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Differential effects of empty and filled intervals on duration estimation by pigeons: Tests of an attention-sharing explanation

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Abstract

Pigeons were trained in a within-subjects design to discriminate durations of an empty interval and a filled interval. Even when different stimuli were used to mark empty intervals and to signal filled intervals, pigeons judged empty intervals to be longer than equal-length filled intervals. This timing difference was not a result of pigeons timing marker duration on empty interval trials. Increasing marker duration did not produce an overestimation of the empty time intervals. It was suggested that this timing difference could be due to a reduction in attention to temporal processing on filled interval trials when visual stimuli are used. Consistent with this hypothesis, it was found that empty intervals were judged longer than filled intervals when testing occurred in a darkened test room, but not when the test room was illuminated. In addition, no timing difference was observed when different auditory stimuli were used as markers for empty intervals and as signals for filled intervals.
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Keywords: Time perception; Attention-sharing; Pigeons; Temporal bisection; Internal clock; Psychometric function; Time discrimination

1. Introduction

The ability of animals to perceive and remember time has often been investigated with a temporal bisection procedure. In this procedure, animals are initially trained to correctly choose between two responses ("short" or "long") following one of two training durations. When accuracy is sufficiently high, intermediate durations are introduced, but responses on these trials are not reinforced. A psychophysical function is generated from this procedure and the point of subjective equality (PSE) is determined. The PSE is the value on the time dimension at which the animal displays indifference between choosing either the "short" or the "long" response. Studies with animals (Church and Deluty, 1977; Gibbon, 1986) and humans (Allan, 1992) have reliably found that the PSE is at the geometric mean of the two training durations.

Several interpretive frameworks have been developed to explain the results of animal studies on the perception and memory of time intervals. These include scalar timing theory (Church, 2006; Gibbon et al., 1984), the behavioral theory of timing (Killeen and Fetterman, 1988), the learning to time model (Machado, 1997), multiple time scale theory (Staddon and Higa, 1999), neural network models (Church and Broadbent, 1990; Dragoi et al., 2003), and spectral timing theory (Grossberg and Schmajuk, 1989). Scalar timing theory, the most dominant theory of interval timing, has been used to explain the results of both human and animal timing experiments (Allan, 1992, 1998; Allan and Gibbon, 1991; Ferrara et al., 1997; Penney et al., 2000; Wearden, 1991). This mathematical theory has been articulated as an information processing model of interval timing with a clock, a memory, and a decision stage (Church, 2006; Gibbon and Church, 1984; Gibbon et al., 1984). The clock stage consists of a pacemaker, switch, and accumulator. The pacemaker emits pulses that are gated into the accumulator when the switch is closed. The switch is controlled by attention and closes when attention is directed to a stimulus or event to be timed. Training in a temporal bisection task results in reference memory consisting of two distributions corresponding to the remembered values of either the short or the long signal duration from trials in which the correct response was made and reinforced. On each trial, after a stimulus has been timed, one value from the short reference memory distribution and another from the long reference memory distribution are sent to the comparator (decision stage). The comparator computes ratios based on the current value in the accumulator and the two values retrieved from reference memory. Response choice is determined by the similarity of the

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value in the accumulator to the short or the long value retrieved from reference memory. If the response choice is correct (reinforced), the value in the accumulator is stored in the appropriate distribution in reference memory.

Previous research has demonstrated that an animal's temporal judgments are affected by nontemporal stimulus factors (Buhusi and Meck, 2000, 2006a; Buhusi et al., 2002; Fetterman, 1996; Stubbs et al., 1984). For example, temporal discrimination accuracy in animals is affected by stimulus modality (Meck, 1984; Roberts et al., 1989; Stubbs et al., 1984), stimulus intensity (Kraemer et al., 1995; Wilkie, 1987), and duration of food access versus light duration (Spetch and Wilkie, 1982). Rats time auditory signals more accurately than visual signals (Meck, 1984), whereas the reverse is found for pigeons (Roberts et al., 1989). Rats also appear to judge visual signals as being shorter than auditory signals of the same duration (Meck, 1991).

Santi et al. (2005) recently demonstrated that rats judged filled intervals to be longer than empty intervals of equal length. This occurred even when the ambient houselight condition and the duration of the intertrial interval (ITI) were clearly differentiated from those of the empty interval. Thus, it was unlikely that the difference in timing of filled and empty intervals could be attributed to rats resetting their clock during a long empty interval due to the similarity of ambient conditions during the ITI and empty intervals (Kaiser et al., 2002; Zentall, 1997, 2005). The psychophysical functions, the PSE, and the difference limen (DL) indicated that filled intervals were timed more precisely and they were perceived as longer than empty intervals of the same duration. The psychophysical functions superimposed across anchor duration sets for filled intervals and for empty intervals, but the filled interval and empty interval functions did not superimpose. These results were the first clear evidence of a filled interval illusion in rats, and they suggested that this difference may reflect a clock rate effect (greater for filled intervals) rather than a switch latency effect (slower for empty intervals).

Initial studies of duration estimation with empty and filled intervals in pigeons appeared to be consistent with the effects reported in rats. For example, Mantanus (1981) reported that pigeons' temporal discriminations were more accurate with filled intervals than with empty intervals. Kraemer et al. (1997) corrected for a number of design and general test procedure problems present in the Mantanus study, and they reported that pigeons judged the duration of a filled interval to be longer than an empty interval of equivalent physical duration. This result was consistent with the finding of Mantanus because, at the intermediate and at the longest stimulus duration, the filled interval resulted in a higher percentage of long responses than the empty interval. Thus, accuracy at the long stimulus duration was higher for filled intervals than for empty intervals. However, as noted by Miki and Santi (2005), the Kraemer et al. finding is somewhat surprising in that it was based on a between-subjects comparison. Penney et al. (2000) have argued that the internal clock model of timing assumes that the detection of a timing difference requires that the accumulator values for the different signal properties be stored within a single reference memory distribution representing the short values for the two signal

properties and within a single reference memory distribution representing long values for the two signal properties. This mixing of signal properties within the short and the long reference memory distributions would presumably only be possible if the two different types of signals were timed within the same session. Although the signal properties that they specifically considered involved different stimulus modalities (auditory and visual), similar theoretical mechanisms would be expected to underlie timing differences based on other nontemporal signal characteristics, such as whether the interval is filled or empty.

Miki and Santi (2005) trained pigeons in a within-subjects design to discriminate durations of a filled interval (2 and 8 s of light), and durations of an empty interval (2 and 8 s bound by two 500 ms light markers). Filled intervals required a response to one set of colored comparisons, whereas empty intervals required a response to a different set of colored comparisons. Psychophysical testing indicated that empty intervals were judged to be longer than equivalent durations of a filled interval. This finding was replicated when the anchor durations used during training were changed to 1 and 4, or 4 and 16 s. Most importantly, the difference between the PSE for the empty intervals and the PSE for filled intervals increased as the magnitude of the anchor-duration pairs increased. In addition, the DLs for empty intervals were smaller than those for filled intervals, and they also increased as the magnitude of anchor-duration pairs increased. An analysis of the Weber fractions (DL/PSE) provided evidence for superimposition of the empty and filled timing functions across the different sets of anchor durations. These results suggest that the accumulation of subjective time was greater for empty intervals than for filled intervals. This difference in timing appeared to be the result of a clock rate difference rather than a switch latency difference.

Previous experiments in humans (Block and Zakay, 1997; Zakay and Block, 1996, 1997), and in animals (Buhusi and Meck, 2006a,b,c; Lejeune et al., 1999; Sutton and Roberts, 2002) have shown that time intervals are underestimated if subjects engage in nontemporal information processing while timing. This result has been interpreted in terms of attentional resources being diverted away from timing. For example, Sutton and Roberts (2002) noted that an animal may need to divide its attention between processing temporal properties of the stimulus and processing other, nontemporal features of the stimulus or environment. Using this attention-sharing concept, Miki and Santi (2005) proposed that the timing difference between empty and filled intervals could arise if pigeons devoted less attention to temporal processing during filled intervals than during empty intervals. Less attention to processing time on filled interval trials could occur if other stimuli present in the chamber drew attention away from temporal processing. Consequently, it may be that empty intervals of darkness allowed pigeons to focus attention on timing signal duration with no competition from nontemporal (visual) features in the chamber. Filled intervals of light, on the other hand, might have allowed for visual features in the chamber (such as the opening to the food hopper, scattered pieces of grain below the grid floor of the chamber, etc.) to attract attention, thereby reducing attention to processing the temporal properties of the signal. This could have resulted in an underestimation of filled intervals relative to empty intervals.