University of Alberta

Memory For Filled Time Intervals In Pigeons

by

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I. Introduction

A procedure that is often used to investigate discrimination learning in pigeons, as well as other animals, is matching-to-sample (MTS). In the standard MTS paradigm, a pigeon is presented with three pecking keys. A stimulus such as a shape, color, or line orientation is projected on the center key, which is the sample stimulus. The pigeon is expected to peck this key, in order to ensure that it is in fact attending to it. At this point, or after a predetermined fixed interval of time (e.g., 5 s), the two side keys are illuminated with comparison stimuli, one of which matches the sample stimulus. There is an equal probability that the stimulus that matches the sample will appear on either the left or the right comparison key. If the pigeon pecks the key that matches the sample stimulus, it is reinforced (e.g., 2-s of food access) and a new presentation of the sample stimulus occurs. If, however, the pigeon pecks the key that does not match the sample stimulus, no reinforcement is given and a new presentation of the sample stimulus occurs. Which of the two or more different stimuli is presented as the sample varies from trial to trial.

An extension of this standard MTS task is called delayed matching-to-sample (DMTS) and it is commonly used to investigate short-term memory capabilities in pigeons. It was first developed by Blough in 1959 and is "the primary analytical tool used to investigate working memory processes in pigeons" (Grant, Spetch, & Kelly, 1997, p. 217). This procedure incorporates a delay interval between the presentation of the sample stimulus and the onset of the two comparison stimuli. In the DMTS paradigm, a pigeon is presented with three pecking keys in which a sample stimulus (e.g., a shape, color, or line orientation) is projected on the center key for a fixed duration. In order to ensure that the pigeon is in fact attending to this sample stimulus it is required to peck the key. At the point where the pigeon has pecked the sample stimulus, or the fixed duration of the sample stimulus is completed, a delay is introduced (e.g., 2 s) with none of the three keys illuminated. Once the delay interval, which may vary in length, is completed, the pigeon is presented with two comparison stimuli, one of which matches the particular sample stimulus that was presented prior to the delay. As in the standard MTS procedure the pigeon is required to peck the comparison key which matches the sample stimulus in order to receive reinforcement (i.e., food). Learning the relation between the sample stimulus and the appropriate comparison stimulus is achieved through training sessions until stable accuracy is shown, and then test trials with longer delays are introduced. During the interval between the sample stimulus and the comparison stimuli it is believed that the subject may be encoding covertly in order to aid in the retention of information about the test stimuli. The performance of a subject on a delay test is thought to be directed by codes that are activated by the sample and remain active throughout the delay interval. It is speculated that this may be occurring with the aid of maintenance rehearsal processes. More specifically, "a working memory representation, or code, is required to bridge the delay that intervenes between sample termination and presentation of the comparison stimuli" (Grant et al., 1997, p.218).

The DMTS task can also be modified to test memory for the duration of past events. In experiments such as these, a symbolic delayed matching-to-sample (SDMTS) procedure is used in which the sample stimuli are mapped onto visually different comparison stimuli. The comparison stimulus chosen is only a reflection of the sample stimulus since there is no physical correspondence between the two. In this procedure, a trial begins with a sample stimulus (e.g., 2- or 8-s events), the offset of this sample stimulus is followed by a delay of some duration, after which two choice stimuli are presented (e.g., red or green colored keys). For example, Spetch (1987) trained pigeons on the SDMTS task with no delay (0 s) between the sample stimulus (2- or 8-s events) and the choice stimuli (red or blue colored keys). These sample events were "filled" intervals in which food access was presented in combination with illumination of the house light, located behind the response panel, for the entire period. The relation between event duration and comparison key color was assigned randomly and counterbalanced across the birds. This type of procedure is frequently used in studies looking at memory for duration intervals as it provides opportunity for subjects to respond to sample stimuli which are not easily presented as comparison stimuli (e.g., time, number).

A number of experiments have looked at pigeon's memory for time intervals using duration samples in an SDMTS task. For example, Spetch and Wilkie (1982) looked at pigeons' memory for 2- and 10-s durations of food access and houselight illumination. Variations in the length of the delay between these samples and the comparison stimuli extended from 0 to 20 s. Results showed that accuracy was greater for shorter samples than longer samples after longer delays. That is subjects showed a strong tendency to choose the comparison stimulus associated with the short sample after longer delays. This observed tendency was called the choose-short effect (CSE).

In a later study, Spetch (1987) increased the delay between the sample stimulus and the comparison stimuli from 0 s to values of 5, 10, and 20 s across successive stages of training. These were dark delays that occurred after termination of the sample stimulus. Spetch's results with these increased testing delays indicated that when tested at delays longer than those during a baseline training phase pigeons demonstrate a CSE. After training with 5-, 10-, and 20-s delays, testing with even longer delays consistently resulted in a CSE, thus it appears to be a general effect with delays longer than those in the training sessions (e.g., Gaitan & Wixted, 2000; Grant & Kelly, 1998; Kraemer, Mazmanian, & Roberts, 1985; Santi, Hornyak, & Miki, 2003; Spetch & Rusak, 1989; Spetch & Wilkie, 1982, 1983).

The dominant theoretical explanation for the CSE is provided by the subjective shortening model (Spetch & Wilkie, 1983). This model assumes that pigeons code durations analogically in a retrospective manner (i.e., counts that accumulate during an interval) rather than categorically (i.e., short and long). The CSE is produced by the shortening of this analogical representation (i.e., loss of counts) during a delay value greater than that of training. According to this interpretation, the working memory representation of the sample becomes systematically shorter over the duration of the delay interval between the sample and the comparison stimuli. When this shortened working memory representation is later compared to the reference memory of the sample at time of decision, the discrepancy between the two representations produces the CSE.

Other theoretical accounts of the CSE have been offered. For example, Gaitan and Wixted (2000), expanding the ideas of past researchers, suggest that whenever one sample differs in salience from the other, one can expect asymmetrical retention functions because subjects tend to transform the time discrimination task into a signal detection task. Specifically, subjects transform the task into one that is based on the presence or absence of the more salient sample which, in the case of filled time intervals, would be the longer sample. This explanation assumes that upon presentation of the comparison stimuli, the subject attempts to retrieve the memory of the most salient sample (i.e., long sample). If the memory is retrieved then the subject chooses the comparison associated with the more salient sample (i.e., long sample) but if, however, the memory is not retrieved the subject chooses the comparison associated with the less salient sample (i.e., short sample). This interpretation also asserts that as the delay between the sample and the comparisons increases the memory of the more salient sample would begin to fade, and at sufficiently long delays would fade completely in which case upon attempt of retrieval the subject would be unsuccessful and would choose short.

A second alternative interpretation is the confusion hypothesis offered by Sherburne, Zentall, and Kaiser (1998) which asserts that the CSE is being caused by subjects' confusion between the intertrial interval (ITI) and the delay interval. Specifically, pigeons trained with a dark ITI and later tested with a dark delay interval may interpret the delay interval followed by comparison stimuli as a no sample trial and then choose short. Unfortunately this account does not elaborate on how exactly this confusion between ITIs and delay intervals causes the CSE to occur or how the delay interval would cause memory of the past sample to reset later allowing for a no sample decision to be made. These alternative theoretical accounts have less explanatory power than that of subjective shortening and therefore they will not be further discussed.

Several studies (Santi, Ross, Coppa, and Coyle, 1999; Grant, 2001; Santi et al., 2003) extended the findings with filled intervals by studying empty (i.e., spent in the dark). In Grant's experiment, there were two groups of pigeons, consistent and inconsistent. In the consistent group, trials began with a 1-s presentation of a red light on all the keys (the "start" marker) followed by a dark interval of 2 or 8 s. These dark intervals ended with 1-s of green lights on all keys ("stop" marker) which was followed by a short variable delay varying from 1 to 3 s in 0.5-s intervals. This variable delay was followed immediately by a white line slanted to the right on one comparison key and a white line slanted to the left on the other, each slant appeared an equal number of times on each side. In the inconsistent group, the procedure remained the same except that red and green were equally often start and stop markers. After training, Grant (2001) performed extended-delay testing in which all parameters of the experiment remained the same as in initial training except that the delay between the termination of the stop marker and the onset of the comparison stimuli was varied across three values. In the first phase of testing the values were 2 ± 1 s, 0.5 s, and 10 s. In the next phase the values were 2 ± 1 s, 10 s, and 20 s.

Both Santi et al. (1999, 2003) and Grant (2001) found a choose-long effect (CLE) in their experiments with empty intervals at long delays. The CLE describes the pigeons' greater tendency to choose the long comparison when given a delay interval longer than the training delay. Santi et al. (1999) found that accuracy dropped more on short sample trials in comparison to long sample trials as the delay increased. In accordance with Santi et al., Grant (2001) also found that at delays longer than the training delay results showed a robust choose-long effect.

These previous experiments show that a substantial CSE occurs when subjects are tested with retention delays longer than those in training on trials with filled sample stimuli. However, an opposite CLE is found when the sample stimuli are empty intervals.

In a previous research project, Grant and Talarico (in press) compared memory for empty and filled intervals under comparable conditions. This was undertaken in an attempt to determine if the different phenomena (i.e., CSE and CLE) are in fact a result of different memory processing for the empty and filled sample intervals, or due to a difference in procedure. Subjects were randomly assigned to two groups, either empty or filled, in which the interval duration consisted of either 2 or 8 s of a dark interval ("empty") or a black dot with a white background on the center pecking key ("filled"). Both groups were trained and tested with 1-s start and stop markers and variable delays.

Results showed that pigeons trained with empty intervals (top panel of Figure 1, next page) displayed the expected CLE during delay testing in accordance with results by both Santi et al. (1999) and Grant (2001). However, in contrast to prior research by Spetch (1987) in which a robust CSE was found when training consisted of filled intervals, pigeons in this experiment showed only a CSE tendency with filled intervals (bottom panel of Figure 1) that was not significant.

II. Experiment 1

The purpose of the following experiment was to determine why a nonsignificant CSE was obtained with the filled intervals by Grant and Talarico (in press). One possibility is that the use of start and stop markers altered the way in which the filled samples were coded. Specifically, the use of start and stop markers may have caused the intervals to be coded categorically as "short" and "long" or, perhaps, prospectively as "peck red" and "peck green", rather than analogically. Since categorical coding would

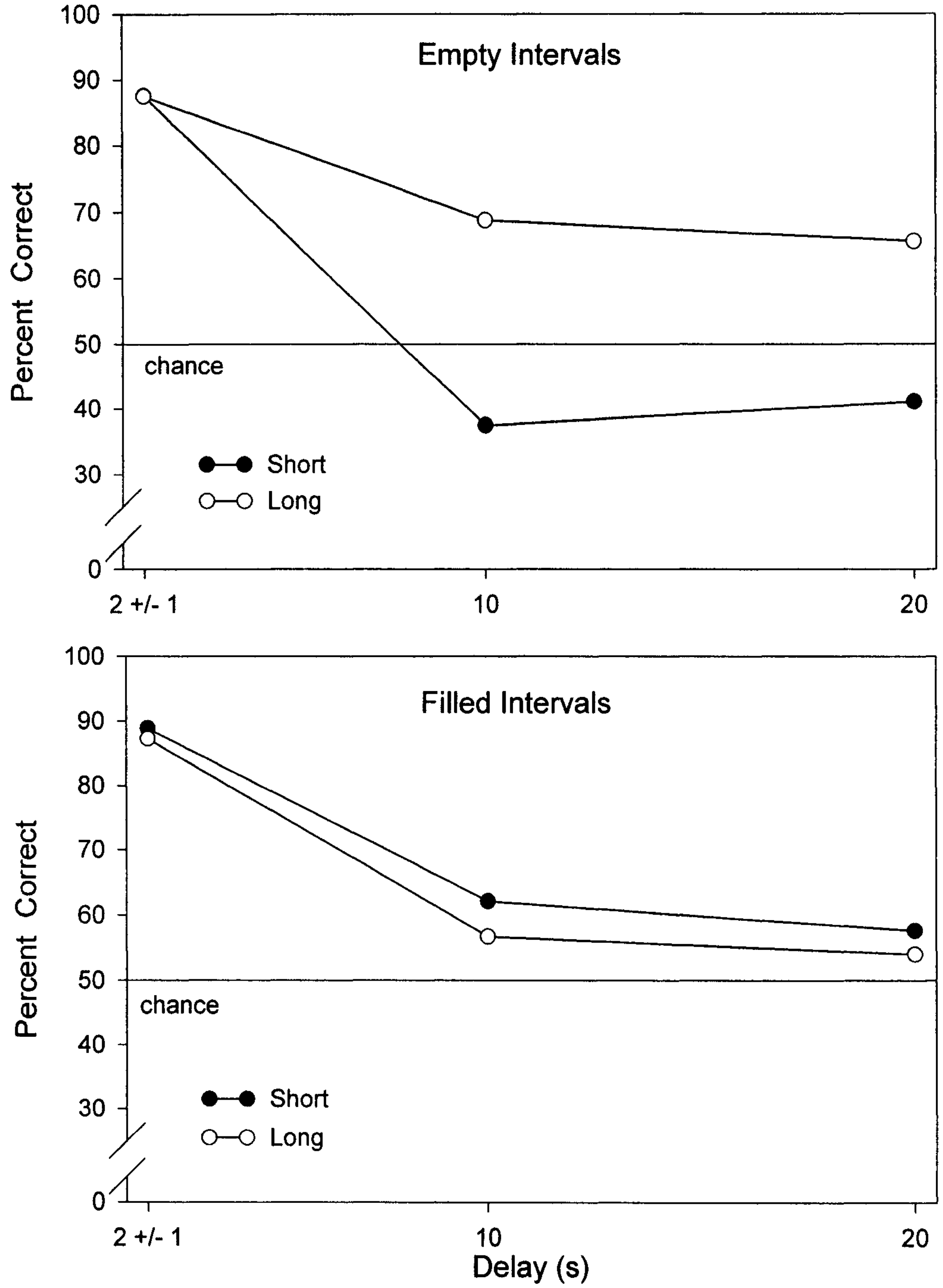

Figure 1. Percentage of correct responses as a function of delay on short- and long-sample trials with empty intervals (top half) and filled intervals (lower half) in the first delay test in Grant & Talarico (in press), Experiment 1. Each data point for the 2 ± 1-s delay interval is based on 1344 observations and for the other delays, each data point is based on 224 observations.

preclude the operation of subjective shortening during the delay, a CSE would not be anticipated.

A second possibility is that use of a variable delay procedure was responsible for the reduced CSE. However, other studies have used a variable delay during training and obtained a robust CSE. For example, Spetch and Rusak (1992) compared two groups of pigeons, one group given a constant delay value (5-s) and the other group presented with variable delays (2-, 4-, 6-, and 8-s) during training using 2- and 8-s samples of an illuminated grain feeder. They were looking to see how variable delay training would affect pigeons' performance on extended delay tests. Results showed that variability in the training delay did not affect performance either during acquisition or during delay testing where both groups displayed a large CSE at longer delays.

Similarly, Dorrance, Kaiser, and Zentall (2000) trained pigeons' on an event duration task with 2- and 10-s of light illumination on the center pecking key using variable delay intervals (0-, 1-, 2-, and 4-s) to examine the effects of experience with delay intervals from the start of training. In this study two groups were utilized that differed in terms of whether or not the ITI and the delay interval were the same (Group Dark-Dark) or different (Group Light-Dark). In terms of procedure, group Dark-Dark was identical to subjects from other experiments (Grant & Kelly, 1998; Grant & Talarico, in press; Spetch & Rusak, 1992) in that both the ITI and the retention interval were periods of darkness within the testing chamber. Hence, it would be expected that they would show results similar to those that have been previously displayed by subjects. However, in this case, the typical CSE was not found, although there was a trend in that direction.

It may be further noted that Grant and Kelly (1998) used the same variable delay procedure with delay values 2 ± 1 s with filled intervals and obtained a significant CSE. In that study, each trial began with the presentation of a preparatory stimulus which was terminated by a single peck to this key or the passage of 5 s, whichever occurred first. The termination of the preparatory stimulus was immediately followed by the presentation of a temporal sample (2- or 8-s). The preparatory stimulus was different from the start signal utilized by Grant and Talarico (in press) in two ways. First, it was not presented for a fixed amount of time (1-s) on every trial before the sample stimulus was presented. Second, its length depended on the pecking behavior of the subject since it could be very short if pecked immediately or longer if not pecked at all. It should also be noted that Grant and Kelly (1998) did not have a stop signal of any sort presented after the temporal sample was terminated and before the delay interval, as was the case in Grant and Talarico (in press).

A third possible reason behind the nonsignificant CSE trend in Grant and Talarico (in press) may be that the start and stop markers altered the values of the analogical representations of short and long, rather than altering how the samples were coded. Specifically, it may be that pigeons in group-filled timed the markers (1 s each) and added their durations to the duration of the filled intervals. If this was the case, the functional short and long samples would have been 4 and 10 s, rather than 2 and 8 s. Most experiments have employed a short-duration to long-duration ratio of 1:4 or 1:5. It may be that a short-duration to long-duration ratio of 2:5 does not produce a robust CSE.

In order to test between these possible accounts of the nonsignificant CSE obtained by Grant and Talarico (in press), three groups were trained and tested with variable delays using solely filled intervals. One group (group marker) was trained and tested with 2- and 8-s intervals marked with the addition of 1-s start and stop markers, as was the case for group filled in Grant and Talarico (in press). The second group (group 2/8) was trained and tested following the procedure used by Spetch (1987) in which the sample stimuli are 2- and 8-s intervals without the addition of start and stop markers. The third, and final group (group 4/10), was trained and tested with 4- and 10-s intervals without start and stop markers.

It was anticipated that in extended-delay testing group-marker would show a CSE tendency, as was found by Grant and Talarico (in press). Group 2/8 followed Spetch's (1987) procedure closely (except for use of a variable delay), therefore it was anticipated that results would show the same strong CSE as previous groups have during extended-delay testing. The third group, group 4/10, was included in order to determine whether the birds in the group including stop and start markers would begin timing at the onset of the start marker and stop timing at the termination of the stop marker. The results from this group are expected to reveal the important factor responsible for the diminished CSE in Grant and Talarico (in press). If a strong CSE is evident, it would appear that start and stop markers were responsible for the decrease in the CSE shown in group marker. In contrast, if only a moderate CSE is shown in group 4/10, it would appear that this was due to the fact that 4- and 10-s intervals produce a weaker CSE than 2- and 8-s because of their longer nominal duration, and/or lower short-to-long ratio.

Method

Subjects

Twenty-four naïve, adult (6 months to one year) Silver King pigeons imported from Ontario served as subjects. They were all reduced and maintained at 80% of their free-feeding weight throughout the duration of the experiment. The pigeons were housed individually in wire mesh cages between sessions and were provided with unlimited amounts of water and grit. The colony room in which the birds were housed was maintained on an alternating 12-hr light-dark cycle, in which light was onset at 6 am. Eight pigeons were assigned at random to each of the three groups: group 2/8, group 4/10, and group marker.

Apparatus

Training and testing was conducted in eight identical operant chambers, each measuring 29.0 x 29.0 x 24.0 cm (height x length x width). In each chamber, a horizontal alignment of three circular pecking keys was centered along one end wall. The key alignment was raised 22.5 cm from the barred-floor base of the chamber. A force greater than 0.15 N applied to any key was recorded as a keypeck. Affixed behind each key was an Industrial Electronics, Inc. (Van Nuys, CA) in-line projector which was used to illuminate the keys with white circles, horizontal and vertical lines, and red, green and yellow colors. A 5.5-cm high x 5.0-cm wide rectangular opening, which provided access to a retractable food magazine, was located 9.0 cm directly beneath the edge of the middle key. A 28-volt lamp, within the magazine opening, was activated when the food magazine was raised. Each chamber was enclosed in a sound- and light- attenuating booth. Within each booth, an exhaust fan provided ventilation and an external white noise generator provided masking auditory stimulation. All experimental booths were isolated in the same darkened running room. The only illumination inside the chamber was provided by the activation of keylights and the magazine light. Experimental events were controlled from, and responses were recorded by, a microcomputer located in an adjoining room. Experimental sessions were conducted six days per week, and began at approximately the same time each day for each of the three groups.

Procedure

Preliminary training. All 24 birds were trained to eat from the magazine and then autoshaped to peck at red, green, horizontal line, and vertical line presented on the center key within their individual operant chambers. Once all birds were reliably pecking each of the stimuli and eating from the feeders, SDMTS training began.

Training. For groups 2/8 and 4/10, trials began with an interval duration of 2- or 8-s, or 4- or 10-s (depending on group) of a black dot with a white background on the center pecking key. Following this, a delay varying between 1 and 3 s (in 0.5-s increments) was interpolated before the comparison stimuli were presented. For group-marker the procedure was identical to that of group 2/8 except for 2 procedural adjustments. First, trials began with a 1-s presentation of circles on all three pecking keys, which served as the start marker for the interval duration. Second, the end of the interval, before the variable delay was presented, was marked by a stop marker. The stop marker was a yellow light on each pecking key for 1 s.

In each of the three experimental groups the eight subjects were further divided into two subgroups in terms of the comparison stimuli (horizontal/vertical and red/green). In the horizontal/vertical subgroup, two birds were reinforced, with 2.5 s of magazine-illuminated access to mixed grain from the food hopper, for pecking the horizontal line in the case of short (2 or 4 s) intervals and the vertical line in the case of long (8 or 10 s) intervals. The remaining two subjects in the subgroup were reinforced for the opposite designations. For birds in the red/green subgroup, two birds were reinforced for pecking the red key in the case of short (2 or 4 s) intervals and the green key in the case of long (8 or 10 s) intervals. The remaining two subjects were reinforced for the opposite designations. On all trials a peck to either of the comparison stimuli on the side keys resulted in the termination of both of them, followed by either reinforcement or non-reinforcement.

The sessions in each of the three groups consisted of an equal number of short- and long-sample trials. The correct comparison stimulus was randomly displayed on either the right or the left pecking key across trials but it was ensured that the correct comparison appeared equally often on either side for each sample duration within a session.

All sessions contained 64 trials, 32 with each sample duration, each concluding with the onset of an intertrial interval (ITI) consisting of a random duration that varied between 10 and 30 s in 5-s increments (M = 20 s). In order to be advanced from SDMTS training to extended-delay testing, pigeons were required to display performance of 85% or higher accuracy over two consecutive blocks of four sessions each after 96 sessions of training.

Extended-delay Testing. All aspects of the extended-delay testing phase were identical to the SDMTS training phase for each experimental group except that the delay between the stop marker, or interval duration, and the comparison stimuli varied across three values. The three different delay values that intervened between the stop marker, or interval duration, and the comparison stimuli were 1 to 3 s with 0.5-s increments (baseline), 10 s, or 20 s. The sessions were comprised of 75% of trials, which were randomly chosen, involving the same delay value as in the training phase (1 to 3 s with 0.5-s increments). The remaining 25% were randomly-divided into 12.5% of trials involving a 10-s delay value, and the remaining 12.5% of trials with a 20-s delay value. Each of the 3 delay values occurred equally often with short- and long-samples, and the position of the correct comparison stimulus was balanced within sample-type and delay-interval factors. A total of 12 testing sessions (3 blocks of 4 sessions each) were conducted. Each testing session was preceded by a baseline session, identical to that of SDMTS training, in order to maintain performance. In all analyses reported in this thesis, $\underline{p} < .05$ was adopted as the criterion for significance.

Results

Training. In group 2/8 and group marker, six of eight birds met criterion after Block 24 of training (Sessions 92-96) while four of seven birds met criterion at this point in group 4/10. After some additional training six more birds met criterion, one bird in group 2/8 (Block 26), two birds in group marker (Block 25), and three birds in group 4/10 (two in Block 29 and one in Block 32). At the completion of all training trials twenty-two birds moved onto testing, 7 in group 2/8, 8 in group marker, and 7 in group 4/10. The eighth bird in group 2/8 never met criterion and therefore was not tested in this experiment and the eighth bird in group 4/10 died. The results from the training sessions are shown in Figure 2 (next page) in which the rate of acquisition can be established by each curve's slope. From looking at the figure there is evidence of some tendency for faster acquisition in group 2/8 from Block 5 to 13. Apart from this divergence, all three groups appeared to follow the same general pattern throughout training sessions. All

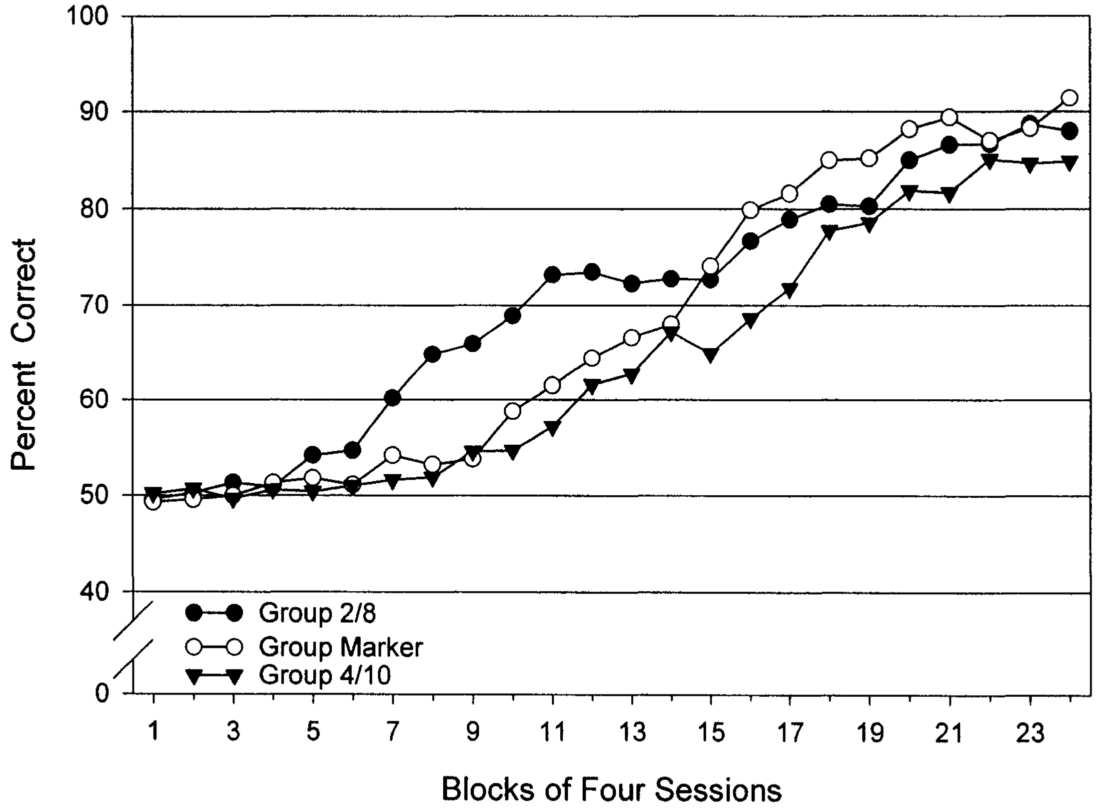

Figure 2. Percentage of correct responses as a function of blocks of four sessions in groups 2/8, marker, and 4/10 in the first 96 sessions of the training phase. Each data point is based on 1792 observations for group 4/10 and on 2048 observations for groups 2/8 and marker.

three groups' terminal acquisition was within the range of upper 80% to lower 90%.

A Block x Group analysis of variance (ANOVA) was conducted on the data from all three groups and revealed a significant main effect of block, F(23, 437) = 79.13. The analysis also showed a significant interaction, F(46,437) = 1.57, likely reflecting the faster rate of acquisition displayed by group 2/8.

Extended-delay Testing. The data from the extended-delay test for all three groups (2/8, marker, and 4/10) are shown in Figure 3 (next page). For subjects in all groups a decrease in performance on both short- and long-sample trials at the 10-s delay is observed. In group marker and group 4/10, performance decreased more so in the case of long trials versus short trials at the 10-s delay. However, in group 2/8 performance on short trials showed a greater drop in performance in comparison to long trials. At the 20-s delay, performance was higher on short trials in comparison to long trials for all three groups. Furthermore, performance of group marker and group 4/10 on long trials dropped to below chance.

A Block x Sample Duration x Delay x Group ANOVA was conducted on data from all three groups and revealed a significant effect of delay, F(2,38) = 460.22. The analysis also revealed a significant Sample Duration x Delay interaction, F(2,38) = 4.14. When comparing the means of short- and long-sample accuracy, a reliable CSE was found in that there was no difference between short- and long-sample trials at the variable training delay or at the 10-s delay, but there was a significant difference for the 20-s delay, F(1,21) = 5.05.

The data from the extended-delay test for all three groups independently are shown in Figure 4 (page 19). The results from group 2/8 are shown in the top graph,

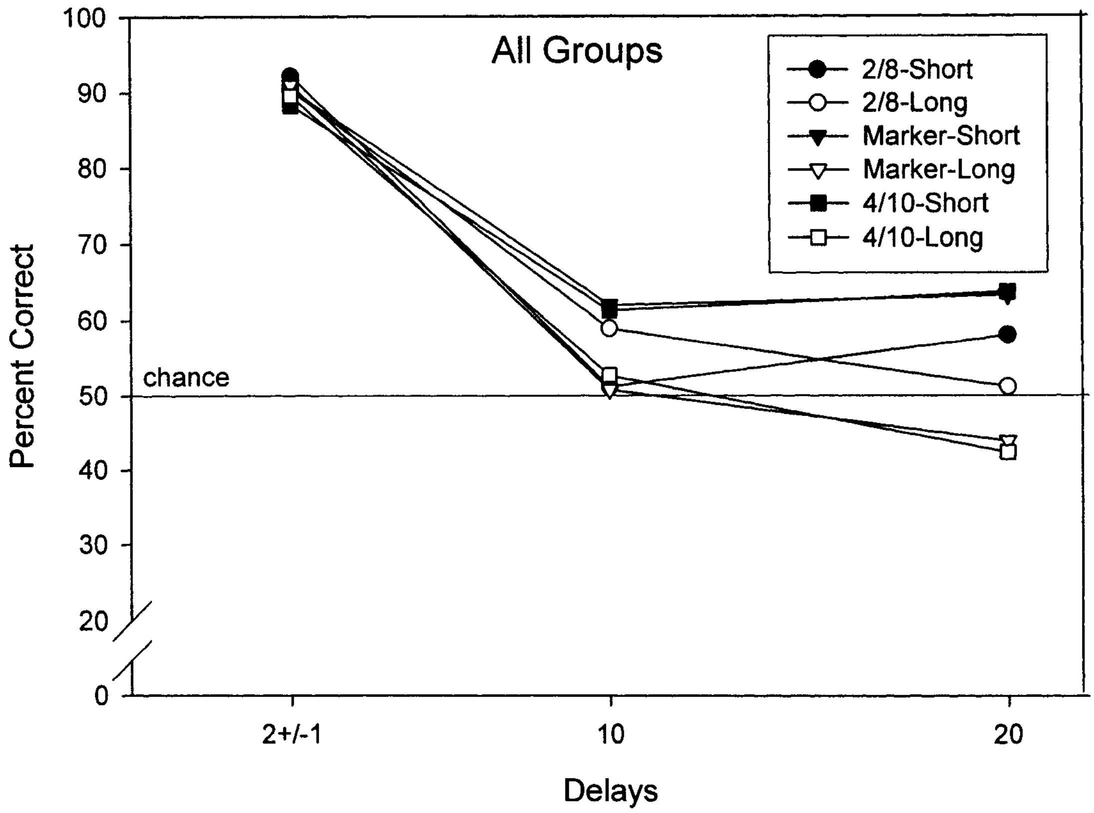

Figure 3. Percentage of correct responses as a function of delay on short- and long-sample trials for all three groups (2/8,marker, 4/10) in extended-delay testing. Each data point for the 2±1-s delay is based on 2016 observations for groups 2/8 and 4/10 and on 2304 observations for group marker. For the other delays, each data point is based on 336 observations for groups 2/8 and 4/10 and on 384 observations for group marker.

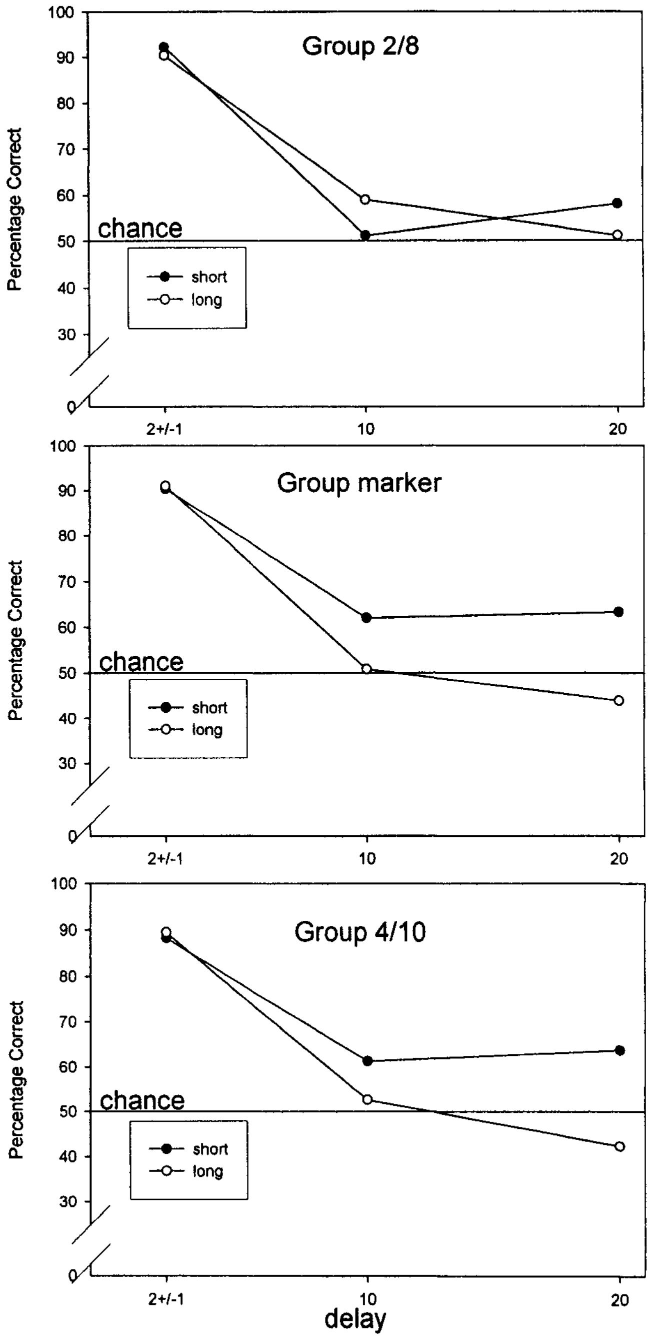

Figure 4. Percentage of correct responses as a function of delay on short- and long- sample trials for group 2/8 (top), group marker (middle), and group 4/10 (bottom) in extended-delay testing. Each data point for the 2±1-s delay is based on 2016 observations for groups 2/8 and 4/10 and on 2304 observations for group marker. For the other delays, each data point is based on 336 observations for groups 2/8 and 4/10 and on 384 observations for group marker.

group marker in the middle graph, and group 4/10 in the bottom graph.

For subjects in group 2/8 (top panel of Figure 4), performance was slightly higher on long-sample trials at the 10-s delay but this tendency appeared to reverse at the extended-delay of 20 s. A Sample Duration x Delay ANOVA was conducted on the data from group 2/8 and revealed only a significant effect of delay, F(2,12) = 215.58.

Group marker (middle panel of Figure 4) and group 4/10 (bottom panel of Figure 4) showed similar functions when looked at separately in that both groups showed a choose-short tendency at both the 10- and 20-s delays. That is, both groups showed better performance on short-sample trials at the 10-s delay and this difference in percentage correct between short- and long-sample trials increased further at the 20-s delay. Results from separate Sample Duration x Delay ANOVAs done on the data from each group showed a significant effect of delay, F(2,12) = 131.76 in group marker and F(2,12) = 126.43 in group 4/10. Neither group marker nor group 4/10 showed a significant CSE in that the Sample Duration x Delay interaction was not significant in either analysis.

Discussion

As predicted based on the findings of Grant and Talarico (in press), the data from group-marker showed a weak CSE tendency that was not statistically significant. However, unlike the predicted CSE in group 2/8, data showed the reverse effect to a minor extent at the 10-s delay and then showed a weak CSE at the 20-s delay. These results from group 2/8 are extremely surprising when compared to the robust CSE found in Spetch (1987) since the procedure was highly similar except for the use of a variable delay. Group 4/10 showed a CSE tendency at the extended delays, but as was the case in group marker this effect was not significant.

So, all three groups showed a weak CSE tendency at the 20-s delay but no group demonstrated a significant CSE. A possible reason for this decrease in magnitude of the CSE, especially in group 2/8, may be the variable delay used in training. Although the use of a variable training delay did not seem to effect the magnitude of the CSE in Spetch and Rusak (1992), it did appear to negatively effect the CSE in Dorrance, Kaiser, and Zentall (2000). Furthermore, although Grant and Kelly (1998) used an identical 2±1 s variable delay training procedure and found a CSE, this CSE was not as robust as that which would be expected based on past research.

III. Experiment 2

The purpose of the second experiment was to investigate the possible effects of removing the variable delay in both training and testing with filled intervals of 2- and 8-s, with and without start and stop markers, and 4- and 10-s intervals without start and stop markers on the CSE. Specifically, the experiment was designed to determine the effects of training a subset of each group of pigeons (2/8, marker, and 4/10) from Experiment 1 with a new task utilizing one of the two alternate types of filled intervals than that tested in Experiment 1. For example, half of the pigeons trained with 2- and 8-s intervals in Experiment 1 were now trained with 2- and 8-s intervals with the addition of start and stop markers, and the other half of the pigeons previously trained with 2- and 8-s were now trained with 4- and 10-s intervals. Table 1 shows the training conditions in Experiment 1 and 2 for all pigeons.

Transfer of Subjects in Groups 2/8, Marker, and 4/10 to New Training Regime

Subjects	**Experiment 1 Training**	**Experiment 2 Training**
871-74	2/8:L	Marker:C
875-78	2/8:C	4/10:L
881-84	Marker:L	4/10:C
885-88	Marker:C	2/8:L
891-94	4/10:L	2/8:C
895, 6, 8	4/10:C	Marker:L

Note – L, line comparisons; C, color comparisons.

In this experiment pigeons were trained in a SDMTS procedure that was the same as in the first experiment with three exceptions. First, each initial group from Experiment 1 (group 2/8, marker, and 4/10) was further divided into two separate subgroups and trained with one of the two interval types not previously utilized in training. Second, training employed a 0-s delay that was present on all trials instead of the variable delay used in Experiment 1. Third, the dimension of comparison stimuli was transferred between colors and line orientations. That is, pigeons trained with colors in Experiment 1 were trained with line orientations in this experiment, and pigeons trained with line orientations in Experiment 1 were trained with colors in this experiment. Hence, the task trained in Experiment 2 was different from that trained in Experiment 1 both in terms of the samples and comparisons.

Method

Subjects and Apparatus

The subjects (n=8 in group 2/8 and group marker, and n=7 in group 4/10) and the apparatus were the same as in Experiment 1.

Procedure

Training. For the birds in all three groups, training sessions were identical to those in Experiment 1 except for the fact that subjects were presented with different time interval types (see Table 1 on previous page) and a 0-s delay rather than a variable delay. Furthermore, subjects who were previously trained and tested with color comparisons were now trained with line orientations on the comparison keys on the new task. Similarly, subjects previously trained and tested with line orientations were now trained with color comparisons on the new task. As in Experiment 1, sessions contained 64 trials, 32 with each sample duration, each concluding with the onset of an intertrial interval (ITI) consisting of a random duration that varied between 10 and 30 s in 5-s increments (M = 20 s). Pigeons were required to display performance of 80% or higher accuracy over two consecutive blocks of four sessions in order to be advanced to extended-delay testing from SDMTS training.

Extended-delay Testing. All aspects of the extended-delay testing phase were identical to those in Experiment 1 with two exceptions. First, subjects were now being tested on the new time interval types which they had learned. Second, the delay values in this phase of testing were 0 s (baseline), 10 s, or 20 s rather than 1 to 3 s with 0.5-s increments (baseline), 10 s, or 20 s. Delay values were equated into trials in the same fashion as described in Experiment 1. A total of 8 testing sessions (2 blocks of 4 sessions each) were conducted, each preceded by a baseline session which was identical to training sessions.

Results

Training. After Block 13 of training (Sessions 49-52) all eight birds in group 2/8, five of seven birds in group marker, and seven of eight birds in group 4/10 met criterion and moved on to extended-delay testing. Because the three groups were not equivalent in terms of prior training history, analysis of rates of acquisition was deemed inappropriate. Terminal acquisition for all three groups ranged from lower 80% to higher 90% and did not differ significantly.

Extended-Delay Testing. The data from extended-delay testing for all three groups (2/8, marker, 4/10) are shown in Figure 5 (next page). For subjects in all groups a decrease in performance on long-sample trials at both the 10- and 20-s delay is observed. This decrease in performance is largest in groups 2/8 and 4/10 whereas the decrease in performance on long-sample trials in group marker is markedly smaller.

A Block x Sample Duration x Delay x Group ANOVA conducted on data from all three groups revealed a significant effect of delay, F(2,34) = 451.36, as well as sample duration, F(1,17) = 14.71. The analysis further revealed a significant Sample Duration x Delay interaction, F(2,34) = 15.60 which represents a significant CSE.

Independent data for each group from extended-delay testing are shown in Figure 6 (page 26). The results from group 2/8 are shown in the top graph, group marker in the middle graph, and group 4/10 in the bottom graph. All three groups show a similar trend of a decrease in performance on both short- and long- sample trials with the greater decrease being long-sample accuracy falling to below chance levels at both the 10- and 20-s delays.

The functions in group 2/8 (top panel of Figure 6) and group 4/10 (bottom panel of Figure 6) are very similar in that both reflect a robust CSE. Results from separate Sample Duration x Delay ANOVAs done on the extended-delay test data for each of these two groups showed a significant effect of delay, F(2,14) = 170.86 in group 2/8 and

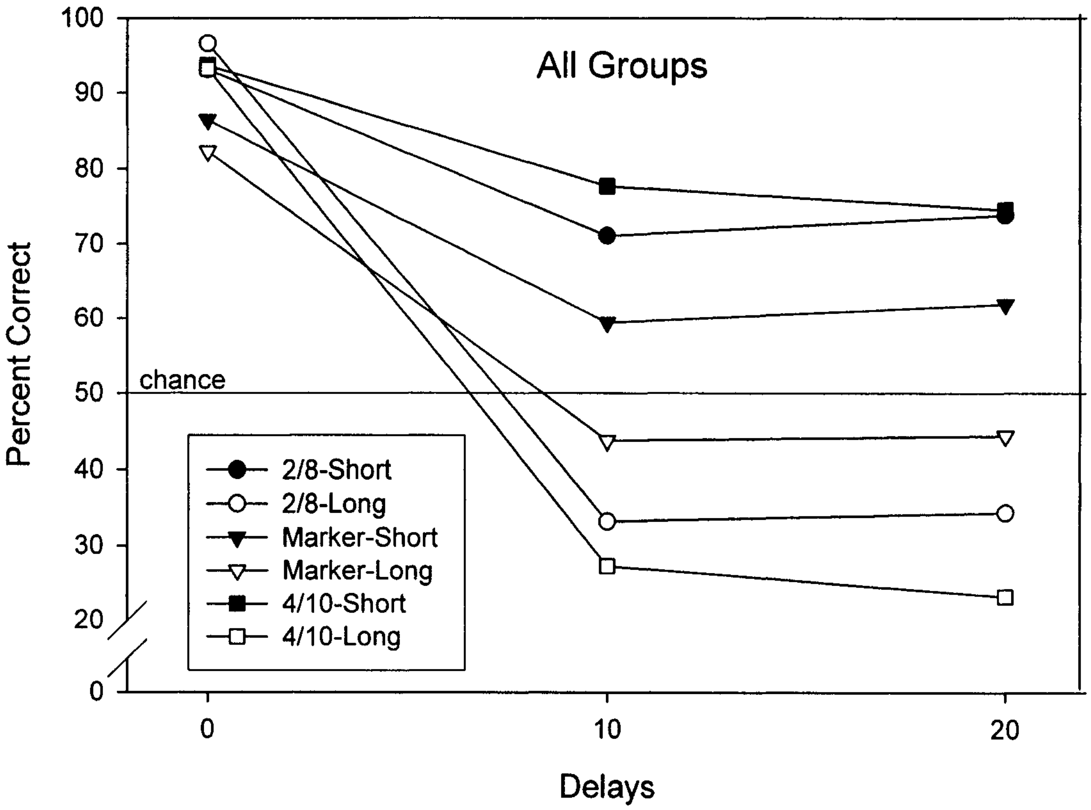

Figure 5. Percentage of correct responses as a function of delay on short- and long- sample trials for all three groups (2/8, marker, 4/10) in extended-delay testing. Each data point for the 2±1-s delay is based on 1536 observations for group 2/8, on 960 observations for group marker, and 1344 observations for group 4/10. For the other delays each data point is based on 256 observations for group 2/8, 160 observations for group marker, and 224 observations for group 4/10.

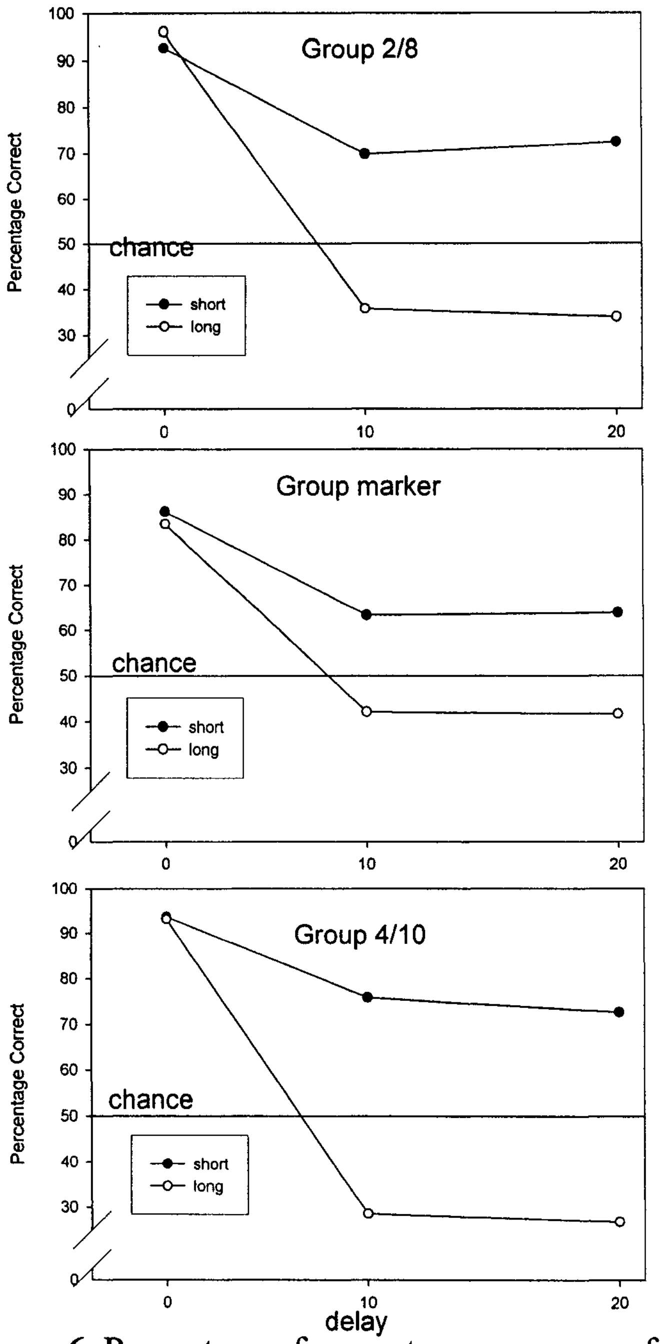

Figure 6. Percentage of correct responses as a function of delay on short- and long- sample trials for group 2/8 (top), group marker (middle), and group 4/10 (bottom) in extended-delay testing. Each data point for the 0-s delay is based on 1536 observations for group 2/8, 960 observations for group marker and 1344 observations for group 4/10. For the other delays, each data point is based on 256 observations for group 2/8,160 observations for group marker, and 224 observations for group 4/10.

F(2,12) = 301.13 in group 4/10. Both groups also showed a significant effect of sample duration, F(1,7) = 6.71 in group 2/8, and F(1,6) = 43.67 in group 4/10. Moreover, both group 2/8 (F(2,14) = 8.20) and group 4/10 (F(2,12) = 29.85 showed a significant CSE in that the Sample Duration x Delay interaction was significant in both analyses.

In comparison to groups 2/8 and 4/10, group marker (middle panel of figure 6) showed slightly lower accuracy on all trials at the 0-s delay, and although at the 10- and 20-s delays performance was greater on short-sample trials, the difference between accuracy on short- and long-sample trials was far less than that shown by groups 2/8 and 4/10. A Sample Duration x Delay ANOVA was conducted on the data from group marker and revealed only a significant effect of delay, F(2,8) = 77.55. Although the Sample Duration x Delay interaction was not significant, $F < 1$, revealing no significant CSE, there was a CSE trend in this group.

Discussion

Both groups 2/8 and 4/10 showed a robust CSE in extended-delay testing, however group marker showed only a CSE tendency that was not statistically significant. These findings suggest that the variable delay implemented in the training and testing phases of Experiment 1 did have an affect on the results of groups 2/8 and 4/10. The change in procedure to one without a variable delay did not have a large effect on results for group marker in that a weak, and statistically nonsignificant CSE was obtained in both experiments reported in this thesis. Hence, the present results suggest that both use of a variable training delay and use of start and stop markers reduces the magnitude of the CSE.

IV. General Discussion

The experiments reported in this thesis were performed in order to gain further knowledge regarding the timing of filled intervals in pigeons. Experiment 1 was conducted specifically to determine why a nonsignificant CSE was obtained with filled intervals in Grant and Talarico (in press). It was speculated that this reduction in CSE could be based on the introduction of start and stop markers which may be causing intervals to be coded in a non-analogical fashion precluding subjective shortening. A second possibility that was considered was that the variable delay procedure may be the cause of the reduced CSE; however this was not anticipated as other studies (Grant & Kelly, 1998; Spetch & Rusak, 1992) had used this procedure and found a CSE.

To test these possible accounts of the reduced CSE three groups of naïve pigeons were trained and tested using solely filled intervals with a variable delay procedure. The first group (group marker) was trained and tested with 2- and 8-s intervals marked with the addition of 1-s start and stop markers, the second group (group 2/8) was trained and tested with 2- and 8-s intervals without the addition of start and stop markers, and the third group (group 4/10) was trained and tested with 4- and 10-s intervals without the addition of start and stop markers. It was anticipated that group marker would show a nonsignificant CSE similar to the findings of Grant and Talarico (in press). Group 2/8 was anticipated to show the same strong CSE as comparable groups in past research have shown (e.g. Spetch, 1987). The results from group 4/10 were expected to reveal which factor of the procedure was responsible for the nonsignificant CSE in Grant and Talarico (in press), either the start and stop markers or the 2:5 short-duration to long-duration ratio that may have resulted from the birds timing the start and stop markers.

Results from extended-delay testing in Experiment 1 did not show a significant CSE in any of the three groups. This was surprising, particularly in regards to group 2/8, as the procedure for this group, except for the variable delay, was highly similar to that of Spetch (1987) where a robust CSE was obtained. Not only was a CSE not found in group 2/8 but at the 10-s delay the choose-short tendency was reversed with performance being slightly higher on long-sample trials. Furthermore, group marker and group 4/10 both showed a choose-short tendency at both extended-delays but neither was significant. These results led to the question of whether or not the variable delay procedure was the reason behind these unexpected results.

Experiment 2 was conducted to aid in understanding why Experiment 1 did not reveal a significant CSE in any of the three groups, more specifically to investigate the possible effects of removing the variable delay procedure in training and testing. New experimental groups were formulated from the subjects in Experiment 1 by assigning half of the pigeons from each group in Experiment 1 to a new group with one of the two alternate types of filled intervals and comparison stimuli than that tested in Experiment 1. Pigeons were trained in a SDMTS task identical to that of Experiment 1 except for three adjustments. First, subjects from each initial group in Experiment 1 were divided into two separate subgroups each being trained with one of the two interval types not previously utilized in training. Second, the dimension of comparison stimuli was transferred between color and line orientation, specifically subjects previously tested with color comparisons were now trained with line comparisons and vice versa. Third, the variable delay was eliminated and all training trials employed a 0-s delay. It was anticipated that results from these groups would aid in understanding the effects of a variable delay on the timing of filled intervals.

Results from extended-delay testing in this second experiment showed a robust CSE in both group 2/8 and group 4/10, but only a choose-short tendency was displayed by group marker. The implications of these findings are that the variable delay procedure does have an effect on the CSE which is an indication that training with variable delays may cause pigeons to code time intervals non-analogically, perhaps prospectively or categorically. It is possible that the variable delay implemented in training sessions is allowing subjects the time to switch over to categorical or prospective coding. That is, although during the presentation of the sample stimulus the subject may be accumulating counts on a pacemaker as is predicted by analogical coding, given the time during the delay they are switching this analogical representation to one that is categorical (i.e., short or long) or prospective (i.e., peck red or peck green). Since categorical coding would preclude subjective shortening this could be why a robust CSE is not found. It is important to note that it may be that only some of the birds in each group are behaving in this manner on all trials or that all birds are doing this on at least some of the trials. Furthermore, it may not matter whether or not the delay in training is variable, that is, any delay value, fixed or variable, may just as easily provide the opportunity for a change in the coding of time intervals to occur.

Moreover, the fact that group marker did not display a CSE, even after the variable delay was eliminated, suggests that there is something happening with either the start marker, the stop marker, or both markers that is causing pigeons to code time intervals in a different manner. Considering the fact that group 4/10 in Experiment 2 showed a significant CSE it does not appear that subjects are timing the values of the start and stop markers and adding them to the value of the samples. If this were the case, the functional values of the 2- and 8-s samples with the markers would become 4- and 10-s, and we would therefore anticipate similar results as those demonstrated by group 4/10. One possibility for the results shown by group marker could be that the start marker is being utilized by subjects as a preparatory stimulus while the stop marker is acting as a delay, namely in the case where there is a 0-s delay implemented in training and testing trials. Therefore neither marker is being timed either separately or along with the sample stimulus. If this was the case, since the stop marker is behaving as a delay then it is possible that this delay or extension to the delay is just adding to the time available for subjects to switch the way they are coding the samples from analogical to categorical or prospective coding. This would aid in explaining why group marker was the only group that did not show a significant CSE in Experiment 2. Group 2/8 and group 4/10 had 0-s delays on all trials as did group marker but since group marker was the only group with a stop marker of 1s they did have that extra 1 s after the sample stimulus had been presented that may be treated as a delay.

Further research into the effects of variable delay procedures and start and stop markers on remembering intervals of different durations is required. One possibility would be to conduct an experiment utilizing four separate groups, all four trained and tested with 2- and 8-s filled time intervals. The between-group differences would lie in whether or not a variable delay procedure is used, and whether or not start and stop markers are presented. Group marker would utilize 2- and 8-s intervals with the addition of start and stop markers. Group variable-marker would be identical to group marker except for the inclusion of the variable delay procedure. The other two groups, group 2/8 and group variable 2/8 would utilize 2- and 8-s filled intervals without the addition of start and stop markers and would again differ in whether or not a variable delay was used. With this experimental design it would be possible to analyze each variable in isolation, as well as in conjunction with the other, which may allow for a more complete explanation of the mechanisms involved in coding filled interval durations.

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