshorten more on long-sample trials than on the short-sample trials. Consequently, when the comparison stimuli are presented, the remembered total duration of the markers on long-sample trials would be less than that on short-sample trials. As a result, the pigeons could have learned to select the long-associated comparison when the remembered total duration of the markers was low, and the short-associated comparison when the remembered total duration of the markers was high. Increasing the delay interval on empty interval trials would result in further subjective shortening of the memory for marker duration, and as a result a choose-long bias would be observed.

In order to determine if responding on empty interval trials was based on the remembered total duration of the markers, the duration of the second marker was manipulated on probe trials (750 or 1000 ms). An increase in the duration of the second marker would be expected to have little effect on accuracy for the short-sample trials. However, it should reduce accuracy on long-sample trials, if responding on empty interval trials is based on the remembered total duration of the markers.

4.1. Method

4.1.1. Subjects and apparatus

The subjects and apparatus used in Experiments 1 and 2 were also used in Experiment 3.

4.1.2. Procedure

Following the mixed-choice testing of Experiment 2, the pigeons received 5 sessions of marker duration testing. Each test session consisted of 128 regular trials (64 empty intervals and 64 filled interval trials) and 32 probe trials. On probe trials, the duration of the second marker on short and long empty intervals was either 750 or 1000 ms (8 trials at each sample duration $\times$ marker duration combination). On regular trials, the duration of the second marker was maintained at 500 ms. The 0-s baseline delay continued during these test sessions, and the correction procedure remained in effect only on regular trials. All other parameters remained the same as those described for training.

4.2. Results and discussion

The mean percentage of correct matching accuracy for empty intervals during probe testing sessions is shown in Fig. 4. Although not shown in this figure, accuracy for filled intervals was maintained at high levels. Accuracy was 92.6% for filled-short samples and 89.6% for filled-long samples. As can be seen in the figure, accuracy for empty intervals was also at a high level when the duration of the second marker was 500 ms. Accuracy was 88.3% for empty-short samples and 89.1% for empty-long samples. Increasing the duration of the second marker to 750 or 1000 ms appeared to result in a small reduction in accuracy that was equivalent on empty-short and empty-long samples. An analysis of variance indicated that the effect of second-marker duration was statistically significant [$F(2, 16) = 4.07$]. However, neither the main effect of sample duration [$F < 1$], nor the sample duration $\times$ second-marker duration interaction was statistically significant [$F < 1$].

If responding on empty interval trials was based on the remembered total duration of the markers, increasing the duration of the second marker should have produced selective errors on trials in which the long-sample was presented. This was not

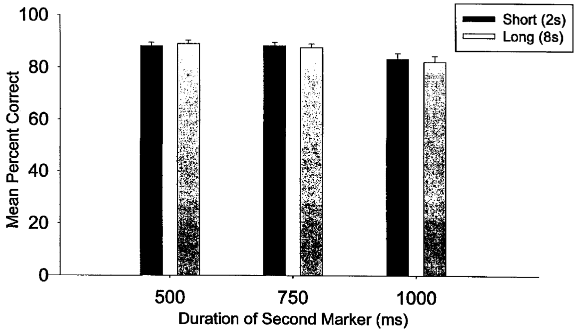

Fig. 4. The mean percentage of correct responding on regular trials initiated by the short- and long-empty intervals, as well as probe trials in which the duration of the second marker for empty intervals was varied (750 or 1000 ms) in Experiment 3. Error bars represent the standard error of the mean.

observed and it is inconsistent with the hypothesis that the pigeons' behavior on empty interval trials was under the control of the remembered durations of the markers themselves.

5. Experiment 4

This experiment was undertaken to determine if the pigeons' responding on empty interval trials was based on the number of markers presented in the last few seconds prior to presentation of the comparison stimuli. On empty interval trials in which the short-sample was presented, two markers were presented in the 3 s prior to presentation of the comparisons. On empty interval trials in which the long-sample was presented, only one marker was presented in the 3 s prior to presentation of the comparisons. Previous studies have indicated that pigeons are capable of responding based on their memory for number of light flashes (Roberts, Macuda, & Brodbeck, 1995; Santi & Hope, 2001). Consequently, correct responding on empty interval trials might have been based on the remembered number of markers, and the choose-long bias might actually be a choose-few bias.

In order to test the viability of this explanation, the discrimination was changed to make a counting strategy ineffective. This was accomplished by changing sample durations from 2.0 and 8.0 s to 0.5 and 2.0 s. If the counting explanation is correct, the birds would be capable of remembering the occurrence of two markers on both the short- and the long-sample trials, and number could no longer serve as a discriminative cue for correct responding.

5.1. Method

5.1.1. Subjects and apparatus

The subjects and apparatus used in Experiments 1–3 were also used in Experiment 4. One bird became ill during delay testing and was removed from the experiment.

5.1.2. Procedure

Following the second-marker duration testing conducted in Experiment 3, the birds were given three sessions of baseline training consisting of 160 trials as previously described. All birds then received 40 sessions of training in which the sample durations for filled and empty intervals were 0.5 s (short) and 2 s (long). The comparison stimulus previously correct for the 8-s sample, was now correct for the 2-s sample, and the comparison stimulus previously correct for the 2-s sample, was now correct for the 0.5-s sample. All other parameters remained the same as those described previously for baseline training.

Delay testing was conducted for 15 sessions of 144 trials each. Within each session, 24 trials for each of the four sample stimuli (empty 0.5 and 2 s and filled 0.5 and 2 s) occurred at the 0-s baseline delay, and 4 trials for each sample occurred at each of the other delays (1, 3, and 9 s). This distribution of delays (66.6% baseline delay and 33.3% other delays) was used so that the reference memory for time samples and their association with the comparison stimuli established during 0-s baseline delay training would remain stable during testing (Spetch & Wilkie, 1983). Delay intervals were spent in darkness. During delay testing, the correction procedure remained in effect only for 0-s delay trials. All other parameters remained the same as those described for training.

5.2. Results and discussion

The mean percent correct responding during the 40 sessions of retraining with empty and filled intervals of 0.5 and 2 s are shown in Fig. 5. As expected, on the first session of retraining, accuracy was below chance following the presentation of the filled-long and empty-long samples as a result of the birds responding to the comparisons previously correct for the short- (2 s) sample durations. However, accuracy was above chance on trials in which the filled-short (0.5 s) sample was presented, because

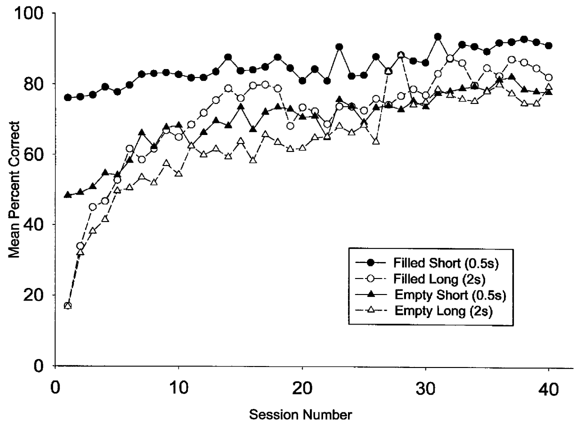

Fig. 5. The mean percentage of correct responding during the 40 sessions of retraining with empty and filled intervals of 0.5 and 2 s during Experiment 4.

a 0.5-s filled interval would be judged more similar to the previous 2-s filled interval (short) than the previous 8-s filled interval (long). Accuracy was at chance for empty-short (0.5 s) intervals on the first session of retraining. If the birds had been counting the markers on empty intervals, one would have expected the birds to respond to the 0.5 s empty interval by responding to the comparison stimulus previously correct for the short-empty interval. On the last session of baseline training, accuracy was 78.9% correct on empty interval trials and 87.6% correct on filled interval trials. This difference was statistically significant [$t(8) = -3.63$].

The mean percentage of correct responding during delay test sessions is shown in Fig. 6. The data for trials in which filled intervals were presented are shown in the top of the figure. For filled intervals, accuracy was very similar following short- or long-sample durations at the three shortest delay intervals. However, at the longest delay of 9 s, accuracy was greater following the short sample than following the long sample. For filled intervals, significant effects of sample duration [$F(1,7) = 11.33$], delay interval [$F(3,21) = 102.21$] and a sample duration × delay interval interaction

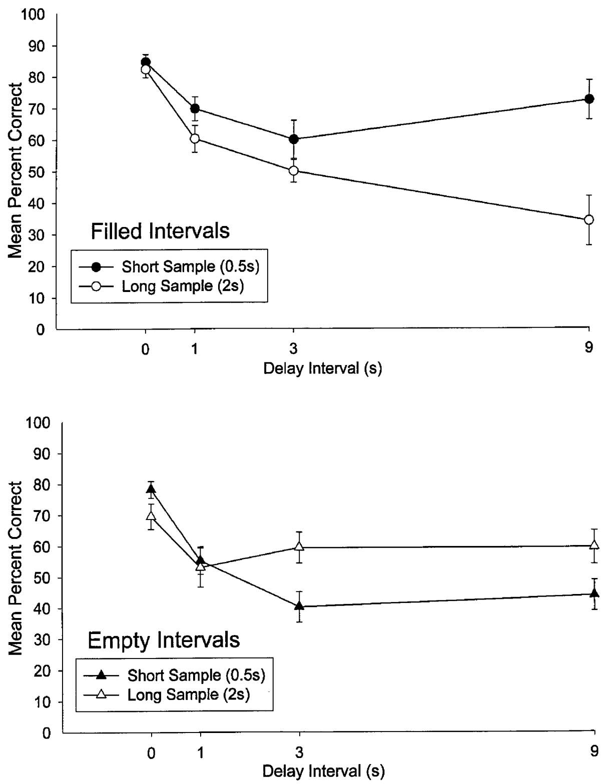

Fig. 6. The mean percentage of correct responding on trials initiated by the short- and long-sample during delay test sessions in Experiment 4. The data for filled intervals are shown in the top panel and the data for empty intervals in the bottom panel. Error bars represent the standard error of the mean.

[$F(3, 21) = 15.79$] were obtained. At delay intervals of 0, 1, and 3 s, there was no difference in accuracy between short-sample and long-sample trials. However, at the 9-s delay, accuracy was significantly greater on the short-sample trials than on the long-sample trials [$F(1, 7) = 22.39$].

The data for trials in which empty intervals were presented are shown in the bottom of the figure. Overall, accuracy decreased more on short-sample trials than on long-sample trials as the delay interval increased. For empty intervals, significant effects of delay interval [$F(3, 21) = 52.61$] and of the sample duration $\times$ delay interval interaction [$F(3, 21) = 11.90$] were obtained. At delay intervals of 0 and 1 s, there was no difference in accuracy between short-sample and long-sample trials. However, at the 3-s delay, accuracy was significantly greater on the long-sample trials than on short-sample trials [$F(1, 7) = 10.21$]. At the 9-s delay, the difference was in the same direction but it was only marginally significant [$F(1, 7) = 4.98$, $p = .06$].

6. General discussion

In Experiment 1, pigeons were trained in a within-subjects design to discriminate durations of a filled interval (2 and 8 s of light) and durations of an empty interval (2- and 8-s bound by two 500-ms light markers). Filled intervals required a response to one set of comparisons (e.g., blue vs yellow), whereas empty intervals required a response to a different set of comparisons (e.g., red vs green). Delay testing and sample stimulus omission both resulted in a choose-short bias on filled interval trials and a choose-long bias on empty interval trials. The results of mixed-choice probe tests, conducted in Experiment 2, ruled out an explanation of the response biases in terms of asymmetrical coding and default responding for both filled intervals and empty intervals. Experiments 3 and 4 investigated the viability of two different explanations for the occurrence of the choose-long bias on empty interval trials. One possible explanation was that the pigeons were timing and summing the duration of the markers themselves, and that the duration of the first marker underwent more subjective shortening on long empty interval trials than on short empty interval trials. Contrary to the predictions of this hypothesis, increasing the duration of the second marker did not result in a selective increase in errors on long-sample trials. Another explanation of the choose-long bias on empty interval trials was that the pigeons were counting the markers that occurred in the last few seconds prior to presentation of the comparison stimuli. On short-sample trials, two markers were presented in the 3 s prior to comparison presentation, while on long-sample trials only one marker was presented in the 3 s prior to comparison presentation. Hence rather than timing the empty intervals, the birds may have based their responding on the number of remembered markers, and the choose-long bias might actually have been a choose-few bias. In Experiment 4, the sample durations were changed to 0.5- and 2-s, in order to minimize the possibility that the birds could use the number of markers as a cue to respond on empty interval trials. A choose-long bias at extended delays on empty interval trials was still evident, although it was not as strong as in the first experiment.

These results extend those previously reported by Santi et al. (1999) and Grant (2001), by showing that robust choose-long biases on empty interval trials and robust choose-short biases on filled interval trials can be obtained when both types of signals are presented within the same session. In addition, Experiment 2 indicated that the asymmetrical coding and default responding hypothesis cannot explain either the choose-short bias for filled intervals or the choose-long bias for empty intervals. The methodology used to test this hypothesis was conceptually similar to the one employed in Grant and Spetch (1994). In both studies, mixed-choice probe trials offered a choice between comparison stimuli associated with the presumed default response codes following exposure to samples that were presumably not coded into working memory. In Grant and Spetch (1994), this was a choice between the two short-associated comparison stimuli for the two sets of filled interval samples with different short and long durations (i.e., 2 and 10 s and 4.5 and 22.5 s). In the present study, mixed-choice probes consisted of a choice between the short-filled associated comparison and the long-empty associated comparison.

One important aspect of the current data for empty intervals, which is different from that reported by Santi et al. (1999) as well as Grant (2001), is the occurrence of a choose-long bias on trials in which the sample stimulus was omitted. In Grant (2001), one group of pigeons was trained with red keylights as the first marker and green keylights as the second marker. Another group of pigeons was trained with red and green randomly presented in the first or second marker position. Neither group of birds exhibited any response bias on trials in which the sample was omitted. The absence of a choose-long bias on sample-omission trials was interpreted by Grant (2001) as evidence against an asymmetrical coding and default responding explanation of the choose-long bias observed at extended delays. The present data indicate that even when a choose-long bias is obtained on sample-omission trials, the asymmetrical coding and default response explanation leads to predictions for the mixed-choice probe trials which are not supported by the data. It is difficult to identify the reason for the discrepancy in results of sample-omission testing. In addition to the nature of the markers used to define an empty interval, there were some salient procedural differences in the two studies. Highly discriminable color comparisons and a fixed 0-s training delay were used in the current study, whereas less discriminable line comparisons and a variable nonzero training delay were used in Grant (2001).

In Santi et al. (1999), when both tone markers were omitted in Experiment 1, or when either the first tone or the first light marker was omitted in Experiment 3, instead of a choose-long bias there was a slight bias to choose-short. Thus, the nature of the response bias evident on sample-omission test trials seems to be independent of the response bias exhibited at extended delay intervals. A choose-long effect for empty interval trials at extended delays has been obtained regardless of whether a strong choose-long bias (current study), a modest choose-short bias (Santi et al., 1999) or no bias (Grant, 2001) occurs on sample-omission trials. This independence of the response bias on sample-omission trials and at extended delay intervals also occurs when memory for filled intervals is tested. When pigeons are trained in an event-duration task with filled intervals, sample-omission tests reliably produce a choose-short bias regardless of whether a choice delayed matching-to-sample task or a successive delayed matching-to-sample task is used (Grant & Spetch, 1991; Spetch & Grant, 1993). However, a choose-short bias at extended delay intervals only occurs when a choice-delayed matching task is used, not when a successive delayed matching task is used (Grant & Spetch, 1991; Spetch & Grant, 1993). Hence, for both filled and empty intervals, the nature of the response bias which occurs on sample-omission trials does not appear to be very diagnostic of the response bias which occurs at extended delay intervals.

While the subjective shortening hypothesis can explain the choose-short effect for filled intervals, it is not clear what mechanism is responsible for the choose-long bias at extended delays on empty interval trials. It does not appear to be a result of timing the markers (Experiment 3) or counting them (Experiment 4). Before assuming that the choose-short effect for filled intervals and the choose-long effect for empty intervals are due to different mechanisms, it might be worth considering whether both effects might be explained by the same mechanism. Gaitan and Wixted (2000) developed a signal-detection account of the choose-short effect which occurs when memory for filled intervals is tested. According to this hypothesis, the choose-short effect arises because the birds' choice responding is based on their memory for the occurrence of the most salient sample. In the case of filled intervals, the long-sample duration would presumably be the more salient event. In the absence of a memory for this event, the detection model claims that the birds respond to the comparison stimulus associated with the short sample. It is possible that in the present experiment, the pigeons learned to respond on the basis of the presence or absence of the samples for both filled and empty intervals. According to the detection model, when the comparisons for filled intervals were presented, a bird would attempt to retrieve a memory for the long filled interval. If the strength of that memory was great enough, it would choose the comparison stimulus correct for the long duration sample. If the strength of that memory was not sufficiently strong, the comparison alternative correct for the short duration sample would be selected. Gaitan and Wixted's detection model can be extended to empty interval trials if it is assumed that the short duration empty interval is a more salient sample stimulus (i.e., two light flashes in 3-s) than the long duration empty interval (i.e., two light flashes in 9-s). Consequently, when the comparisons for empty intervals were presented, a bird would attempt to retrieve a memory for the short empty interval. If the strength of that memory was great enough, it would choose the comparison stimulus correct for the short empty interval. If the strength of that memory was not sufficiently strong, the comparison alternative correct for the long empty interval would be selected.

This extension of the detection model could explain both the choose-short effect which occurs for filled intervals, as well as the choose-long bias which occurs for empty intervals. As Gaitan and Wixted (2000) have noted, the detection model is similar to the asymmetric coding and default response model with respect to the implementation of a default response, but it differs with respect to stimulus coding. According to the asymmetric coding and default responding model, only one of the two sample stimuli is typically coded on each trial. However, according to the detection model both the short and long samples are typically coded, but only the memory of the more salient sample is retrieved. This important difference means that while some of the results of Experiment 2 are inconsistent with the default response account, they are not necessarily incompatible with the detection account. In Experiment 2, the birds were presented on one type of probe trial with a novel choice between the comparison stimuli typically associated with default responding (i.e., filled-short and empty-long). On these trials, the comparisons that normally elicit a search of memory for the more salient sample (i.e., filled-long or empty-short) were not present. As a result, the birds may have instead responded on the basis of their memory for the filled-short or the empty-long samples, because only the retrieval cues for these samples were available to them. The above-chance performance observed on these trials in Experiment 2 would be consistent with successful retrieval of these memories. Hence, for these mixed-choice trials, the data are inconsistent with the default response account, but they are not incompatible with the detection account.

On the other type of probe trial presented in Experiment 2, the novel choice was between the comparison stimuli associated with the two more salient samples (i.e., filled-long and empty-short). On this type of mixed-choice trial, the comparisons that normally elicit a search of memory for the more salient sample (i.e., filled-long or empty-short) are both present. According to the detection model, neither the search for evidence that the long filled interval occurred at the beginning of the trial, nor the search for evidence that the short empty interval occurred at the beginning of the trial would be successful because only the short filled interval or the long empty interval were presented as samples on these trials. Consequently, the detection model would predict chance performance on these trials. When the short filled interval was presented, the birds displayed a preference for the comparison associated with the short empty interval. When the long empty interval was presented, the birds showed a preference for the comparison associated with the filled long interval. These results are inconsistent with the detection model. However, they may not be inconsistent with the detection model if a two-stage retrieval mechanism is proposed. That is, the birds may first retrieve a memory for the type of interval presented, either filled or empty, and only then engage in retrieval of the most salient sample duration. According to this version of the model, on trials which commenced with a filled interval, the birds would search for evidence that the long filled interval had been presented, and respond to the alternative comparison (i.e., the short empty interval) by default. On trials which commenced with the empty interval, the birds would search for evidence that the empty short interval had been presented and respond to the alternative comparison (i.e., the filled long interval) by default.

While the detection model has some notable strengths in explaining the present set of findings, it does not necessarily indicate that the subjective-shortening model is an incorrect explanation of the data from experiments in which only filled intervals are used. As noted by Gaitan and Wixted (2000), one of the strengths of the subjective shortening model is the way in which it predicts the occurrence of a choose-long effect at a delay interval duration which is shorter than the baseline training delay. This result does not follow as naturally from a detection model account. While the focus of the current discussion has been on using the detection model to account for the memory biases that occur with both filled and empty intervals in the current within-subject study, it is possible that the choose-short effect at long delays on filled interval trials was due to a shrinking memory representation, but that the choose-long effect at long delays on empty interval trials was due to a signal detection strategy. It would be worthwhile to extend the current study by training the birds at a baseline delay greater than zero and testing at shorter delays as well as extended delays. A choose-long bias on filled interval trials at delays shorter than the baseline, but no bias on empty interval trials at delays shorter than the baseline might be expected if different mechanisms were operative. No-bias at delays shorter than the baseline delays for both filled and empty intervals would provide some support for the hypothesis that the birds were using a signal detection strategy for both types of trials.

Another factor which could play a role in producing differences between filled and empty intervals is differential pecking behavior during the sample presentation phase of a trial. For example, if more pecks occurred to the long filled sample than to the short filled sample, then the choose-short effect might be explained as a choose-few effect. On empty trials, responding to comparisons might be based on the amount of time spent not responding, and a choose-long bias might be expected. The plausibility of this explanation for the current results does not seem high for several reasons. Although pecks during the sample presentation phase of a trial were not automatically recorded on each trial, informal observation of the birds did not indicate a high incidence of pecks toward the samples. In addition, while a discrete localized visual stimulus might elicit pecking behavior, the choose-short effect has been frequently reported when more diffuse visual cues, such as houselight illumination, are used (Grant & Kelly, 1998; Grant & Spetch, 1991; Leblanc & Soffie, 2001; Spetch & Grant, 1993; Spetch & Rusak, 1989; Spetch & Wilkie, 1983; Wilkie & Wilson, 1990). In fact, the choose-short effect has been obtained even when difficult to discriminate houselight durations of 2 and 3 s were employed (Grant & Kelly, 1996). Finally, in Experiment 2 of the current study, the birds were presented with the empty-long sample followed by a choice between the comparison stimuli associated with the filled-long sample and the empty-short sample. On these trials, they chose the comparison associated with the filled-long sample significantly more than the comparison associated with the empty-short sample. This result is inconsistent with the suggestion that responding to comparisons was based on number of pecks to filled samples and time spent not responding on empty trials.

The main objective of the present study was to provide additional information on the differences in memory performance produced by filled interval and empty interval procedures. It was demonstrated that both a choose-short effect on filled interval trials and a choose-long effect on empty interval trials could be obtained at long delay intervals in a within-subjects design. Experiment 2 provided a clear demonstration that the asymmetrical coding and default responding model does not provide a viable explanation of memory biases for either filled or empty intervals. Finally, the choose-long effect for empty intervals did not appear to be a direct result of pigeons timing and summing marker duration (Experiment 3), nor does it seem to result from pigeons counting the markers (Experiment 4). While the detection model of Gaitan and Wixted (2000) has some strengths in accounting for memory biases obtained under the current experimental procedures, additional empirical investigations are needed to definitively isolate the mechanism or mechanisms responsible for these findings.

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References

Fetterman, J. G. (1995). The psychophysics of remembered duration. *Animal Learning & Behavior, 23*, 49–62.

Gaitan, S., & Wixted, J. T. (2000). The role of "nothing" in memory for event duration in pigeons. *Animal Learning & Behavior, 28*, 147–161.

Grant, D. S. (1993). Coding processes in pigeons. In T. R. Zentall (Ed.), *Animal cognition: A tribute to Donald A. Riley* (pp. 193–216). Hillsdale, NJ: Erlbaum.

Grant, D. S. (2001). Memory for empty time intervals in pigeons. *Animal Learning & Behavior, 29*, 293–301.

Grant, D. S., & Kelly, R. (1996). The role of minimum wait time and sample discriminability in the coding of event duration in pigeons. *Learning and Motivation, 27*, 243–259.

Grant, D. S., & Kelly, R. (1998). The effect of variable-delay training on coding of event duration in pigeons. *Learning and Motivation, 29*, 49–67.

Grant, D. S., & Spetch, M. L. (1991). Pigeons' memory for event duration: Differences between choice and successive matching tasks. *Learning and Motivation, 22*, 180–199.

Grant, D. S., & Spetch, M. L. (1993). Analogical and nonanalogical coding of samples differing in duration in a choice-matching task in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 19*, 15–25.

Grant, D. S., & Spetch, M. L. (1994). The role of asymmetrical coding of duration samples in producing the choose-short effect in pigeons. *Learning and Motivation, 25*, 413–430.

Grant, D. S., Spetch, M. L., & Kelly, R. (1997). Pigeons' coding of event duration in delayed matching-to-sample. In C. M. Bradshaw, & E. Szabaldi (Eds.), *Time and behaviour: Psychological and neurobehavioural analyses* (pp. 217–264). Amsterdam: Elsevier.

Kelly, R., & Spetch, M. L. (2000). Choice biases in delayed matching-to-sample duration with pigeons: Manipulations of ITI and delay illumination. *The Quarterly Journal of Experimental Psychology B, 53*, 309–323.

Kraemer, P. J., Mazmanian, D. S., & Roberts, W. A. (1985). The choose-short effect in pigeon memory for event duration: Subjective shortening versus coding models. *Animal Learning & Behavior, 13*, 349–354.

Leblanc, P., & Soffie, M. (2001). The choose-short effect in rat memory for event duration: The subjective-shortening model. *Behavioural Processes, 56*, 31–40.

Roberts, W. A., Macuda, T., & Brodbeck, D. R. (1995). Memory for number of light flashes in the pigeon. *Animal Learning & Behavior, 23*, 182–188.

Santi, A., Bridson, S., & Ducharme, M. J. (1993). Memory codes for temporal and nontemporal stimuli in many-to-one matching by pigeons. *Animal Learning & Behavior, 21*, 120–130.

Santi, A., Ducharme, M. J., & Bridson, S. (1992). Differential outcome expectancies and memory for temporal and nontemporal stimuli in pigeons. *Learning and Motivation, 23*, 156–169.

Santi, A., & Hope, C. (2001). Errors in pigeons' memory for number of events. *Animal Learning & Behavior, 29*, 208–220.

Santi, A., Ross, L., Coppa, R., & Coyle, J. (1999). Pigeons' memory for empty time intervals marked by visual or auditory stimuli. *Animal Learning & Behavior, 27*, 190–205.

Sherburne, L. M., Zentall, T. R., & Kaiser, D. H. (1998). Timing in pigeons: The choose-short effect may result from pigeons' "confusion" between delay and intertrial interval. *Psychonomic Bulletin & Review, 5*, 516–522.

Spetch, M. L. (1987). Systematic errors in pigeons' memory for event duration: Interaction between training and test delay. *Animal Learning & Behavior, 15*, 1–5.

Spetch, M. L., & Grant, D. S. (1993). Pigeons' memory for event duration in choice and successive matching-to-sample tasks. *Learning and Motivation, 24*, 156–174.

Spetch, M. L., & Rusak, B. (1989). Pigeons' memory for event duration: Intertrial interval and delay effects. *Animal Learning & Behavior, 17*, 147–156.

Spetch, M. L., & Rusak, B. (1992). Temporal context effects in pigeons' memory for event duration. *Learning and Motivation, 23*, 117–144.

Spetch, M. L., & Wilkie, D. M. (1983). Subjective shortening: A model of pigeons' memory for event durations. *Journal of Experimental Psychology: Animal Behavior Processes, 9*, 14–30.

Wilkie, D. M., & Wilson, R. J. (1990). Discriminal distance analysis supports the hypothesis that pigeons retrospectively encode event duration. *Animal Learning & Behavior, 18*, 124–132.