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Choose-long errors at delays shorter than the training delay persist when enhanced between-trial summation of duration memories are precluded in pigeons

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ABSTRACT

Pigeons were trained to match 2- and 10-s durations of houselight to red and green comparisons. Following acquisition with a 0-s baseline delay, they were tested with delays of 0, 10 and 20 s. There was a strong tendency to choose the short-associated comparison stimulus at both the 10- and 20-s delays (i.e., a choose-short effect) and no bias at the 0-s delay. This test was repeated after baseline training with a constant 10-s delay. As in the first delay test, a choose-short effect was obtained at the 20-s delay. In contrast to the first test, no bias was obtained at the 10-s delay and a strong tendency to choose the long-associated comparison (i.e., a choose-long effect) was obtained at the 0-s delay. Importantly, the choose-long effect was obtained under conditions which insured that the temporal spacing between a 0-s delay trial and the preceding trial was equal to that in training. These results are inconsistent with the temporal summation account of the choose-long effect and are most readily interpreted within a perspective emphasizing the subjective shortening of temporal memories over time.

Trials in the delayed matching-to-sample procedure begin with presentation of one of two or more stimuli as a sample stimulus. The sample is followed, typically after a delay interval that varies in duration across trials, by two or more comparison stimuli. Which comparison is correct (and hence pecking it is reinforced) on any particular trial depends upon which sample was presented at the beginning of the trial. Across trials, both the stimulus presented as the sample and the spatial position of the correct comparison stimulus are varied.

The symbolic or arbitrary delayed matching procedure has proven to be a particularly useful tool in the analysis of short-term retention in pigeons. Of particular relevance to the present research is the use of the symbolic matching procedure to study memory for the duration of an event. In the first such study, Spetch and Wilkie (1982) examined pigeons' memory for 2- and 10-s durations of food access and houselight illumination. Following training with a 0-s delay, pigeons were tested with delays ranging from 0 to 20 s. For both food and light samples, accuracy was greater for short samples than long 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*. The choose-short effect is a robust phenomenon and has been demonstrated in a large number of studies (e.g., Gaitan and Wixted, 2000; Grant, 2006; Grant and Kelly, 1996, 1998; Grant and Spetch, 1991, 1993, 1994; Grant and Talarico, 2004; Kraemer et al., 1985; Santi et al., 1993, 2003; Spetch and Rusak, 1989; Spetch and Wilkie, 1982, 1983; Talarico and Grant, 2006).

Spetch and Wilkie (1983) developed the subjective shortening account of the choose-short effect. The subjective shortening account is most readily conceptualized within the information processing model of timing developed by Church and associates (Church, 1978; Gibbon and Church, 1984; Roberts and Church, 1978). According to this model, an internal clock represents time as the accumulation of pulses emitted by a pacemaker. According to the subjective shortening account, the choose-short effect is produced by the shortening of this representation of time (e.g., loss of counts in working memory) during a delay interval greater than that of training. Hence, testing a pigeon immediately following termination of a long sample (i.e., at a 0-s delay) results in a high proportion of correct choices because the representation of the sample duration in working memory corresponds closely to the reference memory representation of a long sample established during training with a 0-s delay. Because the working memory representation is held to subjectively shorten, at longer delays (e.g., 10 and 20 s) the working memory representation of a long sample corresponds less closely to the reference memory representation of a long sample, and corresponds more closely to the reference

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memory representation of a short sample, thereby leading to an increased tendency to choose the short-associated comparison as delay increases.

Spetch (1987) noted that the process of subjective shortening should result in an error pattern opposite to the choose-short effect, a *choose-long effect*, when pigeons are tested at delays shorter than the delay used in training. Specifically, training at a fixed nonzero delay should result in foreshortened representations of event duration being associated with particular comparison responses in reference memory. Choose-long errors would predominate at delays shorter than that employed in training because the durations represented in working memory would not have sufficiently foreshortened, and therefore would be subjectively longer than the durations represented and associated with particular comparison responses in reference memory. To test this prediction, Spetch trained pigeons with 2- and 8-s presentations of food as the sample and a constant 10-s delay. When tested at shorter delays of 0- and 5-s, a choose-long effect was obtained, a result replicated by Spetch and Rusak (1989).

Zentall and his associates (Dorrance et al., 2000; Sherburne et al., 1998; Zentall, 2005) have proposed an alternative interpretation of choose-short and choose-long effects. According to this view, the choose-short effect arises when pigeons are unable to discriminate between a delay interval and the intertrial interval and, therefore, treat the delay as an intertrial interval. Because the comparisons have never been presented at the end of an intertrial interval, the animal responds as if no sample had been presented. Because no sample is judged to be more similar to a short sample than to a long sample, pigeons tend to choose the short-associated comparison following a delay.

To account for the choose-long effect, Zentall (2005) argued that the effects of the sample on the preceding trial or trials combine with the effects of the sample on the current trial, a notion proposed by Spetch and Rusak (1989) in their temporal summation hypothesis. This account anticipates that reducing either the duration of the ITI or the delay, relative to that on training trials, would increase the effects of prior trials and hence make the working memory representation of both samples be longer than on training trials, leading to choose-long errors. Hence, this temporal summation account can explain the choose-long effects reported by Spetch (1987) and Spetch and Rusak (1989) when pigeons were tested with delays shorter than the training delay. Temporal summation from prior trials would also explain choose-long and choose-short effects reported by Spetch and Rusak (1989) when ITI was manipulated in testing. In particular, pigeons were trained with a fixed ITI of 45 s separating all trials within a session. During testing, the ITI was manipulated within session and was either shorter (i.e., 5 and 15 s), longer (i.e., 75 and 90 s), or the same (i.e., 45 s) as in training. Choose-long errors predominated when the preceding ITI was shorter than the training ITI whereas choose-short errors predominated when the preceding ITI was longer than the training ITI (see also Spetch and Rusak, 1992, Experiment 2). Spetch and Rusak (1989) suggested that these results might reflect different amounts of between-trial temporal summation at different ITI lengths. According to this account, choose-long errors with shorter ITIs (i.e., 5 and 15 s) reflect enhanced between-trial temporal summation relative to that on baseline trials with a 45-s ITI. Choose-short errors with longer ITIs (i.e., 75 and 90 s) reflect less between-trial temporal summation relative to that on baseline trials with a 45-s ITI.

The purpose of the present experiment was to test the temporal summation account of the choose-long effect obtained when pigeons are tested with delays shorter than the delay used in training. This was accomplished by training pigeons with 2- and 10-s durations of houselight mapped to color comparisons. After training with a constant 10-s delay and a constant 60-s ITI, pigeons were tested with delays of 0, 10, and 20 s. During control sessions, the ITI preceding each trial was 60 s, as was the case during training. Experimental sessions were identical except that 10 s was added to each ITI that preceded a 0-s delay trial (i.e., 70-s ITI). The temporal separation between comparison presentation on a 0-s delay trial preceded by a 70-s ITI and the sample presentation on the preceding trial was exactly the same as that between a 10-s delay trial preceded by a 60-s ITI in training and testing. Given the common assumption that temporal memories decay or loose strength passively over time (e.g., Cabeza de Vaca et al., 1994; Grant et al., 1997; Zentall, 2005), the strength of memory from the prior trial or trials should be the same at the time of testing on trials with a 70-s ITI and 0-s delay as on trials with a 60-s ITI and a 10-s delay. Hence, the temporal summation account anticipates that performance at the 0- and 10-s delays should be identical in experimental sessions and, therefore, that no choose-long effect at the 0-s delay would be anticipated. To the extent that between-trial temporal summation plays a role in, but is not the sole cause of, the choose-long effect at shorter delays, the choose-long effect would be stronger in control than in experimental sessions.

1. Methods

1.1. Subjects

The subjects were six experimentally naïve homing pigeons obtained from Vandermere Farms (Edmonton, Alberta). The birds were between 6 and 12 months of age on arrival and were reduced to and maintained at 80% of their free-feeding weight. They were housed individually in wire mesh cages between sessions and were provided with unlimited amounts of water and grit in the home cage. The colony room in which the birds were housed was maintained on an alternating 12-h light-dark cycle, in which light onset was at 6 a.m.

1.2. Apparatus

Training and testing was conducted in six identical operant chambers, each measuring 29.0 × 29.0 × 24.0 cm (height × length × width). In each chamber, a horizontal alignment of three circular pecking keys (each 2.5 cm in diameter, and with side keys separated edge-to-edge from the center key by 3.0 cm) 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 red and green colors. A 5.5-cm high × 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-V lamp, recessed within the magazine opening, was activated when the food magazine was raised. A 28-V houselight was attached to the center of the panel and was 31.0 cm above the floor, a shield on the houselight directed light toward the ceiling of the chamber. Each chamber was enclosed in a sound- and light-attenuating booth. Within each booth, an exhaust fan provided ventilation and, supplemented by 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 activation of key lights and the houselight and magazine light. Experimental events were controlled from, and responses were recorded by, a microcomputer located in an adjoining room. Experimental sessions were conducted 6 days per week, and began at approximately the same time each day.