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Pigeons' memory for number of events: Effects of intertrial interval and delay interval illumination

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Abstract

In Experiment 1, pigeons were trained at a 0-s baseline delay to discriminate sequences of light flashes (illumination of the feeder) that varied in number but not time (2f/4s and 8f/4s). During training, the intertrial interval was illuminated by the houselight for Group Light, but it was dark for Group Dark. Testing conducted with dark delay intervals produced a strong choose-small bias in both groups. All birds then received baseline training with a 5-s dark delay and were subsequently tested at shorter and longer dark delays. A choose-small bias was again observed at delays longer than the training delay, while a choose-large bias occurred at delays shorter than the training delay. Differentiating the ambient chamber illumination during the intertrial interval and the delay interval did not attenuate choose-small or choose-large effects. In Experiment 2, all birds received baseline training with a 5-s illuminated delay and were subsequently tested at shorter and longer illuminated delays. A choose-large bias was observed at delays longer than the training delay, while a choose-small bias occurred at delays shorter than the training delay. In Experiment 3, on intermittent test trials, when the duration of the second flash on small-sample trials was equal to the total flash duration on large-sample trials (i.e., 1600 ms), accuracy fell to approximately chance. These results suggest that pigeons discriminated the sequences of light flashes that varied in number but not in total duration of the sequence by relying on other temporal properties of the sequence rather than by using an event switch to count flashes.

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Several studies have employed a delayed symbolic matching-to-sample (DMTS) procedure to investigate memory for number of events in pigeons (Fetterman, 2000; Fetterman & MacEwen, 1989, 2003; Roberts, Macuda, & Brodbeck, 1995; Santi & Hope, 2001). In a typical experiment on memory for number, trials begin with the presentation of a sample stimulus consisting of a small number or a large number of equally spaced light flashes each lasting 200 ms. For example, the small sample could consist of two flashes of light in 4 s (2f/4s), while the large sample could consist of eight flashes of light in 4 s (8f/4s). A peck to one comparison stimulus (e.g., red) is reinforced if the sample number had been small, while a peck to the other comparison stimulus (e.g., green) is reinforced if the sample number had been large. Following acquisition, memory for number is assessed by inserting delay intervals of varying length between the termination of the sample and the onset of the comparisons. Using this type of procedure, Roberts et al. (1995) found that pigeons continued to respond with high accuracy as the delay interval was increased following the samples consisting of a small number of light flashes (2f/4s), but accuracy dropped to well below 50% correct following the large number (8f/4s). Fetterman (2000) reported a similar finding with rates of stimulus change (slow vs fast) serving as sample stimuli. Delay tests indicated a bias to respond to the comparison stimulus associated with the slow sample. Fetterman (2000) hypothesized that rate discriminations were based on the number of sample events (light flashes) and that the choose-slow bias represented an instance of a choose-small effect. The choose-small effect obtained when memory for number is assessed parallels the response bias exhibited when memory for event duration is assessed.

In studies of memory for event duration, a pigeon may be required to peck a red comparison stimulus after a 2-s sample stimulus and to peck a green comparison stimulus after 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 common finding from this procedure is that at delays longer than baseline training, pigeons respond with high accuracy following the short sample, while accuracy of responding following 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; Spetch, 1987; Spetch & Rusak, 1989, 1992a; Spetch & Wilkie, 1983). This result is commonly known as 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.

These findings, in conjunction with other research on the simultaneous processing of time and number information by rats (Meck & Church, 1983) and pigeons (Roberts & Mitchell, 1994), are consistent with the view that the processing of temporal and numerical information is accomplished by a common mechanism. The nature of this common mechanism has been articulated differently by various theoretical perspectives. Meck and Church (1983) advanced a dual-mode version of scalar timing theory which proposed that the same pacemaker-accumulator system processes both time and number. Broadbent, Church, Meck, and Rakitin (1993) have proposed a

connectionist model of timing and counting, while Staddon and Higa (1999) have advanced a multiple-time scale model in which both time and number are stored as values of a decaying memory established either by a continuous signal (duration) or a sequence of events (number).

If temporal and numerical processing is accomplished by a common mechanism, then variables which affect memory for number should have the same effect on memory for event duration and vice versa. While much of the previous research on memory for event duration involved training at a 0-s baseline delay, a few studies have trained pigeons at a longer baseline delay (e.g., 5 or 10 s) and then tested at delays shorter or longer than the baseline delay. In contrast to the choose-short effect observed at test delays longer than the baseline delay, testing at delays shorter than the baseline delay results in a choose-long effect (Spetch, 1987; Spetch & Rusak, 1989). If time and number processing involves a common mechanism, one would expect tests of memory for number to reveal a choose-large effect at delays shorter than the training delay.

Santi and Hope (2001) trained pigeons to discriminate sequences of light flashes (illumination of the feeder) that varied in number but not time (2f/4s and 8f/4s), and in time but not number (4f/2s and 4f/8s). They demonstrated that the choose-small bias for number samples and the choose-long (functionally choose-small) bias for time samples reported by Roberts et al. (1995) could be obtained in a within-subjects design. A choose-long bias for time samples occurred because pigeons coded time samples in terms of the number of flashes occurring in the last few seconds of a sequence. Consequently, the “time samples” in both Roberts et al. (1995) and Santi and Hope (2001) were processed by the birds as if they were number samples. More importantly, in Experiment 3, Santi and Hope (2001) trained the birds with a 5-s baseline delay and subsequently tested them at shorter and longer delays. A choose-large bias reliably occurred at the test delays which were shorter than the baseline training delay, while a choose-small bias was again observed at delays longer than the baseline delay for both number samples and number-coded time samples during one of the two sets of delay tests. These findings provide additional empirical support for conceptualizing memory for number and time in terms of a common mechanism.

A popular theoretical explanation of the choose-short effect proposes that temporal samples are analogically coded in working memory and undergo subjective shortening as the delay interval is increased (Spetch, 1987; Spetch & Wilkie, 1982, 1983). Thus, a temporal sample is assumed to establish a working memory representation which reflects the cumulative nature of that sample. For example, the code could represent that number of pulses generated by an internal clock (Meck & Church, 1983) that accumulate over the duration of a sample, and the “subjective shortening” of the coded duration could be conceptualized as the gradual loss of pulse counts over a lengthy delay interval. As a consequence, the working memory code for a long-duration sample would subjectively shorten and become increasingly similar to the pulse count associated with short samples in reference memory. As a result, choice of the comparison stimulus that is correct on short-sample trials becomes increasingly probable.

A similar explanation can account for the choose-small effect that occurs when memory for number of events is tested. If each event in a sequence of events results in the accumulation of a fixed number of pulses, the total number of accumulated pulses would provide an analogical representation of the number of events that had been presented. After a lengthy delay interval, the pulse counts for a numerically large sample would deteriorate over the delay interval, causing the pulse count for the large sample to be closer to the reference memory pulse count for the small sample at a 0-s delay. As a result, choice of the comparison stimulus that is correct on small-sample trials becomes increasingly probable. The analogical coding/subjective shortening hypothesis also predicts the choose-large effect when test delays are shorter than the baseline training delay. If the pulse counts in working memory are lost over a delay period, then when trained with a constant 5-s baseline delay, the pulse counts stored in reference memory would be smaller than they would be if no delay was used during training. When tested at delays shorter than the 5-s delay, the pulse counts in working memory would be larger than those which had been stored in reference memory during training. Consequently, choice of the comparison stimulus that is correct on large-sample trials becomes increasingly likely as the test delay becomes shorter than the 5-s baseline delay. Thus, the analogical coding/subjective shortening hypothesis can account for choose-short and choose-long effects in tests of memory for event duration, as well as choose-small and choose-large effects in tests of memory for number of events.

Spetch and Rusak (1992b) demonstrated that the similarity of the ambient illumination condition during the intertrial interval (ITI) and the delay interval was an important determinant of the occurrence of a choose-short effect. They regarded this finding as consistent with their relative duration hypothesis which maintained that sample duration was judged relative to a temporal background which included the ITI and the delay. Similarity of the stimulus conditions during the ITI and the delay presumably made it easier for pigeons to treat these two intervals as part of a common temporal background. Response biases during delay testing were assumed to reflect the discrepancy between the current sample-to-background ratio and the ratio established in reference memory during training. Thus the relative duration hypothesis was an extension of the subjective shortening model rather than an alternative to it.

The instructional failure/confusion hypothesis provides an alternative approach to biased-forgetting effects in the assessment of animal memory (Cohen & Njegovan, 1999; Kaiser, Zentall, & Neiman, 2002; Sherburne, Zentall, & Kaiser, 1998; Zentall, 1997, 1999). It views the dependency of the choose-short effect on the contextual similarity of the ITI and the delay interval from the perspective of “instructional failure or confusion”. Accordingly, pigeons trained with the houselight-off during the ITI may confuse the novel dark delay presented at test with the ITI. Therefore, when the comparison stimuli are presented after the delay interval, the pigeon may experience “instructional failure” and respond as though no sample had occurred. Because no sample is judged to be closer to the short-sample code than it is to the long-sample code in reference memory, a choose-short bias is observed (Grant, 1991; Sherburne & Zentall, 1993; Wixted, 1993). To test this hypothesis Sherburne et al. trained two

groups of pigeons to match “short” (2 s) and “long” (10 s) white light on the center key to red and green comparison stimuli with a 0-s delay. One group of pigeons was trained with the houselight on during the ITI (Group Light) and the other with the houselight off during the ITI (Group Dark). Both groups were then tested with both illuminated and dark ITIs and illuminated and dark delay intervals. The instructional failure/confusion hypothesis predicts that the choose-short effect will only occur when the illumination condition in the ITI used during training is the same as the illumination condition in the delay interval used during test. However, when the illumination condition in the delay interval differs from that in the ITI used during training, no confusion should result and the choose-short bias should be eliminated. Sherburne et al. obtained results consistent with these predictions. The choose-short effect only occurred when the ITI condition used in training was the same as the delay condition used at test and was eliminated under all other conditions.

Recently, Dorrance, Kaiser, and Zentall (2000) suggested that delay interval novelty was another factor that contributed to the choose-short effect. They demonstrated that even when the ambient conditions during the ITI and delay were the same, the choose-short effect at extended delays could be eliminated if pigeons experienced variable delay intervals (i.e., 0–4 s) from the start of training. They suggested that this occurred because the pigeons no longer confused the ITI with the delay interval due to their training experience with variable delay intervals. However, in contrast to their findings, robust choose-short effects have been reported in other studies following training with variable delays (i.e., 1–3 s in Grant & Kelly, 1998; 2–8 s in Spetch & Rusak, 1992a).

Because the research described earlier suggests that the response biases in memory for number are a product of the same processes as the response biases shown in memory for time, it would be anticipated that similarity of the ambient illumination condition during the ITI and the delay interval should be an important determinant of the occurrence of a choose-small effect. Indeed, Fetterman and MacEwen (1989) reported that a choose-small bias in memory for number of responses was attenuated when the houselight was off during the ITI but on during the delay. However, in this study, the samples were the number of responses required to complete a fixed ratio (FR) 10 and FR 40. Consequently, number of pecks was confounded with the time taken to complete the requirement, so the choose-small effect could actually have been a choose-short effect.

Experiment 1

The objective of the present study was to examine the effect of similarity of the ambient illumination condition during the ITI and delay with respect to the choose-small and choose-large biases obtained in tests of memory for number of light flashes in the pigeon. The pigeons in this study had previously been trained to discriminate sequences of light flashes (illumination of the feeder) that varied in number but not time (2f/4s and 8f/4s). This previous training was given with a dark ITI. In Experiment 1, one group of pigeons (Group Dark) continued to be trained with a dark ITI, while

the other group (Group Light) received training with an illuminated ITI. In the first phase of Experiment 1, the pigeons were trained with a baseline delay of 0 s and subsequently tested with dark delay intervals of 0, 5, 10, 15, and 20 s. In the second phase, the birds in both groups received baseline training with a 5-s dark delay and subsequent testing at delays longer and shorter than the 5-s baseline delay.

Method

Subjects

Twelve adult Silver King pigeons, maintained at approximately 80% of their free-feeding weight, and housed individually with constant access to water and grit, served as subjects. Postsession feedings of Purina Pigeon Chow were provided to maintain their target weights. The colony room was illuminated on a 12:12 light:dark cycle by fluorescent light turned on at 6:00 am each day. Testing was conducted 5 days a week between 9:00 am and 3:00 pm. The birds had previously been trained to discriminate sequences of light flashes that varied in number, but not in time, and in time but not in number (Santi & Hope, 2001).

Apparatus

Four Coulbourn modular operant test cages (Model #E10-10), each housed within isolation cubicles (Model #10-20), were used. Each cubicle utilized baffled air intake exhaust systems and ventilation fans. Each test cage contained three horizontally aligned, translucent plastic keys positioned approximately at a pigeon's standing sight line. Behind each key was a projector which displayed red, green, or white onto a frosted rear projection screen (Coulbourn Model #E21-18). Vertical and horizontal lines were presented as white bars with a black background. Directly below the center key there was a 5.7×5 cm opening which, during reinforcement, provided access to a hopper containing mixed grain. Within the opening was a lamp (Coulbourn Model #E14-10 with bulb #S11819X) that was illuminated only during reinforcement. Located 6.5 cm above the center key was a houselight that directed light upward to reflect light from the top of the cage (Coulbourn Model #14-10). The organization of all experimental events and recording of response choices was performed by a microcomputer system located in the same room.

Procedure

0-s DMTS number training and testing. All birds received 12 sessions of baseline training in the delayed matching-to-sample task with number samples in accordance with their previous training (Santi & Hope, 2001). Each trial commenced with a sample presentation in which the hopper light flashed on and off throughout a sequence. Each sequence began and ended with a 200-ms light flash. The remainder of the 200-ms flashes occurred at equally spaced time intervals between the beginning and ending flash. Throughout all of the experiments reported in this paper, the sample presentation always occurred in a darkened chamber (i.e., the hopper light flash was the only source of illumination during the sample presentation period). The small sample

consisted of two flashes in 4 s (2f/4s), and the large sample consisted of eight flashes in 4 s (8f/4s). For six birds, color comparisons were presented after the number samples and red was correct following the small (2f/4s) sample, while green was correct following the large (8f/4s) sample. For the remaining birds, line comparisons were presented after the number samples. Vertical was correct following the small sample, and horizontal was correct following the large sample. Different comparisons were used because the birds had previously been trained to discriminate sequences of light flashes that varied in number, but not in time (the number comparison dimension), and in time but not in number (the time comparison dimension). The comparisons in this study were those that the birds had received after number samples. For all birds, a single peck to the comparison stimuli turned them off and if correct permitted 4-s access to mixed grain from the food hopper. Incorrect responses to the comparison stimuli resulted in a 4-s blackout followed immediately by the presentation of the same sample 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 four trials, all combinations of the two sample stimuli with comparison stimuli counterbalanced on the left and right side keys occurred once. The order of presentation was randomized individually for each bird. The intertrial interval (ITI), spent in darkness, was 15 s, and each session consisted of 160 trials.

Following these 12 sessions of baseline training, the birds were assigned randomly to either Group Dark or Group Light with an equal number of color comparison and line comparison birds in each group. All parameters of training remained as described above except for the illumination condition during the ITI. Group Light received nine sessions with the houselight on during the ITI, and Group Dark received nine sessions with the ITI dark. On the ninth and final day of training, Group Dark averaged 90.2% correct on the small-sample trials and 94.2% correct on the large-sample trials. Group Light averaged 90.6% correct on the small-sample trials and 93.3% correct on the large-sample trials.

Delay testing was conducted for 15 sessions of 160 trials each. Within each session, 48 trials for each of the two samples (small and large) occurred at the 0-s baseline delay, and 8 trials for each sample occurred at each of the other delays (5, 10, 15, and 20 s). Delay intervals were spent in darkness. This distribution of delays (60% baseline delay, 40% other delays) was used so that the reference memory of number samples and their association with the comparison stimuli established during 0-s baseline delay training would remain stable during testing (Spetch & Wilkie, 1983). 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-s DMTS number training and testing. The pigeons were given five sessions of the baseline training with a 0-s delay to ensure stable performance before proceeding with 5-s DMTS number training. The training conditions during this phase were identical to those previously described except that a 5-s dark delay interval was inserted between the end of the sample stimulus and the onset of the comparison stimuli. After 39 sessions of training with a 5-s delay interval, Group Dark–Dark

(dark ITI and dark delay) averaged 84.0% correct on the small-sample trials and 82.3% correct on the large-sample trials. Group Light–Dark (light ITI and dark delay) averaged 79.0% correct on the small-sample trials and 73.8% correct on the large-sample trials. Delay testing was conducted for 15 sessions of 160 trials each. Within each session, 48 trials for each of the two samples (small and large) occurred at the 5-s baseline delay, and 8 trials for each sample occurred at each of the other delays (0, 10, 15, and 20 s). All delay intervals occurred in darkness. During delay testing, the correction procedure remained in effect only for 5-s baseline delay trials. All other parameters remained the same as those described for training.

In all the statistical analyses reported in this article, the rejection region was $p < .05$.

Results and discussion

0-s DMTS number testing

The mean percentage of correct responding during delay test sessions is shown in Fig. 1. The data for Group Dark are shown in the top of the figure and the data for Group Light in the bottom of the figure. For both groups, accuracy dropped much more on the large-sample trials than on the small-sample trials as the delay interval increased. There was a significant effect of sample type [$F(1, 10) = 18.57$], delay interval [$F(4, 40) = 381.00$], and a sample type \times delay interval interaction [$F(4, 40) = 13.45$]. At the 0-s delay, accuracy was slightly higher on the large-sample trials than on the small-sample trials [$F(1, 10) = 11.80$]. However, at all delays greater than 0 s, accuracy was much higher on small-sample trials than on large-sample trials [$F(1, 10) = 26.21, 13.40, 14.94, \text{ and } 16.47$]. The only significant effect associated with the group variable was a group \times delay interval interaction [$F(4, 40) = 3.72$]. Group Dark exhibited significantly higher accuracy than Group Light at the 5-s delay [$F(1, 10) = 7.64$], but not at any of the other delays.

These delay test data replicate those reported by Roberts et al. (1995) and Santi and Hope (2001). A clear choose-small bias occurred at all delays greater than 0 s, suggesting that the pulse counts for the large sample had deteriorated over the delay interval, causing the pulse count for the large sample to be closer to the reference memory pulse count for the small sample at a 0-s delay. This choose-small bias occurred regardless of whether the illumination condition in the ITI was the same (Group Dark) or different (Group Light) from that in the darkened delay interval.

While the finding of a significant choose-small bias for Group Light could be viewed as inconsistent with the instructional failure/confusion hypothesis, it is important to note that Group Light had considerable previous experience with dark ITIs. Consequently, the 24 sessions of combined training (9 sessions) and testing (15 sessions) with an illuminated ITI may not have been sufficient to overcome confusion between the ITI and the delay. The delay test data following 5-s delay training provided a better test of the confusion hypothesis, because in this case Group Light had a total of 68 sessions of training with an illuminated ITI (i.e., 10,880 trials) prior to delay testing. For 39 of the 68 sessions (i.e., 6240 trials) they experienced a difference in the illumination condition between the ITI and the delay prior to delay testing.

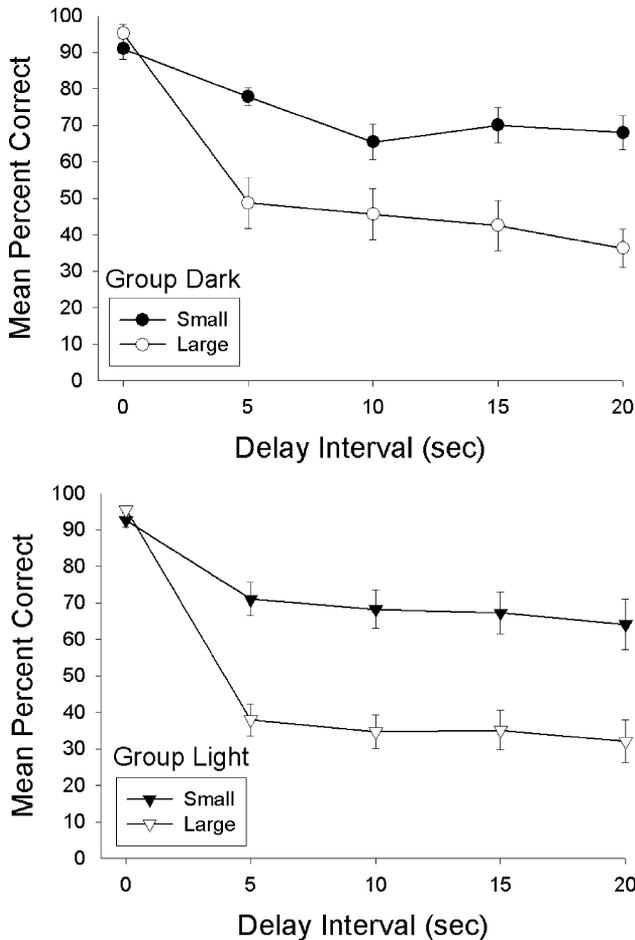


Fig. 1. The mean percentage of correct responding on small- and large-sample trials during delay test sessions following training with a 0-s delay interval. The data for Group Dark are shown in the top panel and the data for Group Light in the bottom panel. Error bars represent the standard error of the mean.

5-s DMTS number testing

The mean percentage of correct responding during delay test sessions is shown in Fig. 2. The data for Group Dark–Dark are shown in the top of the figure and the data for Group Light–Dark in the bottom of the figure. For both groups, at the baseline delay of 5 s, accuracy was equivalent on trials in which the small and the large samples were presented. At the 0-s delay, a choose-large effect was evident, whereas at delays longer than the 5-s baseline a choose-small effect occurred which appeared to be stronger for Group Light–Dark than for Group Dark–Dark. An analysis of variance of these data indicated a significant effect of delay [$F(4, 40) = 56.77$], as well as a significant sample type by delay interval interaction [$F(4, 40) = 13.01$]. Neither the main effect of group nor any of the interactions involving the group factor were

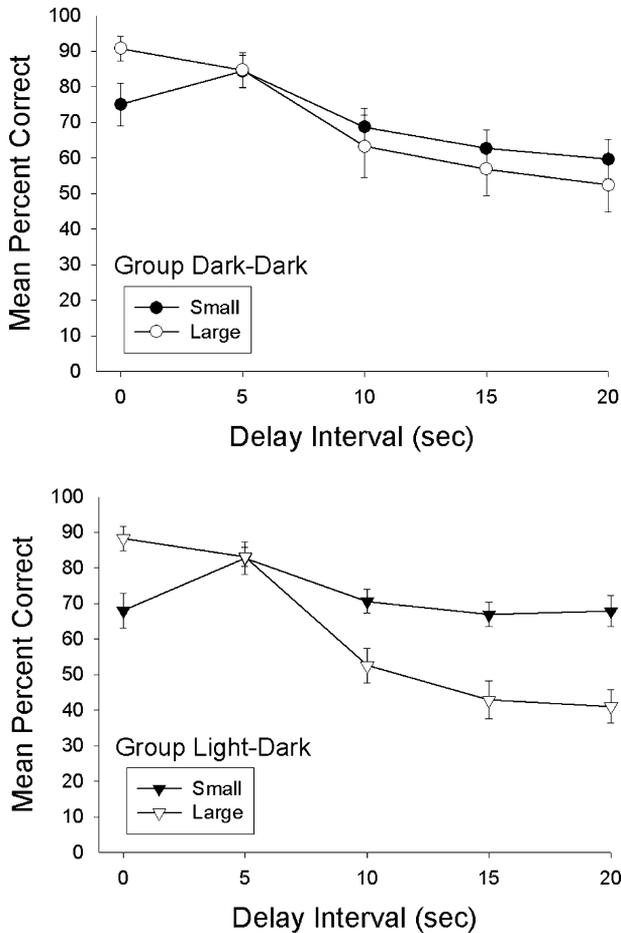


Fig. 2. The mean percentage of correct responding on small- and large-sample trials during delay test sessions following training with a 5-s dark delay interval. The data for Group Dark–Dark are shown in the top panel and the data for Group Light–Dark in the bottom panel. Error bars represent the standard error of the mean.

statistically significant. A simple main effect analysis of the sample type \times delay interval interaction indicated that, at the 5-s baseline, accuracy was equivalent on small- and large-sample trials ($F < 1$). However, at the 0-s delay, accuracy was significantly greater on trials in which the large sample had been presented than on trials in which the small sample had been presented [$F(1, 10) = 54.13$]. At delays greater than the baseline delay of 5 s, accuracy was significantly greater on trials in which the small sample had been presented than on trials in which the large sample had been presented at the 15-s [$F(1, 10) = 5.84$] and the 20-s delay [$F(1, 10) = 5.45$].

The results of delay testing from a 5-s baseline delay were consistent with those obtained following delay testing from a 0-s baseline delay. At delays longer than

baseline, there was a significant bias to respond to the comparison correct for small. In addition, at delays shorter than baseline a choose-large bias was obtained. Thus neither the choose-small nor the choose-large bias was eliminated when the illumination condition in the ITI was differentiated from that in the delay interval. This result is particularly notable in the case of 5-s baseline delay training, because all birds had considerable experience with the illumination condition that prevailed during subsequent delay testing. The present findings are inconsistent with the instructional failure/confusion hypothesis, but consistent with the analogical coding/subjective shortening hypothesis. If the choose-small effect occurs as a result of a deterioration in pulse counts over a delay interval, then the addition of a light in the ITI should have no effect on the bias, as was found here. Testing at delays shorter than baseline also showed strong biases to respond large for both groups. This is also a result predicted by the subjective shortening account.

While the present findings of asymmetrical retention functions for Group Light–Dark are inconsistent with those previously reported in some studies of memory for event duration (Dorrance et al., 2000; Sherburne et al., 1998; Spetch & Rusak, 1992b), it is unlikely that they can be attributed to a differential impact of ITI–delay similarity on temporal memory as opposed to numerical memory. Kelly and Spetch (2000) trained pigeons to match short (2 s) and long (8 s) food samples to red and green comparison stimuli at a 5-s baseline delay, and they also obtained results inconsistent with the instructional failure/confusion hypothesis. Choose-short effects occurred at extended delays both when the illumination condition in the ITI was the same as that in the delay interval and when the ITI was illuminated and the delay interval was dark. Thus, it does not appear as though results inconsistent with the confusion hypothesis are unique to numerical discriminations. It is also important to note that, while birds in Group Light–Dark of the current study had previous experience with a dark ITI, the birds in the comparable groups of the Kelly and Spetch (2000) study were experimentally naive and robust choose-short effects were observed both in Group Light–Dark and Group Dark–Dark. Therefore, even when the ITI and delay are functionally differentiated from the beginning of training, strong response biases during delay testing can be obtained. The results obtained by Kelly and Spetch in their Light–Dark group are consistent with those obtained in the present study, and they suggest that the confusion hypothesis does not provide a completely satisfactory explanation of response biases in memory for event duration or memory for number.

Experiment 2

The second experiment of this study was conducted to investigate an alternative way of disambiguating the ITI from the delay interval by introducing illumination during the 5-s baseline delay interval. The event duration memory study by Kelly and Spetch (2000) showed parallel retention functions when the ITI was dark and the delay interval was illuminated. This occurred because individual subjects exhibited different response biases in the Dark–Light condition. Some exhibited a choose-short

bias, while others exhibited a choose-long bias. Kelly and Spetch suggested that the pigeons who showed a choose-long bias may have been timing through the delay. Because previous research has suggested that numerical discriminations involve the use of an event switch rather than a time switch, it may be possible to avoid the problem of having some pigeons time the illuminated delay interval as in Kelly and Spetch (2000). If pigeons count the number of flashes by use of the event switch, it seems unlikely that they would time the illuminated delay interval and add this duration to their flash count in memory. Thus, using an illuminated delay interval in a memory for number task may allow for a clearer assessment of the effect of disambiguating the ITI from an illuminated delay than has been possible in studies of memory for event duration.

However, it is also possible that the number samples in the present study could be coded by the operation of a timing switch in stop mode. If each 200-ms flash duration was timed and the count added to a total for each sample sequence, the two number samples could be easily discriminated. If pigeons were timing the total duration of feeder illumination, then this timing behavior might generalize to the illumination of the houselight during the delay interval, and responding might be based on a pulse count reflecting both feeder-flash duration and delay interval duration. In this case, a choose-large bias would be expected when birds are first exposed to a 5-s illuminated delay interval, as well as a choose-large bias when birds are tested at delays greater than the baseline delay and a choose-small bias when they are tested at delays shorter than the baseline delay.

Method

Subjects and apparatus

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

Procedure

Following the delay testing of Experiment 1, the pigeons were returned to the constant 5-s baseline training delay condition. Once accuracy became stable, the illumination condition in the delay interval was changed from dark to light for all birds by turning on the houselight. Thus, Group Dark–Dark now became Group Dark–Light and Group Light–Dark now became Group Light–Light. Both groups received 42 sessions of training with a constant 5-s illuminated delay interval. All other parameters remained the same as those previously described. On the final day of training Group Dark–Light averaged 76.5% correct on the small-sample trials and 73.6% correct on the large-sample trials. Group Light–Light averaged 69.8% correct on the small-sample trials and 73.4% correct on the large-sample trials.

Delay testing was conducted for 15 sessions of 160 trials each. Within each session, 48 trials for each of the two samples (small and large) occurred at the 5-s baseline delay, and 8 trials for each sample occurred at each of the other delays (0, 10, 15, and 20 s). Delay intervals were illuminated by the overhead houselight. During delay testing, the correction procedure remained in effect only for 5-s baseline delay trials. All other parameters remained the same as those described for training.

Results and discussion

The mean percentage of correct responding during the last session of training with a dark 5-s delay and the first session of training with an illuminated 5-s delay is shown in Fig. 3. Turning the houselight on during the 5-s delay reduced accuracy in both groups. For Group Dark–Light, the reduction was much greater for small-sample trials than for large-sample trials. An analysis of variance of these data indicated a significant effect of sample type [$F(1, 10) = 26.64$], session [$F(1, 10) = 83.36$], sample type \times session [$F(1, 10) = 14.92$], and sample type \times session \times group [$F(1, 10) = 6.74$]. A simple main effect analysis indicated that the sample type \times session interaction was significant for Group Dark–Light [$F(1, 10) = 20.86$]. For Group Dark–Light, accuracy on small-sample and large-sample trials was equivalent on the last session of training with a dark 5-s delay [$F < 1$]. However, on the first session of training with an illuminated 5-s delay, accuracy was significantly lower on small-sample trials than on large-sample trials [$F(1, 10) = 31.66$]. While the sample type \times session interaction was not significant for Group Light–Light [$F < 1$], accuracy was significantly lower on small-sample than on large-sample trials [$F(1, 10) = 6.09$]. In addition, accuracy was significantly lower on the first session of training with an illuminated 5-s delay [$F(1, 10) = 36.22$].

The mean percentage of correct responding during delay test sessions is shown in Fig. 4. The data for Group Dark–Light are shown in the top of the figure and the data for Group Light–Light in the bottom of the figure. For both groups, at the baseline delay of 5 s, accuracy was equivalent on trials in which the small and the large samples were presented. At the 0-s delay, a choose-small effect was evident in both groups. At delays longer than the 5-s baseline a choose-large effect was clearly evident for Group Dark–Light. An analysis of variance indicated a significant effect of

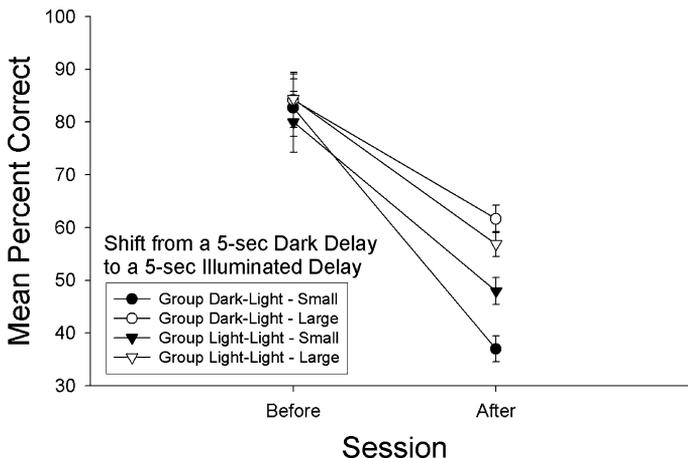


Fig. 3. The mean percentage of correct responding on small- and large-sample trials during the last session of baseline training with a 5-s dark delay interval and the first session of baseline training with a 5-s illuminated delay interval for Group Dark–Light and Group Light–Light. Error bars represent the standard error of the mean.

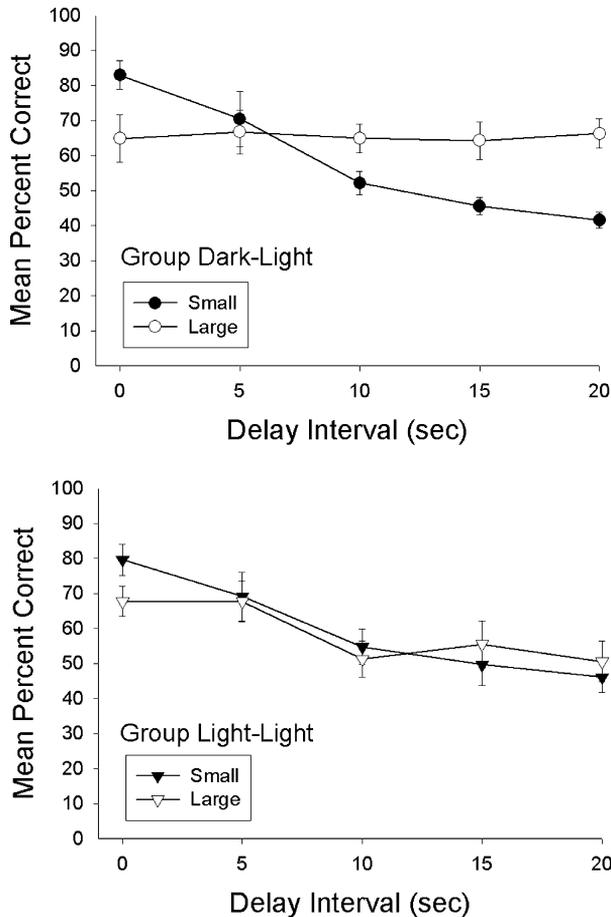


Fig. 4. The mean percentage of correct responding on small- and large-sample trials during delay test sessions following training with a 5-s light delay interval. The data for Group Dark-Light are shown in the top panel and the data for Group Light-Light in the bottom panel. Error bars represent the standard error of the mean.

delay [$F(4,40)=27.24$], as well as a significant sample type \times delay interaction [$F(4,40)=10.09$]. Neither the main effect of group nor any of the interactions involving the group factor were statistically significant. The apparent differences between the two groups at delays greater than the 5-s training delay may make it seem like there should have been an interaction involving groups. However, the data for Group Light-Light are somewhat misleading because one bird in this group showed a very large choose-small bias. Fig. 5 shows the data for birds in Group Light-Light with this outlier bird removed. It is clear from this figure that the remaining birds in Group Light-Light, like those in Group Dark-Light, displayed a choose-large bias at delays longer than the 5-s baseline. A simple main effect analysis of the sample type \times delay interaction from the overall analysis indicated that, at the 5-s baseline,

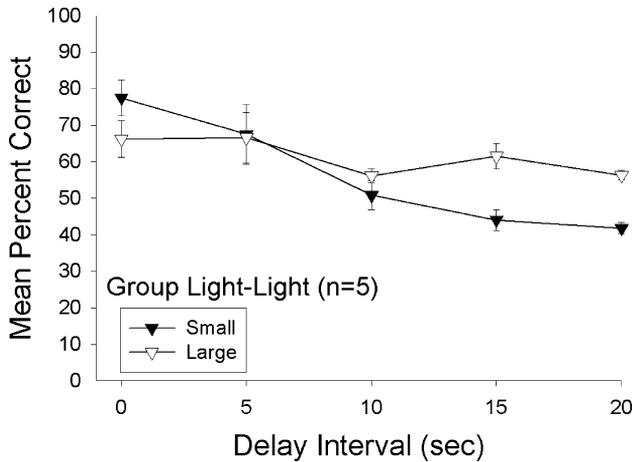


Fig. 5. The mean percentage of correct responding on small- and large-sample trials during delay test sessions for Group Light-Light with the data for one outlier bird removed. Error bars represent the standard error of the mean.

accuracy was equivalent on small- and large-sample trials ($F < 1$). However, at the 0-s delay accuracy was significantly greater on trials in which the small sample had been presented than on trials in which the large sample had been presented [$F(1, 10) = 31.85$]. At delays greater than the baseline delay of 5 s, accuracy was significantly greater on trials in which the large sample had been presented than on trials in which the small sample had been presented but only at the 20-s delay [$F(1, 10) = 5.93$].

Overall, these results suggest that the presence of the houselight during the delay interval was somehow adding to the perceived number of events which had been signaled by flashes of the hopper light. On the first session in which light was introduced during the 5-s baseline delay interval, accuracy on large-sample trials was above chance (62% for Group Dark-Light, and 57% for Group Light-Dark), while accuracy on small-sample trials was below or at chance (37% for Group Dark-Light and 48% for Group Light-Dark). During delay testing, when illuminated delays longer than the 5-s baseline were presented, a choose-large bias occurred. When illuminated delays shorter than the 5-s baseline were presented, there was a choose-small effect for both groups. These biases are the opposite of those found in Experiment 1, and they suggest that the presence of the light in the delay interval was adding pulse counts to the accumulator. This would produce a bias to respond large when the light was first introduced into the delay interval. As expected, this bias disappeared with continued training as the new pulse counts for small-sample and large-sample trials became established in reference memory. During subsequent delay testing, a shorter delay than that used in training would result in a smaller total pulse count, causing a choose-small bias, while a longer delay than that used in training would produce a larger total pulse count and, therefore, a choose-large bias would emerge.

It seems unlikely that the birds would use an event switch (and number accumulator) for the numerical samples, a run switch (and temporal accumulator) for the illuminated delay interval, and then base their response on the sum of these two

accumulator values. The more likely explanation is that birds may have discriminated the number samples on the basis of temporal features rather than number. For example, they may have cumulatively timed each flash of the hopper light during the sample presentation period and then continued to time the duration of the houselight during the delay interval. To assess this explanation, the duration of the second flash on small-sample trials was manipulated in Experiment 3.

Experiment 3

Experiment 3 was conducted to test whether the pigeons were summing the total duration of the flashes which occurred in a sequence rather than using an event counter to discriminate between the 2f/4s and 8f/4s samples. This was accomplished by presenting intermittent test trials in which the duration of the second flash on small-sample trials was either 400, 800 or 1600 ms. If birds used an event switch to discriminate 2f/4s from 8f/4s, adding time to the second event on small-sample trials would not be expected to reduce accuracy very markedly. However, if birds were timing the duration of each flash, then changing the duration of the second flash from 200 to 1600 ms on small-sample trials would result in the birds being more likely to classify the sample as large, and consequently exhibiting a significant reduction in accuracy on these trials. Results supporting a timing explanation would also have implications for previous studies of number discriminations in pigeons which used similar procedures for varying number of events while holding flash duration and the total time of a sequence constant (Roberts et al., 1995; Roberts & Mitchell, 1994; Santi & Hope, 2001).

Method

Subjects and apparatus

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

Procedure

Following the delay testing of Experiment 2, Group Dark and Group Light were given four sessions of training with a 0-s baseline delay (the group labels now only refer to illumination in the ITI because the delay interval was 0 s). All birds then received five sessions of flash duration testing. Each test session consisted of 96 regular trials (48 small-sample and 48 large-sample trials) and 24 probe trials. On probe trials, the duration of the second flash for the small-sample was either 400, 800, or 1600 ms (eight trials at each of the three probe durations). In order to maintain the total duration of the sequence of events constant at 4 s during probe trials, the gap between flashes was reduced by an amount equal to the increment in flash duration. Responses on probe trials were randomly followed by 4-s access to mixed grain with a probability of .50. The 0-s baseline delay continued during test sessions, and the correction procedure remained in effect only on regular trials. All other parameters remained the same as those described for training.

Results and discussion

The mean percentage of correct responding as a function of sample type is shown in Fig. 6. The data for Group Dark are shown in the top of the figure and the data for Group Light in the bottom of the figure. For both groups, accuracy was above 90% correct for both large-sample and small-sample regular trials. As the duration of the second flash on small-sample probe trials was increased from 200 to either 400, 800, or 1600 ms, accuracy decreased for both groups. An analysis of variance indicated that the effect of sample type was significant [$F(4, 40) = 20.77$]. There was no main effect or interaction effect involving the group variable. Bonferroni multiple comparisons tests showed that accuracy on the small-1600-ms trials was significantly lower

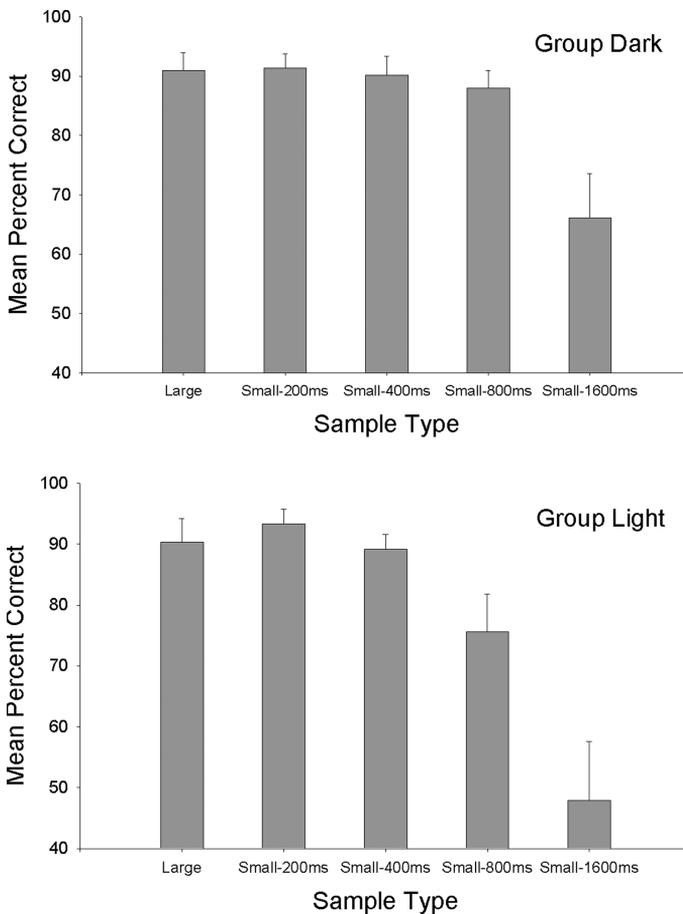


Fig. 6. The mean percentage of correct responding on regular small- and large-sample trials, as well as probe trials in which the duration of the second flash on small samples was varied (400, 800 or 1600 ms). The data for Group Dark are shown in the top panel and the data for Group Light in the bottom panel. Error bars represent the standard error of the mean.

than on the remaining small-sample trials (200, 400 or 800 ms). There were no significant pairwise differences among the small-sample trials with second flash durations between 200 and 800 ms.

When the duration of the second flash on small sample trials was equal to the total flash duration on large-sample trials (i.e., 1600 ms), accuracy fell to approximately chance levels (56.7% correct) overall. This result is consistent with the findings of Experiment 2, and it suggests that the birds may have discriminated the sequences of light flashes on the basis of temporal features rather than number.

General discussion

In Experiment 1, delay testing conducted from a 0-s baseline resulted in strong choose-small effects regardless of whether the illumination condition in the ITI was the same (Group Dark) or different (Group Light) from that in the darkened delay interval. Delay testing from a 5-s baseline delay produced results which were consistent with those obtained following delay testing from a 0-s baseline delay. At delays longer than baseline, there was a significant bias to respond to the comparison correct for small. In addition, at the delay shorter than the baseline, a choose-large bias was obtained. Thus, neither the choose-small nor the choose-large bias was eliminated when the illumination condition in the ITI was differentiated from that in the delay interval. The occurrence of the choose-large effect in Experiment 1 is a theoretically significant finding because it is predicted by the analogical coding/subjective shortening hypothesis, but it cannot be as easily explained by the instructional failure/confusion hypothesis.

Although all birds in this study had participated in a previous study in which the ITI was dark, Group Light–Dark experienced 68 sessions (i.e., 10,880 trials) with an illuminated ITI prior to the delay testing conducted from the 5-s baseline training delay in Experiment 1. In addition, for 39 of these 68 sessions (i.e., 6240 trials), Group Light–Dark experienced an illuminated ITI and a 5-s dark delay prior to the delay testing conducted in phase two. If 4640 trials of training with an illuminated ITI plus 6240 trials of training with an illuminated ITI and a dark delay are considered sufficient to eliminate any possible confusion between them, then the present findings, along with those of Kelly and Spetch (2000), are incompatible with the instructional failure/confusion hypothesis explanation of choose-short or choose-small effects. Individual birds in Group Light–Dark of the Kelly and Spetch (2000) study experienced between 816 to 3360 trials of training in Experiment 1A, and 2198–3264 trials of training with an illuminated ITI and a 5-s dark delay prior to testing at extended delays. Both Groups exhibited significant choose-short biases at extended delays. By way of comparison, Group Light in Sherburne et al. (1998) received on average a total of 2016 trials prior to delay testing in which they exhibited parallel retention functions when the delay was different from the trained ITI. Amount of prior training with an ITI condition that is distinctive from the delay condition would not seem to be a critical factor in explaining why the present study and Kelly and Spetch (2000) observed asymmetrical retention functions in Group Light–Dark, while

Sherburne et al. observed parallel retention functions. Despite the extensive amount of training given to the birds prior to testing in the current study, there may still be some doubt about the role played by their initial training under conditions in which the ITI and delay were both dark. While a definitive answer to this question would require a replication of our experiments with naive birds, it is important to note that Kelly and Spetch (2000) used naive birds in their study. They observed robust choose-short effects both in Group Light–Dark and Group Dark–Dark. Therefore, even when the ITI and delay are functionally differentiated from the beginning of training, strong response biases during delay testing can be obtained.

While the analogical coding/subjective shortening hypothesis provides a better overall account of the data from Experiment 1 than the instructional failure/confusion hypothesis, there are some aspects of the data which are puzzling. Although Group Dark–Dark exhibited a robust choose-small effect following delay testing from a 0-s baseline, the magnitude of this effect was diminished following delay testing from a 5-s baseline. Nevertheless, a choose-large effect was still clearly evident at the delay shorter than the 5-s baseline delay in Group Dark–Dark.

In Experiment 2, the birds received baseline training with a 5-s illuminated delay. Testing at shorter and longer illuminated delays produced a different pattern of response biases than those observed in Experiment 1. A choose-large bias was observed at delays longer than the baseline delay, and a choose-small bias occurred at the delay shorter than the baseline delay. The choose-large bias at extended illuminated delay intervals appeared to be larger for Group Dark–Light than for Group Light–Light. However, a choose-large bias was clearly evident in the data for five of the six birds in Group Light–Light. In addition, both groups exhibited a choose-small effect at the test delay that was shorter than the baseline training delay and the group \times sample type \times delay interval interaction was not statistically significant. These results suggest that birds in both groups were utilizing temporal properties of the event sequences rather than number as the basis for responding to comparisons.

In Experiment 3, on intermittent test trials, the duration of the second flash on small sample trials was increased and accuracy fell to approximately chance levels. This result was consistent with the findings of Experiment 2, and it provided partial support for the hypothesis that the birds coded number samples by timing and summing the duration of flashes in each sequence rather than by using an event switch to count feeder flashes. However, it is noteworthy that on small-sample trials, in which the second flash duration was increased to 1600 ms, accuracy did not fall below chance levels. If the birds had been exclusively responding on the basis of total flash duration, then one would have expected a very strong tendency to respond to the comparison correct for large samples on these probe trials. This raises the possibility that instead of responding on the basis of flash duration, the birds may have relied on the duration of the gaps between flashes. In Experiment 3, as flash duration was increased on test trials, the duration of the gap was decreased to keep the total duration of the event sequence constant at 4 s. Thus, on probe trials with a 1600 ms flash, the gap duration for small samples was reduced from 3600 to 2200 ms. The duration of individual gaps on large-sample trials was 343 ms and the sum of the gap durations

was 2401 ms. If the birds had just timed the duration of each individual gap without summing, it would be difficult to understand how a gap duration of 2200 ms on 1600 ms flash probe trials would be confused with the 343 ms gap on large-sample trials. On the other hand, if the birds had been responding on the basis of the sum of the gap durations, then just as in the case of a reliance on total flash duration, one would have expected a very strong tendency to respond to the comparison correct for large samples on 1600 ms probe trials. This would be expected because the sum of the gap durations on large-sample trials was 2401 ms and the gap duration on 1600 ms probe trials was 2200 ms.

While total flash duration and total gap duration may appear to be equally plausible alternatives based on the results of Experiment 3, it should be noted that total flash duration provides a much better discriminative cue for responding to comparisons than total gap duration. The ratio of total flash duration on large-sample trials to total flash duration on small-sample trials was 4:1. The ratio of total gap duration on small-sample trials to total gap duration on large-sample trials was approximately 1.5:1. In addition to discrimination difficulty, the assumption that total gap duration was the variable controlling responding has difficulty accounting for the results of Experiment 1. If the remembered duration of gaps decreased (due to analogical coding/subjective shortening) as the delay interval was lengthened, then there should have been a choose-large effect in Experiment 1 not a choose-small effect. However, a choose small-effect might have been expected in Experiment 1, if novel dark delay intervals were confused with gaps (due to instructional confusion/ambiguity). This seems much more plausible for delay tests which followed 0-s baseline delay training than for those which followed 5-s baseline delay training. In addition, one would expect that the illuminated delay intervals in Experiment 2 would not be confused with gaps and that parallel retention functions rather than a choose-large effect would result. While it appears more likely that birds were responding on the basis of total flash duration rather than total gap duration, it is also clear that total flash duration was not the only factor on which comparison responding was based because accuracy did not fall significantly below chance on 1600 ms probe trials in Experiment 3.

Both Roberts et al. (1995) and Santi and Hope (2001) studied memory for number of events by training pigeons to discriminate sequences of 200-ms light flashes that varied in number but not time (2f/4s and 8f/4s). Based on previous studies of the simultaneous processing of time and number in rats (Meck & Church, 1983) and in pigeons (Roberts & Mitchell, 1994), it was argued that pigeons used an event switch, which stayed closed only for a short period each time a flash occurred, in order to transmit pulse counts to a count accumulator. Meck, Church, and Gibbon (1985) estimated that the event switch closed for 200 ms after the initiation of each stimulus on the basis of rats' transfer of discrimination between continuous noise signals to segmented noise signals. Given flash durations of 200 ms in the present experiment as well as in Roberts et al. (1995) and Santi and Hope (2001), it was assumed that the number of events was the variable controlling choice. However, the finding in Experiment 2 that extended illuminated delay intervals biased pigeons to choosing the comparison stimulus correct for large samples requires a reassessment

of this assumption. In Experiment 3, increasing the duration of the second event on small-sample trials (2f/4s) increased the probability of the pigeons classifying the sample as large. These results suggest that the present experiment as well as those of Roberts et al. (1995) and Santi and Hope (2001) were not actually studies of memory for number (see Breukelaar & Dalrymple-Alford, 1998; and Fetterman, 1993; for additional concerns regarding the confound of unintended temporal cues with number).

It might be claimed that pigeons used a counting strategy in Experiment 1 and only switched to a timing strategy in Experiment 2 after the introduction of an illuminated delay interval. While it is difficult to rule out this possibility, it should be noted that on the very first day of training with an illuminated delay interval, accuracy on large-sample trials was above chance (62% for Group Dark–Light, and 57% for Group Light–Dark), while accuracy on small-sample trials was below or at chance (37% for Group Dark–Light and 48% for Group Light–Dark). If the birds had been counting up to this point and the novelty of delay interval illumination produced retroactive interference, then one would expect disruption in the retention of the numerical code, thereby resulting in random choice responding, or a bias to respond to the comparison correct for the small sample. A bias to respond to the comparison stimulus correct for the large sample suggests the operation of a timing strategy.

In summary, the present findings contribute to our understanding of asymmetrical retention for number of light flashes in three ways: (1) they replicate previous findings of asymmetrical retention for these samples at delays longer than the baseline training delay (Roberts et al., 1995; Santi & Hope, 2001) and a reversed asymmetry at delays shorter than the baseline training delay (Santi & Hope, 2001) when the delay interval is not illuminated; (2) they demonstrate that these response biases are not eliminated when the ITI is disambiguated from the delay interval by presenting ambient illumination in the ITI but not the delay interval. Hence they are consistent with the findings of Kelly and Spetch (2000) and incompatible with the instructional failure/confusion hypothesis; and (3) they suggest that pigeons discriminate a small and a large number of equally spaced light flashes each lasting 200 ms by relying on temporal properties of the flash sequence rather than by using an event switch to count flashes. Future studies of memory for number of events will clearly need to vary number independently of the temporal properties of sample sequences to be confident that working memory for an accumulation of pulse counts based on the operation of an event switch is being tested.

Acknowledgments

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