Instructional Ambiguity in the Discrimination of and Memory for the Duration of a Stimulus[*]

Thomas R. Zentall

University of Kentucky, USA

ABSTRACT

The study of timing in animals has often included instructional ambiguity (or a failure to discriminate), an artifact that has often led to the misinterpretation of results. In the case of the peak procedure, used to determine when animals anticipate the time of reinforcement, the effect of gaps in the to-be-timed stimulus depends importantly on whether the gap appears similar in appearance to the intertrial interval. When the two intervals are similar animals appear to reset their clock –as they learned to do between trials. When the two intervals are different the animals appear to pause their clock. In the case of conditional duration discriminations, memory for the durations appears to shorten with the passage of time since their occurrence as indicted by divergent retention intervals, but only when the retention interval is similar to the intertrial interval and the trial appears to occur without a sample. When the retention interval and the intertrial interval are different, parallel functions are often found thus, no such shortening of the interval occurs. Finally two phenomena are examined, (a) the relative categorization of short and long durations depending on what they are being compared with and (b) the subjective passage of time that varies systematically with what the animal is doing while timing.
Key words: timing, peak procedure, conditional discrimination of time, memory, learning, theory, animals.

RESUMEN

Ambigüedad instruccional en la discriminación de y la memoria de la duración de un estímulo. El estudio de la medida del tiempo por los animales ha incluido a menudo la ambigüedad instruccional (o un fallo para discriminar), un artefacto que ha conducido a menudo a una mala interpretación de los resultados. En el caso del procedimiento del vértice, usado para determinar cuando los animales anticipan el momento del refuerzo, el efecto de las interrupciones en el estímulo cuya duración esta siendo medida depende de forma importante de si la interrupción es similar en apariencia al intervalo entre ensayos o no. Cuando los dos intervalos son similares los animales parecen reiniciar su reloj –tal como aprendieron a hacer entre los ensayos. Cuando los dos intervalos son diferentes los animales parecen pausar su reloj. En el caso de las discriminaciones condicionales de la duración, la memoria para las duraciones parece acortarse con el paso del tiempo desde su ocurrencia tal como lo sugiere la existencia de intervalos divergentes de retención, pero solo cuando el intervalo de retención es similar al intervalo entre ensayos y el ensayo parece ocurrir sin una muestra. Cuando el intervalo de retención y el intervalo entre ensayos son diferentes, a menudo se encuentran funciones paralelas, esto es no

ocurre ningún acortamiento del intervalo. Finalmente se examinan dos fenómenos, (a) la categorización relativa de duraciones cortas y largas dependiendo de con que se están comparando y (b) el paso subjetivo del tiempo que varía sistemáticamente con lo que está haciendo el animal mientras mide el tiempo.

Palabras clave: discriminación temporal, procedimiento del vértice, discriminación condicional de duraciones, memoria, aprendizaje, teoría, animales.

The ability of animals to discriminate and remember the duration of temporal intervals has received considerable attention in the past 25 years. The reasons are varied but two are notable. First, the temporal dimension is unique in its abstractness. It is not defined by the presence of certain observable attributes or by the relative relation among objects. Instead, it is marked by the abstract notion of when an event (its start) occurred in time. Thus, unlike many other events that can be identified almost as quickly as they appear, the point on the dimension of time changes continually.

The second reason that the judgment of temporal intervals by animals has been of interest to researchers is because of its importance in the lives of modern humans and the difficulty that we have in separating our natural ability to make temporal judgments from our extensive experience in making those judgments, including our general experience with our culturally invented scale of time and the external machines (clocks) we have invented for its measurement.

The study of timing by animals has been characterized largely by two procedures; one often referred to as the production procedure, the other as the discrimination procedure. In the production procedure the animal is typically presented with a stimulus and reinforcement is provided for the first response that occurs after a fixed time has passed (a fixed interval schedule of reinforcement). If the animal is given a continuous choice between responding and not responding it will generally show the typical 'scalloped' rate of responding from the onset of the stimulus to the time at which the reinforcement occurs. If on selected 'empty' trials reinforcement is omitted and the stimulus is not removed, the resulting mean response function will typically increase to the time at which reinforcement is expected and then it will typically decline such that the resulting function will generally appear bell-shaped (see S. Roberts 1981). That the response function typically is at its maximum at about the time that reinforcement would be delivered has been taken as evidence that animals have a reasonably good ability to judge the passage of time. Because the response function peaks at about the time that reinforcement is expected, this procedure has often been referred to as the peak procedure (W. Roberts, 1998).

In contrast, in the discrimination procedure, on some trials the animal is presented with a stimulus of a particular duration and is then given a choice between two test or comparison stimuli, a response to one of which is reinforced. On the remaining trials, the animal is presented with a stimulus of a different duration after which a response to the other comparison stimulus is reinforced. Most of the research involving the discrimination procedure has been done with pigeons. Because the timing models that have been developed from research using the peak and discrimination procedures have been somewhat different, I will discuss them separately.

THE PRODUCTION OR PEAK PROCEDURE

Research using the production or peak procedure has led to the development of the information processing model of timing (Church, 1978). This model, depicted in Figure 1, consists of three processes: the clock process, the memory process, and the decision process. The clock process consists of a pacemaker which puts out a series of pulses at a constant average rate, a switch controlled by the onset and offset of the to-be-timed signal, and an accumulator which collects those pulses. The memory process consists of working memory which receives input from the accumulator and reference memory which receives and stores the count in working memory when a response is rewarded. The decision process consists of a comparator which receives input from both working memory and reference memory and when the difference in counts between the two memories is sufficiently small (based on the animal's response criterion) it makes a decision to respond.
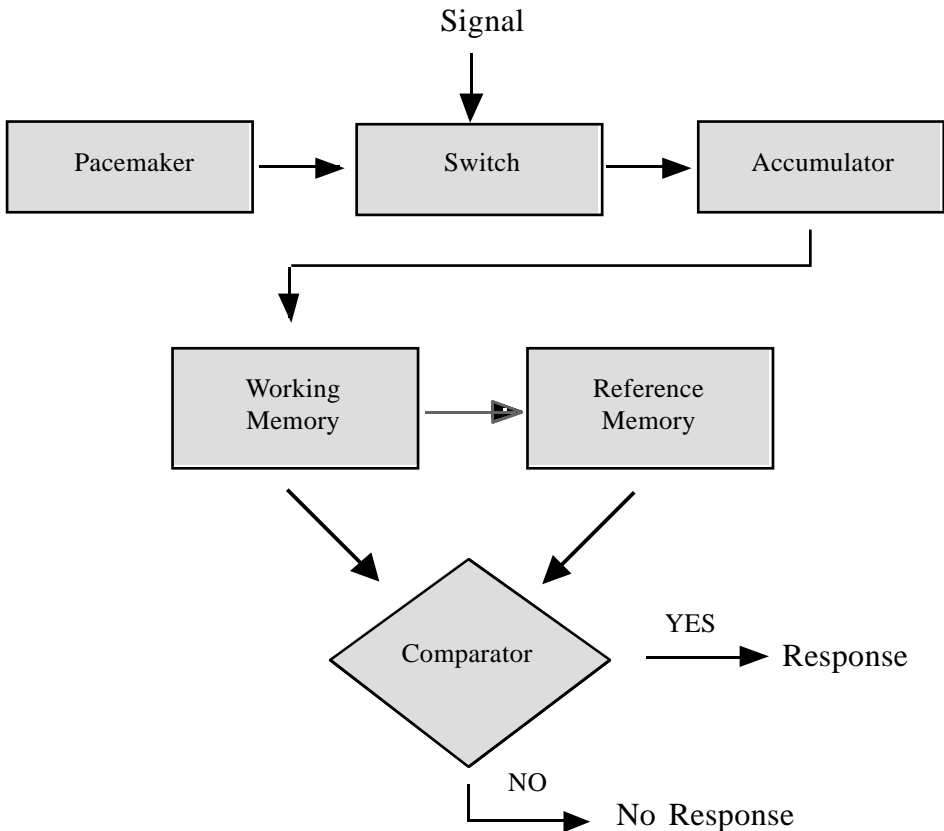

Figure 1. An information processing model of timing. There are three processes: the clock process (involving the pacemaker, the switch, and the accumulator), the memory process (involving working memory and reference memory), and the decision process (involving the comparator).
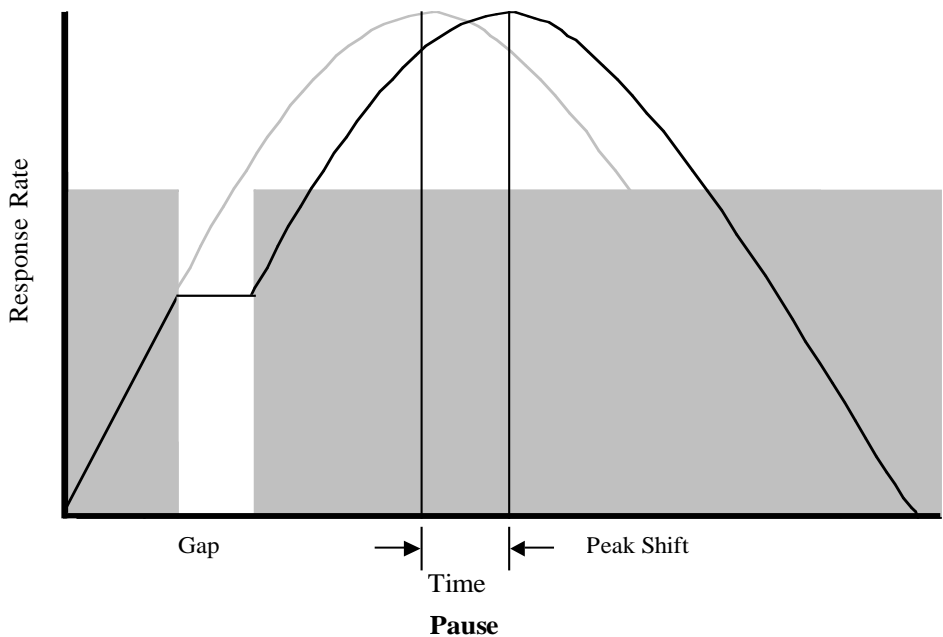
Figure 2. Predicted shift in the peak of responding if the animal pauses its clock (stops when the gap starts and restarts where it left off when the gap ends).

In an alternative model proposed by Staddon & Higa (1999), behavior is controlled by a steadily decaying memory for the start of the interval. According to this theory, the animal's decision to make a response is based on the animal's memory for the strength of that start event at the time of reinforcement. The appeal of this strength model is that it is somewhat simpler than the clock model and it makes some unique predictions (see Staddon, 1970).

GAPS IN THE TO-BE-TIMED SIGNAL

One of the techniques that has been used to understand the functioning of the timing process using the peak procedure has been the use of gaps in the to-be-timed signal (see e.g., S. Roberts, 1981; W. Roberts, Cheng, & Cohen, 1989). These trials are similar to empty trials; however, prior to the time that reward would be expected there is a gap in the signal for several seconds. It is the effect of that gap on the timing process that has been of interest to researchers. The effect of the gap is typically assessed by the effect that the gap has on the time of the peak rate of responding. Three effects can be identified: First, the animal may time through the gap. If this happened, the gap would have little effect on the time of the peak rate of responding. Alternatively, the gap may cause the animal to pause or stop timing for the duration of the gap and

then resume timing when the signal returns. If this occurred, one would expect the time of the peak rate of responding to occur later than it would without the gap (i.e., the peak would shift to the right) by an amount equal to the duration of the gap (see Figure 2). Finally, the gap may cause the animal to reset the accumulated time such that it starts timing from zero again when the signal returns. If this occurred, one would expect the time of the peak rate of responding to occur even later than it would without the gap (i.e., the peak would shift to the right) by an amount equal to the duration of the gap plus the duration of the signal prior to the gap (see Figure 3). Thus, the three hypotheses make quantitatively different predictions about the time of the peak rate of responding.

Interestingly, when the gap procedure has been used, the results have been quite varied. Some experiments suggest that animals pause and then resume timing (Buhusi, Perera, & Meck, 2005; Buhusi, Sasaki, & Meck, 2002; S. Roberts, 1981). That is, the peak of responding is shifted an amount equal to the duration of the gap. Other experiments suggest that they reset (Buhusi *et al.*, 2005; Buhusi *et al.*, 2002; W. Roberts *et al.*, 1989). That is, the peak of responding is shifted an amount equal to the duration of the gap plus the duration of the signal prior to the gap. Still other experiments suggest that they do something in between those two strategies (Buhusi *et al.*, 2005). That is, the peak of responding is shifted further than the duration of the gap but not as far as the gap plus the duration of the signal prior to the gap.
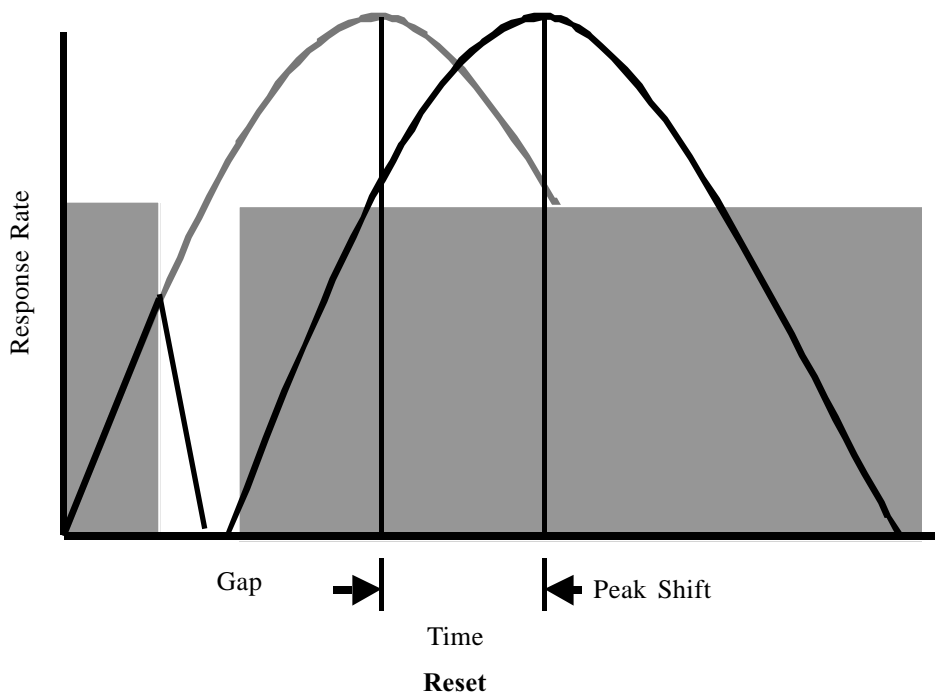

Figure 3. Predicted shift in the peak of responding if the animal resets its clock (resets to zero when the gap starts and restarts when the gap ends).

The empirical effect of inserting a gap in an empty trial appears to depend on a number of variables that have made it difficult to adequately model the results of the various experiments. Some of these variables include, the species tested (rats tend to pause during gaps, S. Roberts, 1981, whereas pigeons tend to reset, W. Roberts *et al.*, 1989), the strain of rat (albino rats tend to pause during gaps, whereas pigmented rats tend to reset, Buhusi *et al.*, 2005, Experiment 1), the modality of the to-be-timed signal (albino rats tend to pause with visual signals but they tend to reset with auditory signals, Buhusi *et al.*, 2005, Experiment 2), the brightness of the signal (pigmented rats tend to pause when the signal is of low intensity but they tend to reset when the signal is of high intensity, Buhusi *et al.*, 2002; Buhusi *et al.*, 2005, Experiment 3), and gap duration (pigmented rats tend to pause when the gap in the visual signal is short but reset when the gap is long, Buhusi *et al.*, 2005, Experiment 2).

The memory-loss or active-decay account

To account for these diverse data as well as for peak shifts that fall between those predicted by pause and reset strategies, it has been proposed that when a gap occurs, the animal stops timing and retains the interval prior to the gap but during the gap, memory for the interval prior to the gap begins to decay (see Buhusi *et al.*, 2005; Cabeza de Vaca, Brown, & Hemmes, 1994). Thus, animals often appear to pause when the gap is short but they appear to reset when the gap is long and memory has an opportunity to decay.

The decay of memory for the interval prior to the gap has also has been used to account for the fact that for pigmented rats and for pigeons, gaps in bright to-be-timed signals tend to result in performance that is closer to resetting, whereas gaps in dim to-be-timed signals tend to result in performance that is closer to pausing (Buhusi *et al.*, 2002). Although one might think that the brighter the to-be-timed interval is, the better it should be remembered, according to the memory decay account, the brighter is the to-be-timed signal the more salient the gap should be; and the more salient the gap, the more it should cause the interval prior to the gap to decay (Buhusi *et al.*, 2005).

The idea of a decaying interval that depends on the duration of the gap and the brightness of the to-be-timed signal may appear to be quite reasonable but the nature of such a decay process is not obvious. The passage of time should make a stimulus less distinct or less discriminable from other stimuli (e.g., a fading color or an increase in the variability of a remembered length or brightness). In fact, there is evidence that gradients of stimulus generalization along dimensions of intensity tend to flatten (or show poorer discriminability) rather than show a peak shift in the direction of shorter duration as the time between training and testing increases (Perkins & Weyant, 1958; Richardson, Williams, & Riccio, 1985). Thus, it is not clear why the forgetting of a duration should necessarily make it appear shorter rather than be remembered generally less accurately.

Furthermore, the magnitude of the hypothesized shortening process appears to be larger than one might intuitively think it should be. Specifically, according to the model suggested by Buhusi *et al.* (2005), if 15 sec into a to-be-timed interval a salient

gap of 5 sec is presented, by the end of the gap the memory for the 15 sec interval would have shrunk to perhaps 1 sec or less (see Cabeza de Vaca *et al.*, 1994, for a similar model). At an intuitive level, such a distortion of remembered time intervals would seem to be maladaptive for an animal. If memory for time intervals is at all important to animals, they should be able to hold in memory a time interval of 15 sec longer than 5 sec without it experiencing such great distortion. Although false memories do occur, they are rather rare and in humans can be generated only by strong extra-experimental associations (see Roediger & McDermott, 2000) or social influence (Loftus, 1997). Thus, the proposition of such an extreme distortion of memory in animals should at least encourage one to look for an alternative account.

The instructional ambiguity[1] account.

To generate an alternative account for the varied results that have been obtained using the gap procedure, it may be useful to imagine the task from the animal's perspective. To better appreciate the decision process that the animal experiences on trials with a gap, it would be helpful to examine the sequence of events that occurs on the original fixed interval trials and how they differ from those on empty trials. On fixed interval trials, the animal learns to start timing when the trial starts and to reset its clock with reinforcement or perhaps with the intertrial interval. When empty trials are introduced, the intertrial interval can still serve as a cue to reset the clock, however, reinforcement is no longer available to reset the clock. The degree to which the onset of the intertrial interval serves to reset the clock is likely to depend on the salience of the to-be-timed signal because the more salient is the to-be-timed signal, the more distinctive should be the start of the intertrial interval. If the signal is quite salient, its offset at the start of the intertrial interval will be salient and that should be sufficient to reset the clock, even if it occurs at an unexpected time (i.e., as a gap prior to the time reinforcement is expected). However, if the signal is not so salient, then its offset may not immediately reset the clock, especially if the offset occurs as a gap at an unexpected time. In that case, the duration of the gap may play a role. The longer is the unexpected offset of the signal, the more likely it should be taken for the intertrial interval and the more likely the clock will reset. Thus, what happens when a gap is introduced during an empty trial should depend on the degree to which the stimulus conditions at the start of the intertrial interval serve to reset the clock.

This relatively simple model of confusion between the gap and the intertrial interval or ambiguity of the gap may be able to account for virtually all of the data that have been reported using the gap procedure. Consider first the results of two studies that actually manipulated the similarity between the intertrial interval and the gap. Kaiser, Zentall, & Neiman (2002) explicitly manipulated the similarity between the intertrial interval and the gap. Whether the gap was short or long, when the gap and the intertrial interval were similar, they found that pigeons tended to reset their clock. However, when the intertrial interval was distinctively different from the gap, the pigeons tended to pause (see Figure 4). Similarly, in a study with rats, Buhusi and Meck (2002, Experiment 2) found that when the intertrial interval and the gap were
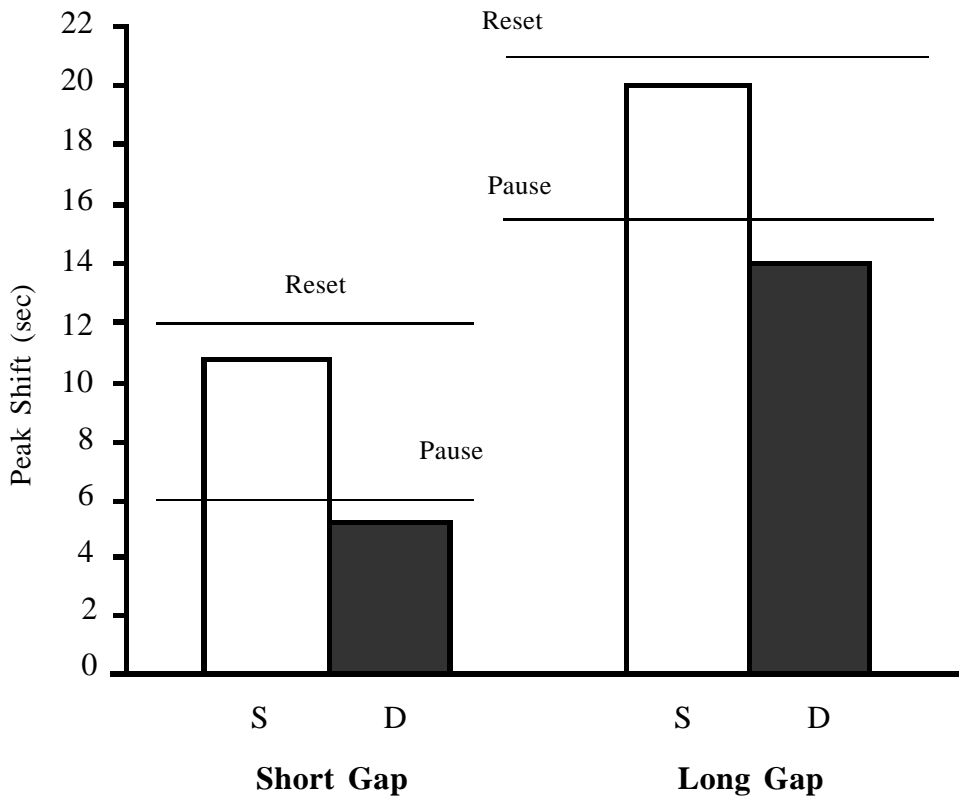
Figure 4. When the gap is the same (S) as the intertrial interval pigeons appear to reset. When the gap is different (D) from the intertrial interval they appear to pause both when the gap is short (6 sec) and when it is long (15 sec).

similar, the rats tended to reset, however, when a distinctive noise was presented during the intertrial interval but not during the gap, the rats clearly paused.

When the intertrial interval is not distinctively different from the gap, results reported with rats are more complex because several variables appear to determine whether they pause or reset. For example, S. Roberts (1981) reported that albino rats paused during gaps. However, Roberts' to-be-timed signals (visual for some rats auditory for others) were not very salient, so the gap was not likely to reset the clock. Similarly, Buhusi *et al.* (2005) reported that albino rats paused with visual signals but when they used auditory signals 3–10 dB louder than those used by Roberts, the rats tended to reset their clock. Buhusi et al. also reported that pigmented rats, which are more visually sensitive than albinos, tended to reset their clock, but only when the visual signal was relatively bright (and the gap was relatively long).

Pigeons too appear to be sensitive to the salience of the to-be-timed signal. When the signal consists of a relatively dim light coming from a small response key (Kaiser *et al.*, 2002) or a dim screen (Buhusi *et al.*, 2002, Experiment 1) pigeons tend

to pause (especially if the gap is relatively brief). When the visual stimulus is more salient, however, the pigeons tend to reset (Buhusi *et al.*, 2002, Experiment 1).

Another variable that appears to affect whether the clock stops or resets is the duration of the gap. When the stimulus conditions during the gap and the intertrial interval are similar, one might expect that the longer the gap, the more like the intertrial interval it would appear and thus, the more likely the animal would reset. That does appear to be the case. In general, when the signals are moderately salient, the longer the gap, the more likely the animals are to reset (Buhusi *et al.*, 2005, Experiment 1, with pigmented rats and Experiment 3; Cabeza de Vaca *et al.*, 1994; W. Roberts, *et al.*, 1989, Experiment 3). In several experiments, when the gap is short, shifts in peak responding have been found that are intermediate between pause and reset. Thus, if the signal is not salient and the gap is similar to the intertrial interval, animals may initially pause but with longer gaps they are likely to reset. In other words, if in training, the intertrial interval is not a salient event and the clock does not reset immediately at the end of the to-be-timed signal, on test trials, a gap similar in appearance to the intertrial interval should have the same effect. However, if in training the intertrial interval is a salient event and the clock resets immediately, on test trials, a gap similar in appearance to the intertrial interval also should have the same effect. But what about gap durations that result in a shift in the peak that is between pausing and resetting? Such an effect could arise by averaging trials on which the animals at times pauses and at other times resets. Alternatively, it may be that the reset process takes a finite amount of time and if the gap ends before the reset process is complete it might result in a partial reset.

It is important to note that although gap ambiguity (together with a salience mechanism that determines when the animal will reset following the onset of an ambiguous gap) can account for the results of much of the research reported using the peak procedure with gaps; this is really not a theory of how animals time intervals. Instead, it is a suggestion that artifacts that may produce ambiguity should be avoided. Thus, to study animal timing appropriately one should make the intertrial interval distinct from other trial events and one should use to-be-timed signals that are appropriately salient for the species under study.

It also should be noted that when the peak procedure is used without gaps, neither ambiguity involving the intertrial interval nor ambiguity involving novel gaps should be a factor. However, one more factor should be considered. The bell-shaped function that often is found on empty trials following fixed interval training has typically been interpreted in terms of a decision rule involving an estimate of the probability that reinforcement will occur at each point in the interval. When viewed from the perspective of the animal, however, it may be more appropriate to view the bell-shaped function as an estimate of the probability that the current trial is a fixed interval trial, rather than an empty trial. The difference in interpretation has important implications for the information processing theory of timing presented in Figure 1. This information processing theory suggests that the decision to respond, based on the absolute difference in counts between what is in working and reference memory, is relatively symmetrical. As long as the absolute difference is small, responding will occur. However, when empty trials are first introduced, the function relating response rate to time from the start of the trial

is not symmetrical (Kirkpatric-Steger, Miller, Betti, & Wasserman, 1996). Instead, the function rises quite steeply but descends quite gradually. It is only with extended training with empty trials that the pigeons learn to discriminate between the two kinds of trial and the ascending and descending functions approach symmetry. This finding suggests that the ascending and descending portions of the response function may represent different underlying processes –timing and discrimination, respectively. This issue needs to be studied further.

THE DISCRIMINATION PROCEDURE

The discrimination procedure differs from the peak procedure in that two stimulus durations are involved and one test or comparison stimulus is correct following presentation of one duration, whereas the other comparison stimulus is correct following presentation of the other duration (see Figure 5). Following acquisition of this task, one can ask about the nature of the temporal dimension by testing with sample durations that fall between the trained values. Of particular interest is the point of subjective equality (i.e., the stimulus duration at which the animals distribute their responses equally between the two comparisons). When animals have been tested this way, the point of subjective equality can best be described by the geometric mean of the two training values (i.e., the square root of the product of the two duration values; Church & Deluty, 1977; Gibbon, 1986).

Memory for Durations

Another question of interest to those who study the discrimination of temporal intervals is the degree to which those intervals can be remembered. Memory for the duration of an interval has been of particular interest because of the curious way in which durations appear to be forgotten. One might expect that memory for a duration
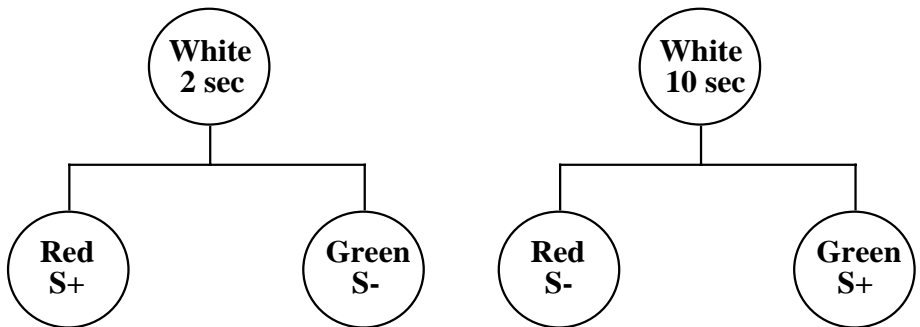

Figure 5. The two trial types that constitute a conditional discrimination involving two stimulus durations (2 sec versus 10 sec).

would become more variable as time passed since the interval was experienced (i.e., as the retention interval increased, a particular stimulus duration would tend to be remembered sometimes as shorter and at other times as longer than its actual duration) and short intervals would be as likely to be confused with long intervals as long intervals would be to be confused with short intervals. But that is not what has been found.

The choose-short effect

Imagine the following task: If the initial stimulus was presented for 2 sec, choice of the red comparison stimulus would be rewarded, whereas if the initial stimulus was presented for 10 sec, choice of the green comparison stimulus would be rewarded. Once the 'rules' associated with correct choice have been acquired such that matching accuracy by the pigeon is high, a delay that varies from trial to trial is inserted between the offset of the initial stimulus and the onset of the comparison stimuli requiring that the pigeon remember the stimulus duration.

When matching accuracy is plotted against delay for trials involving the two durations of the initial stimulus, the typical results are somewhat surprising. Although matching accuracy on trials involving the short, 2-sec initial stimulus suffer very little with increasing delay, matching accuracy on trials involving the long, 10-sec initial stimulus deteriorates very quickly with increasing delay (Spetch & Wilkie, 1982). Intuitively one might expect that the stimulus that was presented for a longer duration would be remembered better, but this was not the case.

Subjective shortening of memory for duration

The explanation given for this 'choose short effect' is that the duration of the initial stimuli becomes subjectively shorter as time passes since the offset of the stimulus. As the delay increases, this subjective shortening effect would cause the 10-sec stimulus to appear more and more like the 2-sec stimulus, thus accounting for the poor perfor-mance on those trials. On the other hand, although subjective shortening would also affect the 2-sec stimulus, this effect would not lead to poorer matching accuracy because the subjective shortening would not cause the 2-sec stimulus to appear to be more like the 10-sec stimulus.

A further surprising result is the rapidity with which this subjective shortening process occurs. That is, a relatively short delay (as short as 4 sec) can result in a 10-sec sample being judged more similar to a 2-sec sample without a delay than to a 10-sec sample without a delay (see Sherburne, Zentall, & Kaiser, 1998). This finding is reminiscent of the extremely rapid forgetting proposed in the last section by the active decay hypothesis. According to the active decay hypothesis, presentation of a 5-sec gap in a to-be-times signal may cause the memory for a pre-gap interval of 15 sec to shorten to almost nothing.

More recently, Spetch & Rusak (1992) have suggested that the duration of the sample may be judged relative to the entire context in which it appears. That is, each sample duration is bounded by the intertrial interval prior to its appearance and by the

delay following its appearance. Thus, the duration of the sample is judged relative to the combined background duration of the intertrial interval and the delay and an increase in the intertrial interval should have the same effect as an increase in the delay –it should result in the subjective shortening of the duration (a choose-short effect). Furthermore, this theory makes the addition prediction that a decrease in the duration of the intertrial interval should have the opposite effect. When one plots the retention functions, it should tend to produce subjective lengthening of the duration (a choose-long effect). Both predictions were confirmed.

When Spetch & Rusak (1992) then manipulated the similarity of the intertrial interval to the delay, they reported a surprising result. When the intertrial interval and delay were both dark (as they typically are) or both lit, a plot of the retention functions indicated that there was a clear choose-short effect. When one was dark and the other lit, however, there was no evidence of a choose-short effect. Instead, the retention functions were quite parallel.

Spetch & Rusak (1992) interpreted their finding in terms of the relative context in which the sample durations appeared (the relative-duration hypothesis). When the intertrial intervals and the delay intervals were similar, they proposed that the pigeons judged the sample duration in the context of those intervals and as either the delay or the intertrial interval increased, they judged the sample durations as getting smaller and smaller. However, when the intertrial intervals and the delay intervals appeared different, they suggested that the pigeons responded randomly and showed no choose short effect.

The instructional ambiguity[1] hypothesis

An alternative to both the subjective shortening and relative-duration hypothesis is the ambiguity hypothesis that considers the similarity between the novel delay and the familiar intertrial interval to result in ambiguity. More specifically, during training, all samples end with presentation of the comparison stimuli and all trials end with the intertrial interval. The 'instruction' inherent in the onset of the intertrial interval is that memory for the sample is no longer required. Now, consider what happens on trials with a delay. Following presentation of the sample, an event occurs that is similar in appearance to the intertrial interval. Following the delay, the comparison stimuli are presented. Thus, presentation of a novel delay may give the impression that the trial ended without presentation of the comparison stimuli and then that the next trial started without presentation of the sample. If this is the effect of the novel delays, what effect might that have on the pigeons' retention functions? Certainly, the presumed absence of a sample would be judged as more similar to a short sample than a long sample. This would be true especially if in training the sample appeared unannounced and there was some variability in the latency of attention to the sample (i.e., some short sample durations were effectively shorter than that actual short sample). One would expect that the effect of such ambiguity on short-sample trial performance would be minimal; however, one would expect the effect on long-sample trial performance to be great. Again, the similarity between the delay and the intertrial interval should cause the pigeon to judge the appearance of the comparison stimuli at the end of the delay as a

trial without a sample, and such trials would likely be judged as more similar to short-sample trials than long-sample trials. Furthermore, the longer the delay the more the delay should appear similar to the intertrial interval and the poorer performance should be on 10-sec sample trials. If the delay is sufficiently long, on long-sample trials, pigeons should choose the comparison that in training was associated with short-samples a majority of the time –and they do.

To test the hypothesis that the delay may be mistaken for an intertrial interval because of their similarity, Sherburne *et al.* (1998) trained pigeons on a conditional interval discrimination (2 vs. 10 sec) with a 0-sec delay and either a bright houselight lit during the intertrial interval or a dark intertrial interval. After acquisition, on test trials, a delay that varied in duration from trial to trial was introduced between the offset of the sample and the onset of the comparison stimuli. On half of the test trials, the delay was dark. On the remaining test trials the houselight was lit during the delay.

The results indicated that for pigeons trained with dark intertrial intervals, when the delays were dark, the retention functions (matching accuracy plotted against increasing delay) diverged; matching accuracy on 2-sec-sample trials was high and flat, whereas matching accuracy on 10-sec-sample trials steeply declined. This is the typical choose-short effect (see top panel of Figure 6). However, when the delays were lit, the retention functions were parallel. That is, when the delays were discriminably different from the intertrial intervals, no choose short-effect was found (see bottom panel of Figure 6).

The results for the group trained with lit intertrial intervals were quite different. For these pigeons, when the delays were lit, the retention functions diverged; matching accuracy on 2-sec-sample trials was high and flat, whereas matching accuracy on 10-sec-sample trials steeply declined. Furthermore, for these pigeons, when the delays were dark the retention functions were parallel. Once again, when the delays were discriminably different from the intertrial intervals no choose-short effect was found.

The results reported by Spetch and Rusak (1992) together with those reported by Sherburne et al. (1998) offer support for the ambiguity hypothesis. A result that the ambiguity hypothesis cannot account for is the effect of manipulating the duration of the intertrial interval reported by Spetch and Rusak. Recall, they reported that when the intertrial interval was made longer, pigeons showed a choose-short effect. The longer the intertrial interval, the poorer performance was on long-sample trials but there was little effect of performance on short-sample trials. When the intertrial interval was made shorter, however, pigeons showed a choose-long effect. The longer the intertrial interval, the poorer performance was on short-sample trials but there was little effect of performance on long-sample trials.

The differential effect of manipulating the duration of the intertrial interval on long and short sample trials may be explained by a mechanism similar to that used to explain the effects of delay, namely a failure to discriminate. In this case, however, one must assume that the effects of the sample on the preceding trial (or trials) combine with the effects of the sample on the current trial to produce a stronger memory trace. To perform well in acquisition, the pigeons must learn to discriminate between the short sample combined with the residual effects of the samples from prior trials and the long sample combined with the residual effects of the samples from prior trials. Now, if one
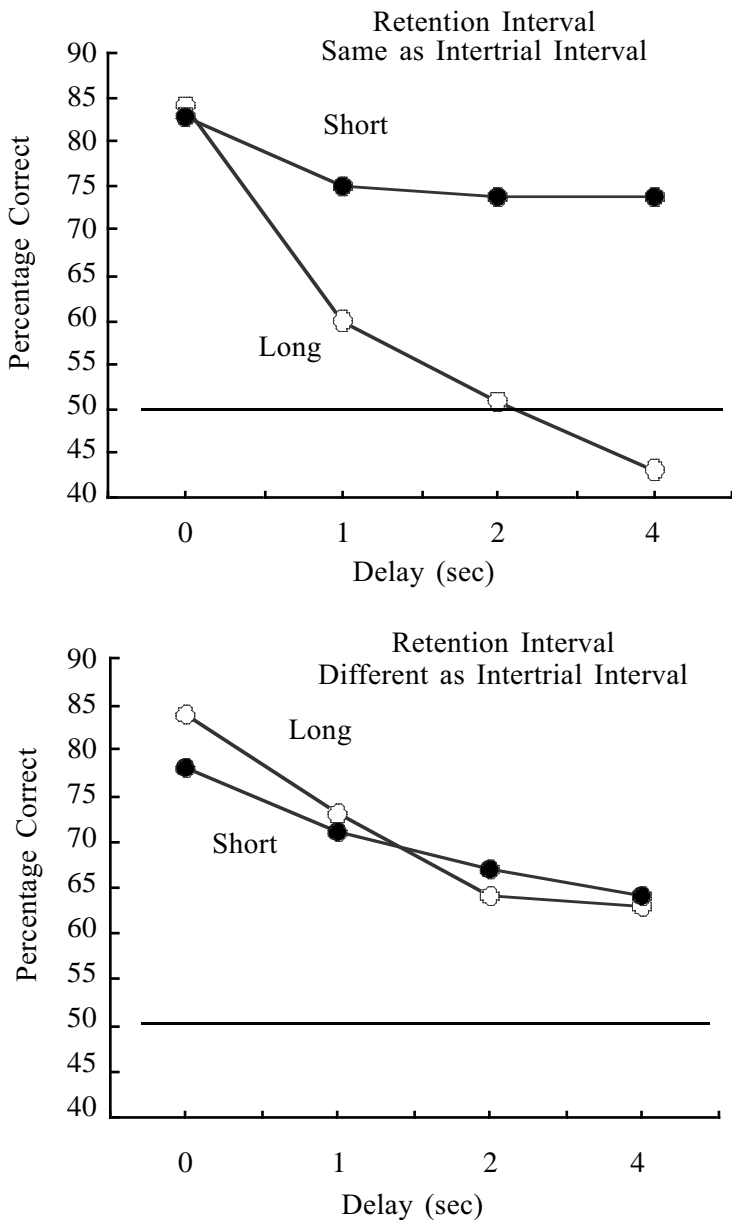
Figure 6. The divergent retention functions found following training with short (2 sec) and long (10 sec) initial stimuli when the retention interval (delay) was the same as (similar in appearance to) the intertrial interval (top) and different from the intertrial interval (bottom).

lengthens the intertrial interval, it should reduce the effect of prior trials on both short- and long-sample trials and make the memory trace of both samples appear somewhat weaker. Thus, the long sample should be more similar in strength to the memory of the short sample from training (with greater residual effects of the samples from prior trials) and a choose-short effect might be expected (see Staddon & Higa, 1999). Similarly, if one shortens the intertrial interval, it should increase the effect of prior trials and make the memory trace of both samples appear stronger. In this case, the short sample (with greater residual effect of prior samples) should be more similar in strength to the memory of the long sample from training and a choose long effect might be expected.

The same mechanism might account for manipulations of the duration of delays. Generally, pigeons are trained with a 0-sec delay and are tested with longer delays. The typical finding is divergent retention functions best described as a choose-short effect. But Spetch & Rusak (1992) trained pigeons with a 10-sec delay and then tested them with longer and shorter delays. When the pigeons were tested with longer delays they showed the typical choose-short effect. When they were tested with shorter delays, however, the pigeons showed a clear choose-long effect. That is, as the delay decreased from the 10-sec delay experienced during training, matching accuracy on long-sample trials remained high, whereas matching accuracy on short-sample trials actually declined. To account for this choose-long effect, once again, one must assume that memory for the sample consists of memory for the current sample combined with the residual memory of prior samples. If the decrease in the duration of the delay from what was experienced during training increases the strength of the combined memory strength, then the strength of the memory on short-sample trials may sometimes exceed the criterion for choosing the comparison associated in training with the long sample.

The effects of manipulating the duration of the intertrial interval and delay following training with constant durations would be expected to occur immediately, but with continued experience with shorter or longer durations, one should see a accommodation to the new durations. That is, one would expect the animals to adjust their decision criterion for the strength of the memory trace for short and long samples to maximize the likelihood of reinforcement.

As noted earlier, the ambiguity hypothesis is not a theory of how animals time intervals. Rather it is alternative account of various theories that have been proposed to account for the effects on timing of interval gaps using the peak procedure and of memory for discriminated stimulus durations. Once ambiguities are eliminated, the resulting procedures may provide important insights about interval timing by animals.

Training with delays

As noted earlier, interpretation of the results of experiments in which retention intervals are assessed following training in the absence of delays is made difficult when delays are similar in appearance to the intertrial intervals. However, even when the delays and intertrial intervals are discriminably different in appearance, the delay may be ambiguous to the animal. Specifically, although the delays may not resemble the intertrial intervals, their novelty following training without delays may disrupt perfor-

mance independent of any purported memory loss.

Furthermore, not only are trials with a delay novel, but it is likely that the degree of novelty is directly proportional to the duration of the delay. Thus, Sargisson & White (2001) have suggested that the sloping retention functions typically found following duration sample training (see Sherburne *et al.*, 1998) may be attributable to the generalization decrement or differential novelty associated with the various delay trials. In the study by Spetch & Rusak (1992) described earlier in which pigeons were trained with a 10-sec delay and tested with longer and shorter delays, the novelty of the delays should have been somewhat reduced but as the tested delays had not been experienced during training, the effect of novelty was not eliminated.

The differential novelty of delay intervals may not appear to be an important factor in disrupting performance; however, the expectation of the appearance of the comparison stimuli may also directly affect the behavior of the pigeon. If the comparison stimuli appear either later than expected or earlier than expected, the pigeon may not be prepared at that time to choose a comparison stimulus.

In an attempt to eliminate the effect of novelty of delays, Dorrance, Kaiser, & Zentall (2000, Experiment 1) exposed pigeons to delays of 0, 1, 2, and 4 sec from the start of training. To preclude the inclusion of training sessions during which the sample-comparison associations were being initially acquired, sessions were considered for a test of memory only if matching accuracy on 0-sec-delay trials exceeded 75% correct for both short and long samples. Not only did Dorrance et al. find no evidence of a choose-short effect –the retention functions on short- and long-sample trials were parallel– but the retention functions were almost flat between 0 and 4 sec. That is, when delays are not novel, the memory for sample duration appears to be quite accurate for at least 4 sec.

In a follow-up experiment, Dorrance *et al.* (2000, Experiment 2) trained pigeons with longer delays (0, 4, 8, and 16 sec). Under these conditions, once again, the retention functions on short-sample and long-sample trials were parallel but now both functions declined with increasing delay. Surprisingly, however, matching accuracy at the longest delay (16 sec) was still significantly above chance (above 60% correct) –a result that is not typically found when delays are novel. Thus, training pigeons with delays may provide a less biased estimate of their capacity to remember the duration of a sample, and training them with delays that are different in appearance from the intertrial interval may reduce the likelihood that an artifactual bias will develop to choose one of the comparisons over the other.

RELATIONAL LEARNING IN TEMPORAL DISCRIMINATIONS

Once artifacts are removed from studies investigating how animals time and remember intervals, a clearer picture of timing by animals can be obtained. One area that has been of particular interest to us has been the degree to which the passage of time has relational properties for animals. For example, do estimates of the passage of time depend on what else is being timed or on other intervals with which the timed

interval is being compared? Also, do estimates of the passage of time depend on what else the animal is doing while it is timing? The results of recent experiments provide preliminary evidence that similar processes may affect estimates of the passage of time by humans and other animals.

Are Duration Samples Categorically Coded?

It is generally assumed that what animals store in memory is the absolute duration of the stimulus interval that has been experienced. Whether animals are capable of relational learning has long been an issue (see Lashley & Wade, 1946; Spence, 1936). But whether animals can represent stimulus durations not only in terms of their absolute values but also in terms of the relationship between them, to my knowledge, has not been asked. In other words, humans who have acquired a duration sample conditional discrimination might represent a 2-sec sample as the 'short' sample and a 10-sec sample as the 'long' sample. It is possible that animals also tend to categorize durations this way. Kraemer, Mazmanian, & Roberts (1985) suggested that in a conditional discrimination, pigeons may code two duration samples in a binary fashion as 'short' and 'long.' To test this hypothesis Kraemer *et al*. trained pigeons with three sample durations (0, 2, and 10 sec) and three comparison options, one for each sample. Then, when delays were introduced, they used the distribution of errors to distinguish between the subjective shortening hypothesis and the alternative, coding hypothesis. According to the coding hypothesis, each sample should have a distinctive code, one of which would be 'no-sample.' When delays were introduced, the code for the sample on that trial would tend to be forgotten. When the sample was forgotten it should have elicited a no-sample code. This should occur equally on short (2 sec) sample and long (10 sec) sample trials.

In support of the coding hypothesis, Kraemer *et al*. (1985) found that on long sample trials, as the delay increased pigeons tended to choose the no-sample comparison rather than the short-sample comparison. It should be noted, however, that in this study, the intertrial intervals and the delays were similar in appearance. As noted earlier, when the intertrial intervals and the delays are similar in appearance and the duration of the delay is increased, all delay trials become, in effect, no-sample trials.

The idea that pigeons may categorize intervals according to their relative duration (i.e., as short and long) was studied by Zentall, Weaver, & Clement (2004) using a different approach that does not involve the introduction of ambiguous delays. This design took advantage of the fact that when animals are trained with duration samples and they are tested with sample durations that fall between the trained values, as noted earlier, the point of subjective equality has been found to be very close to the geometric mean of the two training values (Church & Deluty, 1977; Gibbon, 1986).

In the Zentall *et al.* (2004) experiment, pigeons acquired two duration-sample matching tasks. For one task the samples were 2- and 8-sec long with red and green comparisons. For the other task the samples were 4- and 16-sec long with vertical- and horizontal-line comparisons. Note that one of the samples from each task falls at the putative point of subjective equality of the other task. We hypothesized that if the
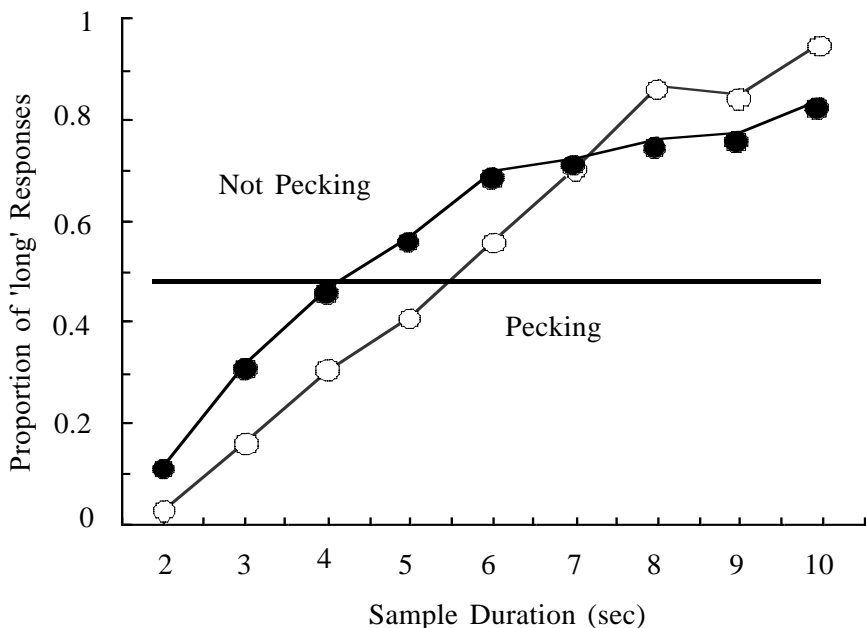
Figure 7. Proportion of choices of the response key associated in training with the long (10 sec) sample as various sample durations between 2 and 10 sec were presented when pecking was required and when the pigeons were required to refrain from pecking. The horizontal line represents equal choice of the two alternatives (the point of subjective equality).

pigeons were representing the samples in each duration discrimination as analogous to 'short' and 'long,' presenting the 8-sec-duration sample (the longer of 2 and 8 sec) with the vertical- and horizontal-line comparisons should result in a bias to choose the comparison associated in training with the longer (16 sec) sample, whereas presenting the 4-sec-duration sample (the shorter of 4 and 16 sec) with the red and green comparisons should result in a bias to choose the comparison associated in training with the shorter (2 sec) sample. We found, in fact, that five out of the six pigeons 'chose long' with the 8-sec sample and all six pigeons 'chose short' with the 4-sec sample. Thus, we found significant evidence for the categorical coding of temporal samples.

The Subjective Experience of the Passage of Time

Recently, we have asked if the passage of time is affected by what the animal is doing while timing (Zentall, Friedrich, & Clement, 2005). Research with humans suggests that the subjective passage of time is systematically affected by the cognitive load in effect while timing (Block & Zakay, 1997; Chastain & Ferraro, 1997; Chaston & Kingston, 2004; Zakay, 1993). The greater the cognitive load for humans, the slower

time appears to pass.

In a within-subject experiment, we asked pigeons to choose comparison stimuli differentially depending on whether the initial stimulus was presented for a short time (2 sec) or a longer time (10 sec). When the initial stimulus was one color (e.g. white), the pigeons were required to peck at it at a rate of one peck per sec (a condition that we judged to involve a moderate cognitive load). Failure to meet the pecking requirement terminated the trial. When the initial stimulus was a different color (e.g., blue), the pigeons were required to refrain from pecking for the duration of the stimulus (a condition that we judged to involve a low cognitive load). In this case, pecking terminated the trial.

Following acquisition of this task, the pigeons were tested with durations of the initial stimulus that varied between 2 and 10 sec and reinforcement was delivered on 50% of the test trials regardless of the pigeons' choice. The results indicted that the point of subjective equality was approximately at the geometric mean when the pigeons were required to refrain from pecking the to-be-times signal. However, it was almost a full sec higher when pecking was required (see Figure 7). These results suggest that for animals too, an apparent increase in cognitive load leads to the judgment that time passes faster than when there is no additional cognitive load.

Conclusions

The purpose of the present article was to identify a source of error in the interpretation of results of several timing experiments that have used either the peak procedure or duration discrimination procedure to assess animal timing and the memory for time. It is suggested that ambiguity at the time of test can produce artifacts that may lead to erroneous conclusions about the effect of gaps in the peak procedure as well as memory for the duration of an event in a temporal discrimination procedure. When those artifacts are removed, very different interpretations may result concerning the processes involved. Evidence is also provided that judgments of the passage of time may be influenced both by the relation between stimulus durations and by the animal's behavior (or cognitive load) during those stimulus durations.

Notes

1 Some readers may feel uncomfortable with the use of the term instructional ambiguity in reference to the changes in procedure that occur between training and testing. I use the term here to emphasize the similarity between what an animal experiences and what a human would experience if placed in similar conditions. Those readers who feel that the term is too anthropomorphic, should substitute the more objective term 'generalization decrement.' In either case, there is a systematic loss of stimulus control that may be misattributed to various memory processes.

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