

Pigeons' timing of an arbitrary and a naturalistic auditory stimulus: tone versus cooing

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Abstract

Previous animal research has traditionally used arbitrary stimuli to investigate timing in a temporal bisection procedure. The current study compared the timing of the duration of an arbitrary, auditory stimulus (a 500-Hz tone) to the timing of the duration of a naturalistic, auditory stimulus (a pigeon cooing). In the first phase of this study, temporal perception was assessed by comparing psychophysical functions for the duration of tone and cooing signals. In the first set of tests, the point of subjective equality (PSE) was significantly lower for the tone than for the cooing stimulus, indicating that tones were judged longer than equivalent durations of cooing. In the second set of tests, gaps were introduced in the tone signal to match those present in the cooing signal, and no significant difference in the PSE for the tone or the cooing signal was found. A repetition of the testing conducted with gaps removed from the tone signal, failed to replicate the difference in the PSEs for the tone and cooing signals originally obtained. In the second phase of the study, memory for the duration of tone and cooing was examined, and a choose-long bias was found for both signals. Based on these results, it appears that, for pigeons, there may be no significant differences in either temporal perception or temporal memory for arbitrary, auditory signals and more complex, naturalistic, auditory signals. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Research on the perception of time in humans has demonstrated that an important role is played by stimulus factors (Goldstone and Lhamon, 1974; Allan, 1979; Poynter, 1989; Block, 1990; Grondin, 1993; Penney et al., 1998; Wearden et al., 1998). For example, when humans time both

visual and auditory durations in the same session, auditory signals are perceived as longer than equal durations of visual signals. Stimulus factors may be equally important in animals' temporal judgements (Stubbs et al., 1984; Fetterman, 1996). For example, past research indicates that either the accuracy of temporal discriminations or temporal perception itself is affected by stimulus properties. Pigeons are more accurate at discriminating between a short and long visual signal than a short and long auditory signal (Roberts et al.,

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1989), whereas rats are better able to discriminate between durations of auditory signals than visual signals (Meck, 1984). In addition, rats appear to perceive an auditory signal as longer than the same duration of a visual signal (Meck, 1991). Both pigeons and rats, perceive an intense signal to be longer than the same duration of a less intense signal (Wilkie, 1987; Kraemer et al., 1995). Finally, there is some evidence suggesting that pigeons perceive a filled interval to be longer than the same duration of an empty interval (Man-tanus, 1981; Kraemer et al., 1997).

A temporal bisection procedure has been used often in research that investigates animals' ability to perceive and remember time. Animals are initially trained to correctly choose between two responses ("short" or "long") following one of two anchor durations. When accuracy is sufficiently high, intermediate durations are introduced, but responses on these trials are never reinforced. A psychophysical function can be generated from this procedure and the point of subjective equality (PSE) can be calculated. The PSE is the value on the time dimension where the subject displays indifference between a short and a long response. At this point, the probability of responding long or short is 50%. Studies with humans (Allan, 1992) and animals (Church and Deluty, 1977; Gibbon, 1986) have reliably found that the PSE is at the geometric mean of the two anchor durations.

Church (1984) proposed an internal clock model that describes how animals perceive and remember durations and make a response decision based on previously reinforced durations. This timing model is composed of three stages: a clock, a memory, and a decision stage. The clock stage consists of a pacemaker, switch, and accumulator. The pacemaker generates pulses that are gated into the accumulator when the switch is closed. The switch closes when attention is allocated to a stimulus or event to be timed. Reference memory consists of two distributions of values (short and long) that have been previously reinforced. The values in these distributions vary as a result of the dynamic rate of the pacemaker (Gibbon and Church, 1984). Two values, one from the short distribution and another from the

long distribution in reference memory, are sent to a comparator. The comparator in the decision stage computes two ratios based on the value in the accumulator and the two values retrieved from reference memory. The ratios determine which response choice will be made. If the response is reinforced, the value in the accumulator is stored in the appropriate distribution in reference memory (memory stage).

Although the function that best characterizes the psychological representation of time has been subject to debate (Staddon and Higa, 1999), the popular view of interval timing postulates that time is accumulated in a linear fashion and ratios are computed to determine the operant choice response (Church and Gibbon, 1982). Given the assumptions of a linear accumulation of time and a ratio comparison process, the internal clock model can account for the finding that the PSE is at the geometric mean of the two anchor durations in a temporal bisection procedure.

A delay interval can be introduced in a temporal bisection procedure to examine memory for visual event durations. In this case, the procedure could be referred to as a delayed matching-to-sample task, and the typical finding for pigeons is a choose-short effect (Spetch and Wilkie, 1982, 1983; Spetch, 1987; Spetch and Rusak, 1989, 1992). That is, when variable-length delay intervals are presented, pigeons show an increasing tendency to peck the comparison stimulus corresponding to the short-duration sample. However, the modality of the event being timed also appears to play a role in the assessment of memory for event duration. Santi et al. (1998) trained pigeons to match short and long durations of light to one set of color comparisons and the same durations of tone to a different set of color comparisons. During delay testing, choose-short errors occurred following light durations, but choose-long errors occurred following tone durations. When the birds were tested with trials in which the tone signal was omitted but with additional time added to the intertrial interval, accuracy dropped indicating that the birds were attending to the tone and not simply timing from the end of one trial to the presentation of comparison stimuli on the next trial. Thus the "choose-long" bias obtained

when memory for tone duration was tested cannot be simply accounted for by the idea that the birds had learned to respond on the basis of time since the end of the previous trial. Santi et al. (1998) suggested that the difference in response biases observed during delay testing for tone and light was probably due to the nature of the stimulus which controls the termination of timing. For a light signal, the offset of the light itself appears to terminate timing. Whereas for a tone signal, the onset of the comparisons in a dark chamber may overshadow the offset of the tone and control the termination of timing.

Most experiments examining timing or memory for time in animals have involved simple unchanging stimuli (e.g., a light or a tone). As noted by Fetterman (1996), these stimuli lack ecological validity because they do not contain the temporal structure that is characteristic of stimuli in the natural environment where stimulus change may serve as an index of the passage of time.

The purpose of the present study was to compare temporal perception and temporal memory for a simple unchanging 500-Hz tone and a more complex auditory stimulus of a pigeon cooing. In the first phase of this study, temporal perception was assessed by comparing psychophysical functions for the duration of tone and cooing signals. In the second phase, memory for the duration of these events was examined.

2. Materials and methods

2.1. Species

Six White Carneaux pigeons, maintained at approximately 80% of their ad lib weights and housed individually with constant access to grit and water, served as subjects. The colony room was illuminated on a 12:12 h light:dark cycle by fluorescent lights. All of the birds had prior experience with timing visual signals and a 1325 Hz tone.

2.2. Apparatus

Three touch screen testing stations located in individual test rooms were used. Each test station consisted of a clear Plexiglas cage (30 cm wide \times 40 cm deep \times 36 cm high) with a large opening cut into the one end wall which was constructed of stainless steel. On both the left and the right side walls adjacent to the stainless steel wall, there were 5.7 \times 5 cm openings that provided access to a hopper filled with mixed grain (Coulbourn Model E14-10). A color SuperVGA monitor (Mitsubishi #SD4311C) with an attached touch frame (Carrol Touch Inc., Frame 8100-9583-01, Card 8200-3224-01) was placed against the opening in the stainless steel wall. The auditory events were generated by or played through a SoundBlaster 16-OEM audiocard with stereo speakers located at the left and the right side walls, next to a hopper that provided access to mixed grain. The cooing signals were produced by editing a wave sound file of a pigeon cooing. The original wave file was 2.94 s in length. The intensity of the auditory events was \approx 80 dB in all three rooms. An IBM-compatible microcomputer, located in the same room, controlled stimulus displays, recorded peck locations, and operated feeders.

2.3. Procedure

Because of their previous experience, no preliminary training was required. All six birds were given training sessions in which each trial began with the presentation of one of four different sample stimuli. On half of the trials, the signal consisted of the presentation of a 500-Hz tone for either 2 or 8 s. On the remaining trials, the signal consisted of the presentation of a pigeon cooing for either 2 or 8 s. After the termination of the tone or cooing signal, two color comparison stimuli (red and green) were immediately presented. The comparison colors were presented in two rectangular response areas, each measuring approximately 3.4 cm \times 3.2 cm (width \times height), one on the left and one on the right side of the monitor (\approx 15.6 cm apart, as measured from their inside edges). Position of the color comparison stimuli was counterbalanced over trials. For three

birds, red was correct following 2 s signals, and green was correct following 8 s signals. For the remaining birds, the relationship between the signal duration and the correct comparison stimulus was reversed. A single response to one of the comparison stimuli turned them off and if correct provided 4 s access to mixed grain randomly presented at either the left or the right hopper opening with a probability of 0.5. Incorrect responses to the comparison stimuli produced a 4 s blackout, followed immediately by re-presentation of the signal 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. When necessary, supplementary feedings of Purina Pigeon Chow occurred after the experimental sessions and on days when the birds were not run. Within each block of eight trials, all combinations of the four sample stimuli (two signal types \times two signal durations) and the two comparison stimulus configurations occurred once. The order of presentation was randomized individually for each bird. All birds received 160 trials per session. The duration of the intertrial interval randomly varied within sessions (4, 8, 16, or 32 s). Training continued until accuracy was at least 85% on both tone and cooing trials for all birds.

In Phase 1, three sets of psychophysical test sessions were administered. The first set consisted of 15 test sessions. Each of the four training signals (2 s or 8 s of tone, and 2 s or 8 s of cooing) was presented with a probability of 0.125 on each trial. On the remaining trials, one of ten intermediate signals (2.6, 3.2, 4.0, 5.0, and 6.4 s of tone or cooing) was presented with equal probability (0.05). The pigeons were still reinforced for responding correctly to comparisons that immediately followed the four training signals, but responses following intermediate signals were never reinforced. Each test session consisted of 160 trials (80 tone trials and 80 cooing trials).

In the second set of psychophysical test sessions, a change was made to the tone signals because the cooing stimulus used in this study contained natural pauses. Instead of a continuous

tone, gaps (no tone) were introduced to mimic the occurrence of natural pauses in the cooing signal. After each bout of cooing, a pause of 500 ms occurred where no vocalization could be heard. Previous timing studies with pigeons and black-capped chickadees have indicated that the internal clock is partially reset when a gap is encountered (Roberts et al., 1989; Cabeza de Vaca et al., 1994; Brodbeck et al., 1998). Although the gaps in these studies were substantially greater than 500 ms, it is possible that the brief pauses in the cooing stimulus may play a role in timing. Therefore, a single gap of 500 ms was inserted after 2.5 s of tone in the 3.2, 4.0, and 5.0 s tone signal (e.g., 2.5 s tone + 0.5 s gap + 0.2 s tone for the 3.2 s signal). For the 6.4 and 8.0 s tone signal, two gaps of 500 ms were inserted, one after 2.5 s of tone and another after 5.5 s (e.g., 2.5 s tone + 0.5 s gap + 2.5 s tone + 0.5 s gap + 0.4 s tone for the 6.4 s signal). Except for the introduction of gaps in the tone signals, the second set of 20 psychophysical test sessions was conducted as previously described. The third set of psychophysical test sessions was conducted for 15 sessions with the continuous tone signals restored as described for first set of tests.

In Phase 2 of the experiment, memory for durations signaled by a tone (without gaps) or by cooing was studied. Unlike the procedures described previously, Phase 2 introduced probe trials with a delay between offset of the auditory signals and the onset of comparison stimuli. Fifteen delay testing sessions were conducted and each session consisted of 144 trials. Twenty-four trials for each of the four training signals occurred at the 0 s delay and four trials for each signal occurred at each of the other delays (1, 3, and 9 s). This distribution of delays was used so that the reference memory of durations and their associations with the comparison stimuli established during 0 s delay training would remain relatively stable during testing (Spetch and Wilkie, 1983). There was no illumination in the test chamber during the delay intervals. The correction procedure remained in effect on 0 s delay trials, but not on trials with delays of 1, 3, or 9 s. All other parameters were the same as those described previously.

3. Results

The mean percentage of long responses as a function of signal duration for tone and for cooing averaged across the first set of 15 test sessions are presented in Fig. 1. For both tone and cooing, the percentage of long responses increased as a function of signal duration. The PSE was estimated from the psychophysical function for each pigeon by conducting linear regressions of the proportion of long responses for each set of three adjacent points in the two functions (tone and cooing). For each pigeon, the regression equation with the greatest slope for each function was used to estimate the PSE by calculating the signal duration associated with 50% of the long responses. These regression equations were also used to calculate the difference limen (DL), which represents the average difference between the signal duration associated with 75% long responses and the signal duration associated with 25% long responses. Finally, the Weber fraction (WF) was calculated as the DL/PSE. Overall, the mean PSE for tone (3.51) was significantly lower than the mean PSE for cooing (3.91), $t(5) = 5.56$, $P < 0.01$. This indicates that pigeons judged a given duration of tone to be longer than an equal-length interval of cooing when both were presented within the same session. Neither the DLs (0.94 for

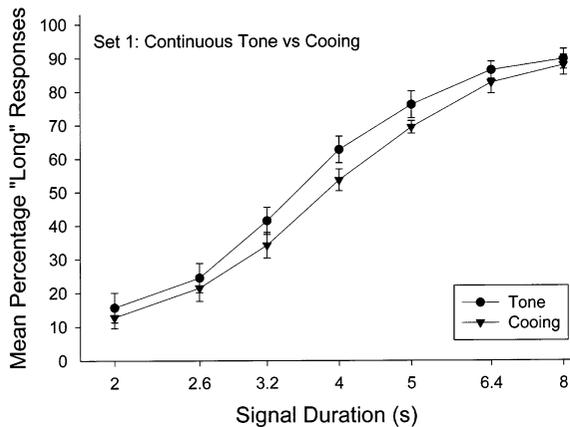


Fig. 1. The mean percentage of long responses as a function of signal type (continuous tone or cooing) and signal duration during the first set of psychophysical test sessions. Error bars represent standard error of the mean.

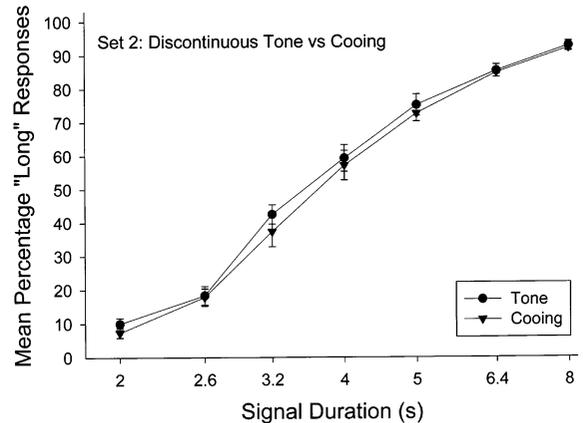


Fig. 2. The mean percentage of long responses as a function of signal type (discontinuous tone or cooing) and signal duration during the second set of psychophysical test sessions. Error bars represent the standard error of the mean.

tone and 1.01 for cooing) nor the WFs (0.26 for tone and 0.27 for cooing) differed significantly, both $t_s < 1.0$. The DL and WF analyses indicated that the pigeons were equally sensitive to the passage of time for the tone and cooing signals.

One possible explanation for the difference in PSEs for the continuous tone signal and the cooing signal was that the cooing signal contained natural pauses. That is, after each bout of cooing (≈ 2.5 s), a pause of ≈ 500 ms occurred where no vocalization could be heard. These brief pauses may have caused counts from the accumulator to be lost during the presentation of the cooing signal. Consequently, the same physical duration of a cooing signal might be experienced as psychologically shorter than the continuous tone signal. If this explanation is correct, then introducing similar length pauses at comparable locations in the tone signal should eliminate the difference in the PSEs. The mean percentage of long responses as a function of signal duration for the discontinuous tone and for cooing averaged across the second set of 20 test sessions is presented in Fig. 2. Unlike the previous test, the psychophysical functions for tone and cooing were very similar. The PSEs for tone (3.61) and for cooing (3.68) were not significantly different, $t(5) = 1.53$, $P = 0.19$. This indicates that the pigeons timed the tone (with gaps) and cooing stimuli similarly.

Neither the DLs (0.85 for tone and 0.85 for cooing) nor the WFs (0.23 for tone and 0.23 for cooing) differed significantly, both $t_s < 1.0$.

The results from the second set of psychophysical test sessions, indicate that the timing difference in the first test may have been due to the presence of pauses in the cooing signal. However, it is also possible that the original timing difference was an unreliable finding and there may be no fundamental differences in the perception of temporal intervals signaled by a simple tone and a more complex auditory stimulus of a pigeon cooing. To determine whether the timing difference was reliable, a third set of psychophysical tests with continuous tone signals was repeated exactly as in the first set.

The mean percentage of long responses as a function of signal duration for the continuous tone and for cooing averaged across the third set of 15 test sessions is presented in Fig. 3. The psychophysical functions for tone and cooing were identical. There was no statistically significant difference in the PSEs for the tone (3.50) and cooing (3.36) signals, $t(5) = -1.40$, $P = 0.22$. Neither the DLs (0.80 for tone and 0.79 for cooing) nor the WFs (0.23 for tone and 0.22 for cooing) differed significantly, both $t_s < 1.0$. Therefore, the pigeons were equally sensitive to timing tone and cooing signals.

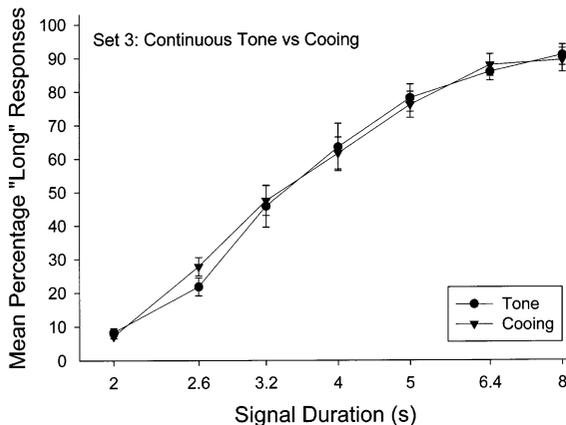


Fig. 3. The mean percentage of long responses as a function of signal type (continuous tone or cooing) and signal duration during the third set of psychophysical test sessions. Error bars represent the standard error of the mean.

An analysis of the data across the three sets of tests was conducted separately for tone and cooing signals. There was no statistically significant difference in the PSE for tone across the three sets of tests $F(2,15) < 1$. This indicates that introducing 500 ms gaps into the tone signals during the second set of tests had no effect on the perceived duration of the tone signals. However, there was a significant difference in the PSE for cooing signals between the first set of tests (3.91) and the third set (3.36), $F(1,10) = 7.63$, $P = 0.02$. In the third set of tests, the PSE for the tone (3.50) and cooing (3.36) functions were compared with the geometric mean (4.0) and the harmonic mean (3.2). One-way single sample t -tests revealed that the PSE for both tone and for cooing differed significantly from the geometric mean ($t(5) = -3.94$ and -2.35 , $P < 0.05$) but not from the harmonic mean ($t's(5) < 1.39$). Overall, the psychophysical test results suggest that there are no reliable differences in the way pigeons' perceive temporal intervals signaled by a simple unchanging tone and a more complex auditory stimulus.

Phase 2 of this study examined memory for temporal intervals signaled by tone or cooing. The mean percentage of correct responding during delay testing for both tone and cooing signals is shown in Fig. 4. The memory functions for signal duration were highly similar for the tone and cooing signals. For both signals, accuracy following the 8 s signal remained high as the delay interval increased, whereas accuracy following the 2 s signals declined as the delay interval increased. An analysis of variance (ANOVA) conducted on the tone data revealed a main effect of signal duration, $F(1,5) = 14.01$, $P < 0.05$, a main effect of delay, $F(3,15) = 40.93$, $P < 0.001$, and a significant interaction, $F(3,15) = 16.56$, $P < 0.001$. Another ANOVA performed on the cooing data revealed a main effect for signal duration, $F(1,5) = 12.53$, $P < 0.05$, a main effect of delay, $F(3,15) = 35.46$, $P < 0.001$, and a significant interaction, $F(3,15) = 7.95$, $P < 0.01$. These results demonstrate that there was a clear choose-long bias shown when a delay interval was introduced between the offset of the auditory signal (either tone or cooing) and the presentation of comparison stimuli.

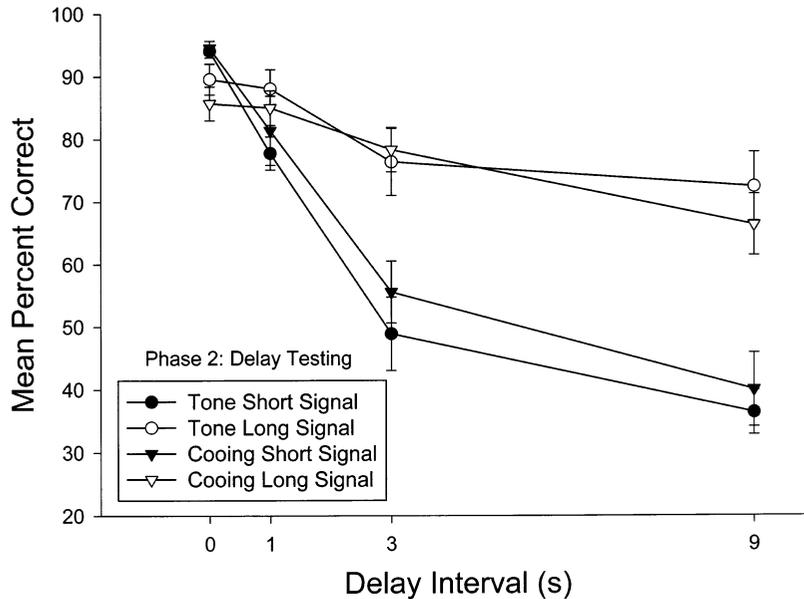


Fig. 4. The mean percentage of correct choices for short and long signal durations as a function of signal type (tone vs cooing) and the delay between the signal and the comparison stimuli. Error bars represent the standard error of the mean.

4. Discussion

The first set of psychophysical tests suggested that pigeons perceived a given duration of tone to be longer than an equal duration of cooing. This timing difference could have been the result of natural pauses (gaps) in the cooing stimulus (Roberts et al., 1989; Cabeza de Vaca et al., 1994; Brodbeck et al., 1998). The purpose of the second set of tests was to determine whether the initial timing difference was the result of brief pauses in the cooing signal. Since no timing difference was found in the second set of tests with pauses inserted into the tone signal, the initial timing difference was either due to the presence of pauses in the cooing signal, or it was unreliable. The third set of psychophysical tests attempted to replicate the timing difference by removing the pauses from the tone signal. No difference in timing was observed. While the original finding may simply be unreliable, it is also possible that pigeons originally timed the cooing signals differently than the tone signals but with experience, timed both signals similarly.

During the third set of psychophysical tests, the PSE for the tone and for the cooing signals was closer to the harmonic mean than the geometric mean. As noted earlier, the dominant timing model postulates that the psychological representation of time changes as a linear function of time with a ratio comparison process. An alternative model, the multiple-time-scale model, proposes that timing is the result of the trace strength of a stimulus rather than an internal clock (Staddon and Higa, 1999). This model postulates that the psychological representation of time changes as a logarithmic function of time. The data from this study are inconsistent with both models because both models predict a PSE at the geometric mean. The present findings of a PSE closer to the harmonic mean would be expected if the psychological representation of time changed as a reciprocal function of time (Church and Deluty, 1977).

Although the pigeons were presented with a novel 500 Hz tone at the start of training in this experiment, they had previously timed tones that were 1325 Hz. The method of accumulating time for the 1325 Hz tones may have transferred to timing 500 Hz tones. This could account for the

finding that the PSEs were the same across all three sets of tests for the tone functions, while the PSE for the cooing functions changed across the test sets. Therefore, the results could be interpreted as indicating that pigeons originally timed the cooing signals in a linear fashion with a ratio comparison process, however, with experience timed the cooing and the tone in a reciprocal fashion.

Past studies have indicated that some stimuli control the onset and offset of the internal clock differently. For instance, when a delay was introduced after the sample stimulus, Santi et al. (1998) found a choose-short effect when pigeons timed visual stimuli. This suggests that pigeons start timing at the onset of the visual signal and stop at the offset of the signal. The choose-short effect has been commonly replicated and is explained by the temporal foreshortening of the value in working memory during the delay (Spetch and Wilkie, 1983). An unexpected finding was a choose-long effect when pigeons timed an auditory stimulus. This finding suggests that pigeons start timing at the onset of the auditory signal and stop when the comparison stimuli are presented.

Although it might be anticipated that naturalistic auditory stimuli might capture attention more easily than an arbitrary, auditory stimulus, so that the onset and offset of the internal clock would be controlled more effectively, a clear choose-long bias was found for both the tone and the cooing signal when delay tests were administered. As a result it appears that arbitrary and naturalistic auditory stimuli control onset and offset of the internal clock in a similar manner.

In summary, the present study was the first to investigate how pigeons time an arbitrary, auditory stimulus (tone) compared to a more naturalistic auditory stimulus (cooing). While there was an initial timing difference, this difference was not evident with further testing. While it is possible that the psychological representation of time could change with prolonged exposure to a novel auditory signal, it is clear that with experience, pigeons time arbitrary and naturalistic auditory stimuli similarly. Furthermore, both types of auditory stimuli control the onset and offset of the internal clock in a similar fashion. The onset of

the comparisons in a dark chamber appears to overshadow the offset of a cooing signal as effectively as the offset of a tone and control the termination of timing.

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