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Pigeons' Memory for Time: Assessment of the Role of Subjective Shortening in the Duration
Comparison Procedure

By

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Bachelor of Arts (Honours), Psychology

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THESIS

Submitted to the Department of Psychology

in partial fulfillment of the requirements for

Masters of Science, Psychology

Wilfrid Laurier University

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Abstract

In Experiment 1, pigeons were trained with a 1-s baseline $s - c$ delay in a duration comparison procedure to peck one key if a comparison duration (c) was 1-s shorter than a standard duration (s), and another key if c was 1-s longer than s . The duration pairs used prevented pigeons from relying on the absolute duration of c on some trials (comparison common) while on other trials they could rely on the absolute duration of c (comparison unique). Pigeons were then tested with equal duration pairs at extended $s - c$ delays of 1, 2, 4, and 8 s. Long responding increased as a function of $s - c$ delay length and at the 8-s $s - c$ delay responding was indicative of a reliance upon the absolute duration of c . In Experiment 2, no-standard probe testing was used to assess whether responding was controlled by the absolute duration of c at the 8-s $s - c$ delay. Long responding on comparison common durations of c was significantly higher than 8-s $s - c$ delay testing, which suggested that the memory of s was still impacting long responding. In Experiment 3, pigeons were trained with white vertical lines superimposed onto the keys to make the trial presentation phase distinct from the intertrial interval (ITI). Extended $s - c$ delay testing with equal duration pairs revealed similar $s - c$ delay functions to Experiment 1 when the lines were present throughout the $s - c$ delay, but not when the lines were absent from the $s - c$ delay. Taken together, these results suggest that subjective shortening can account for the increase in long responding on comparison common trials in Experiment 1 and line-present test trials in Experiment 3.

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Pigeons' Memory for Time: Assessment of the Role of Subjective Shortening in the Duration Comparison Procedure

Time is an inescapable constant in the lives of both humans and animals. On one hand, circadian timing is responsible for large-scale biological processes such as sleeping and wakefulness, appetite, and metabolic rate. On the other hand, interval timing is responsible for smaller-scale temporal processes such as time estimation. Interestingly, in terms of interval timing, animals possess the ability to precisely estimate, produce, and reproduce short temporal durations without the need for an external stimulus to keep track of time (Buhusi & Meck, 2005). Interval timing has been studied not only in humans but a wide variety of species including birds, fish, rodents, and primates.

These abilities suggest the existence of some kind of internal processor through which animals can keep track of time. In fact, some research has suggested that the internal clock works very much like a stopwatch, which can be started and stopped, reset and restarted (Roberts & Church, 1978). Since animals appear to process time using an internal clock, the nature of how animals encode and retain temporal information is an interesting question. Like humans, the ability of animals to retain temporal information may be related to several factors such as the length of retention, attention, and motivation.

Recently, however, researchers have turned to increasingly complex questions aimed at identifying the internal mechanisms responsible for timing in humans and animals. For example, different drugs have been shown to increase or decrease the speed of the internal clock (Meck, 1983) while other drugs have been shown not to disrupt the speed of the internal clock, but instead the representation of temporal information stored in memory (Santi & Weise, 1995). Interestingly, the results of drug studies have led to further research which suggests that several

mechanisms in the brain are responsible for different scales of timing. The cerebellum, for example, has been implicated in timing on the order of milliseconds, which is relevant to its role in the coordination of fine motor movement required in sports, speech, and music (Malapani, Dubois, Rancuel, & Gibbon, 1998). On the other hand, interval timing in the seconds to minute range is dependent on the striatum (Meck, 1996). The 24-hour circadian rhythm, or clock, has been shown to originate from hypothalamic circuitry (Reppert & Weaver, 2002). While it has been shown that these different mechanisms can operate independently of one another, current research is investigating how these mechanisms may interact and turned to developing more sophisticated models of timing that incorporate these different areas of the brain.

Much of the research in timing has originated in or has been supported by animal models and research, since humans and animals share similar underlying structures that are involved in timing. An important question with respect to interval timing in animals has addressed how temporal information is mentally represented and how long it can be remembered. The study of memory for time in pigeons (e.g., Spetch & Wilkie, 1983), rats (e.g., Church, 1980), and monkeys (e.g., Oshio, Chiba, & Inase, 2006) has allowed for the exploration of how animals represent and remember temporal information as well as allowing comparisons to be drawn between other species, including adult humans (e.g., Wearden & Ferrara, 1993) and young children (e.g., Rattat & Droit-Volet, 2001). The current series of experiments will explore how pigeons represent event durations in working memory and will attempt to provide evidence for a temporal foreshortening process in pigeons with a procedure that avoids the methodological artifacts of previous studies (see Zentall, 2007).

Pigeons' memory for time is typically studied using a delayed matching-to-sample (DMTS) procedure whereby a pigeon is required to indicate whether one of two possible sample

durations was presented on a given trial. These sample durations typically consist of the presentation of either a short-sample (e.g., 2 s) or a long-sample (e.g., 8 s) stimulus such as illumination of the houselight or feederlight within the operant chamber. Following trials initiated by the short sample, a pigeon may be required to peck a green key, and following trials initiated by the long sample, to peck a red key. However, when studying pigeons' memory for time, a commonly encountered memory bias known as the choose-short effect often occurs (Kraemer, Mazmanian, & Roberts, 1985; Sherburne, Zentall, & Kaiser, 1998; Spetch, 1987; Spetch & Wilkie, 1983). This choose-short effect is characterized by above-chance accuracy on short-sample trials as a delay is placed between the end of the sample presentation period and the opportunity to respond. Responding to the long sample on the other hand decreases to or below chance the longer the delay that is placed between the end of the sample presentation period and the opportunity to respond.

While several different explanations have been suggested to account for the choose-short effect, two explanations in particular have provided contrasting views as to why this bias in memory occurs. Subjective shortening proposes that the representation for the long sample in working memory shortens and increasingly becomes more similar to the representation of the short sample in working memory as the delay interval (DI) increases (Spetch & Wilkie, 1983). However, the instructional ambiguity/confusion hypothesis explains the choose-short effect in terms of a confusion that can occur when the DI and ITI share similar ambient illumination conditions (i.e., the houselight is either on or off during both the ITI and DI). When similar, the pigeon may confuse the DI with the ITI and upon presentation of the choice stimuli, respond as if it had not perceived a sample as being presented on that trial. With the memory of no-sample being more similar to the short sample, this provokes a bias to respond to the stimulus correct for

the short sample (Sherburne et al., 1998). In addition, if a pigeon is trained with a 0-s baseline delay between sample presentation and presentation of the choice stimuli, the novelty of a test trial (e.g., a DI) may in itself produce an ambiguity/confusion in how to respond, particularly if the ITI and the DI share similar illumination conditions (Dorrance, Zentall, & Kaiser, 2000).

A modified version of the DMTS procedure, known as the pair comparison or duration comparison procedure has also been used to study pigeons' memory for time (Dreyfus, Fetterman, Smith, & Stubbs, 1988; Dreyfus, Fetterman, Stubbs, & Montello, 1992; Fetterman, 1987; Fetterman & Dreyfus, 1986; Fetterman, Dreyfus, & Stubbs, 1989; Fetterman, Dreyfus, Smith, & Stubbs, 1988; Kraemer, 1990). In the duration comparison procedure, rather than being presented with a single sample duration on a given trial and having to match it to a comparison stimulus, a pigeon is presented with a standard duration (s) followed by a comparison duration (c), and the pigeon is required to indicate whether c was either shorter than or longer than s . Similar duration comparison studies have also examined humans' memory for temporal durations (Allan, 1977; Jamieson & Petrusic, 1975a, 1975b, 1976; Jamieson, 1977; Stott, 1935; Wearden & Ferrera, 1993; Wearden, Goodson, & Foran, 2007; Wearden, Parry, & Stamp, 2002; Woodrow, 1935; Woodrow & Stott, 1936). Although it is difficult to draw a direct comparison between pigeons' and humans' memory for temporal durations, more recent research has proposed similar processes to explain the types of errors that both humans and pigeons make when tested with various $s - c$ delays. Most notably, both humans (Wearden & Ferrera, 1993; Wearden et al., 2007; Wearden et al., 2002) and pigeons (Fetterman et al., 1988) have shown a tendency to indicate that $c > s$ at long $s - c$ delays.

The increase in responding $c > s$ at long $s - c$ delays has been suggested to occur through the process of the subjective shortening of s , whereby the representation of s in working memory

degrades over an $s - c$ delay and is then compared to a fresh representation of c during the decision process (Fetterman et al., 1988; Wearden & Ferrera, 1993; Wearden et al., 2007; Wearden et al., 2002). Since humans can be explicitly instructed on how to respond in a duration comparison task, the instructional ambiguity/confusion explanation may not be relevant to humans' performance and the types of errors which they make in the duration comparison procedure. However, in the small body of research examining pigeons' memory for time using the duration comparison design, the similarity of the illumination conditions between the $s - c$ delay and the ITI has not been investigated as a potential source of the increase in long responding as the $s - c$ delay increases.

However, the duration comparison procedure may already potentially prevent confusion between the $s - c$ delay and ITI from occurring, irregardless of the ambient illumination conditions during the $s - c$ delay and the ITI. In the duration comparison procedure, the delay is interposed between s and c , rather than between the presentation of the sample duration and choice stimuli as seen in the DMTS procedure. If pigeons are trained with two durations which are interposed by a short $s - c$ delay right from initial training, a pigeon may develop the expectation of experiencing both s and c on a given trial and it may also be less likely that a pigeon would confuse the $s - c$ delay with the ITI. Since the introduction of the instructional ambiguity/confusion explanation of the choose-short effect, researchers have sought to eliminate sources of confusion in the DMTS procedure so memory rather than responses attributed to confusion can be studied (Dorrance et al., 2000; Sherburne et al., 1998; Zentall, 1997, 1999, 2007). While some research using the DMTS procedure has demonstrated that the choose-short effect can be eliminated by differentiating the ambient illumination conditions during the ITI and DI (Dorrance et al., 2000; Sherburne et al., 1998), other studies have found that simply

differentiating the ambient illumination during the ITI and DI does not always eliminate the choose-short effect (Kelly & Spetch, 2000).

In Experiment 1 of the current study, pigeons were trained on a duration comparison procedure with a 1-s baseline $s - c$ delay to indicate whether c was either 1-s shorter than or 1-s longer than s . Whether subjective shortening or confusion between the $s - c$ delay and the ITI was responsible for pigeons' tendencies to report $c > s$ at long $s - c$ delays was then assessed by testing pigeons with equal duration pair probe trials at $s - c$ delays of 1, 2, 4, and 8 s. In Experiment 2 following $s - c$ delay testing, test sessions were administered where probe trials were presented that consisted solely of the seven different durations of c (Kraemer, 1990). These test sessions were used to elucidate whether responding at long $s - c$ delays was controlled by the absolute duration of c , consistent with an instructional ambiguity/confusion explanation of the increase in long responding at long $s - c$ delays. In Experiment 3, pigeons were trained using a similar procedure as in Experiment 1 except that white vertical lines were presented on all three keys of the operant chamber throughout s , the $s - c$ delay, c , and presentation of the comparison stimuli. Test sessions consisting of equal duration pair probe trials followed where the white vertical lines were either *present* or *absent* during the $s - c$ delay. Whether pigeons confused test trials where the lines were not present during the $s - c$ delay was further used to assess whether an increase in long responding at lengthy $s - c$ delays was produced by the confusion of the $s - c$ delay with the ITI or through subjective shortening.

The Information Processing Model of Animal Timing

The Information Processing Model of Timing has been one of the most widely accepted accounts of how animals perceive time and consists of three distinct processes (Gibbon, Church, & Meck, 1984). The clock process is made up of an internal pacemaker and a switch. When

timing, the switch closes and allows pulses from the pacemaker to be collected in the accumulator. For example, if the pacemaker emits pulses at a rate of 4 pulses per second, the reference memory of a short 2-s sample and a long 8-s sample would consist of 8 and 32 pulse counts respectively. Once the duration being timed has ended, the switch opens not allowing any further pulses to be accumulated. Next, the memory process is made up of working and reference memory. Working memory consists of the analogical representation from the current trial (e.g., 8 pulse counts) and reference memory contains analogical representations from past reinforced trials (e.g., 8 or 32 pulse counts for short- and long-sample trials respectively). In the comparator process the duration timed from a particular trial is then compared to a randomly sampled duration from reference memory and a response decision is made. However, whether animals encode time in an analogical fashion is an important question when studying the types of errors pigeons make when studying memory for time.

Pigeons' Memory for Time and Response Biases in the Delayed Matching-to-Sample Procedure

Typically, studies looking at memory for time in pigeons use the DMTS procedure where a pigeon is trained to discriminate between two different durations (e.g., 2 vs. 8 s). In this paradigm the pigeon receives one of these durations on a given trial and is required to make one response (e.g., red) following short-sample trials (2 s) and the alternative response (e.g., green) following long-sample trials (8 s). Once the pigeon has learned the discrimination, memory testing occurs where the pigeon must remember which sample had been presented over various DIs interposed between the sample presentation period and the opportunity to respond. Response accuracy usually declines as a function of DI length and a choose-short bias occurs, whereby accuracy remains relatively high on short-sample trials and declines to or below chance on long-sample trials as a function of DI length (Spetch & Wilkie, 1983). As previously noted, subjective

shortening explains the choose-short bias as a loss of pulse counts over a DI resulting in the memory of the long sample being more similar to that of the short sample.

Theoretical Explanations of Memory Biases in the Delayed Matching-to-Sample Procedure

Subjective Shortening. Spetch and Wilkie (1983) proposed a theory based on the analogical coding of temporal durations to account for the choose-short effect. Known as the subjective shortening hypothesis this theory posits that as a DI is interposed between the end of the sample presentation phase and the opportunity to make a response choice, the duration in working memory subjectively shortens as a function of DI length. Spetch and Wilkie had originally trained pigeons with a 0-s baseline delay to discriminate between 2 and 8 s of houselight or 2 and 8 s of food access. Pigeons were then tested using variable DIs (5 and 20 s) following sample presentation. It was found that regardless of the type of stimulus, although accuracy on short-sample trials remained relatively high compared to 0-s baseline training, accuracy on long-sample trials declined to below chance even at the 5-s DI. In a second experiment, to investigate whether the subjects were simply forgetting the long sample over the DI, different pigeons were trained to discriminate between short (2 s), medium (6 s), and long samples (8 s). Delay testing indicated that as a function of DI length, accuracy decreased on medium- and long-sample trials but not on short-sample trials. This indicated that the pigeons were not just forgetting the long sample, but as the DI increased, the medium and long samples were more prone to subjective shortening. Overall, Spetch and Wilkie's subjective shortening model explains the choose-short effect in terms of a discrepancy in working memory of a given trial compared to a stable reference memory of past reinforced trials established during 0-s baseline training. As the remembered duration of the long sample (e.g., 8 s) subjectively shortens over a long DI, the remembered duration in working memory may be perceived as being more

similar to the short sample (e.g., 2 s), resulting in a tendency to make the response correct for short.

The Relative Duration Hypothesis. Spetch and Rusak (1989) proposed a modification of the subjective shortening explanation of memory biases that takes the relative duration of a given trial into account. In a DMTS task, they had found that when the ITI was lengthened beyond the baseline value used during training, pigeons showed a choose-short effect. Alternatively, a choose-long effect was also found when the ITI was shortened from the baseline value used during training. Since a similar effect was found for manipulation of the DI, Spetch and Rusak proposed that how pigeons remember temporal durations depends upon the “temporal context” in which they occur. In essence, Spetch and Rusak found that if the temporal context was lengthened by increasing the length of either the ITI or DI a tendency to choose the response choice correct for the short sample was observed. Alternatively, if the temporal context was shortened by reducing the length of either the ITI or DI from that of baseline training, then an opposite tendency to choose the response choice correct for the long sample occurred. Similar to the subjective shortening model, the relative duration modifications were still based on the discrepancy between working and reference memories but it emphasized the analogical coding of the short and long samples being associated with their respective correct responses in the temporal context employed during training (Spetch & Rusak, 1992).

Categorical Coding Models. Kraemer, Mazmanian, and Roberts (1985) proposed a categorical coding, rather than analogical coding model to account for the choose-short effect. A categorical code would require a pigeon to code a temporal sample on some dimension other than time, such as to code a 2-s short-sample trial as “peck-red” and a 10-s long-sample trial as “peck-green”. Instead of explaining the choose-short effect in terms of an analogical code

deteriorating over time as described by subjective shortening, Kraemer et al. suggested that following different samples pigeons would adopt a response strategy based on different categories such as “peck-short” and “peck-long”. However, if the strategy used to “peck-long” is forgotten over a long DI and the remembered stimulus duration would be 0 s, the pigeon would generalize to the “peck-short” code resulting in the choose-short effect. Kraemer et al. had trained pigeons to discriminate between 0, 2, and 10 s of amber light. Pigeons were then tested with various delays ranging from 3 to 21 s and the pigeons were given the opportunity to respond to the short-, long-, or no-sample keys. Results suggested that pigeons adopted some other strategy besides an analogical code because responding to the short-sample key was very low and did not vary across delays. If the subjects had been using an analogical code, then short sample responding should have increased when the long sample had subjectively shortened to the point where it was most similar to the short sample. Comparatively, responding to the long-sample key declined across delays due to the response strategy to “peck-long” being forgotten and the pigeons generalizing to the no-sample key. Kraemer et al. clearly demonstrated that pigeons were capable of adopting a categorical code.

The Instructional Ambiguity/Confusion Hypothesis. It has been found that when the ITI matches the same illumination conditions as those of the DI, a confusion or ambiguity in how to respond can occur. The subject may confuse the DI with the ITI and when presented with the comparison stimuli at the end of a DI, which the subject may perceive as the ITI, may not remember what it had just experienced. Therefore, having “nothing” in memory more closely resembles the short (e.g., 2 s) rather than long sample (e.g., 8 s), provoking a tendency for the pigeon to choose the comparison correct for the short sample. An abundance of evidence for the instructional ambiguity/confusion hypothesis has resulted in its support for explaining why

memory biases occur, particularly in pigeons (Sherburne et al., 1998; Santi et al., 2006; Zentall, 1997, 1999, 2007). However, some research has revealed that the instructional ambiguity/confusion hypothesis does not always account for the choose-short effect. Kelly and Spetch (2000) found that pigeons revealed a symmetrical decline in accuracy on both the short and long samples when the ITI was dark and DI was illuminated. However, when the ITI was illuminated and the DI was dark, a choose-short effect was observed.

The Signal Detection Hypothesis. Spetch and Wilkie (1983) had previously discovered that pigeons respond “short” if no-sample is presented in lieu of the actual short sample. Gaitan and Wixted (2000) examined the role of how important the actual presentation of the short sample (e.g., 2 s) is in the DMTS paradigm. The hypothesis being tested was whether pigeons actually search working memory for the presence of the short sample when faced with the choice stimuli, or instead search working memory for the presence of the long sample. In Gaitan and Wixted’s Signal Detection Hypothesis, the long sample is regarded as the more salient of the two samples, which drives responding based on whether or not it was present on a given trial. When Gaitan and Wixted trained pigeons in a DMTS task where short-sample trials shared the same response alternative as no-sample trials, accuracy remained high for both samples compared to a decline in accuracy on long-sample trials as the length of the delay increased. On the other hand, when long-sample trials shared the same response alternative as no-sample trials, accuracy remained high for both samples compared to a decline in accuracy on short-sample trials as the length of the delay increased. In the case of mapping the correct response for no-sample trials onto the correct response for short-sample trials, it was suggested that the pigeons were responding based on the memory for the presence or absence of the long sample. Inversely, mapping the correct response for no-sample trials onto the correct response for long-sample

trials, it was suggested that the pigeons were responding based on the memory for the presence or absence of the short sample. These results showed that when a discrimination task varies along a dimension such as time, pigeons can turn it into a detection task.

Pigeons' Memory for Time using a Duration Comparison Procedure

Research examining the perception and memory for time in pigeons has been dominated by the use of the DMTS procedure. However, a small body of research has employed a variant of this procedure to study pigeons' memory for time (Dreyfus, Fetterman, Smith, & Stubbs, 1988; Dreyfus, Fetterman, Stubbs, & Montello, 1992; Fetterman & Dreyfus, 1986; Fetterman et al., 1989; Fetterman, Dreyfus, Smith, & Stubbs, 1988; Fetterman, Dreyfus, & Stubbs, 1989; Kraemer, 1990). Fetterman and Dreyfus (1986) first modified the DMTS design to incorporate the presentation of more than a single duration on a given trial. In the majority of their experiments which followed their original adaptation of the duration comparison procedure for studying pigeons' memory for time, Fetterman and colleagues followed a similar procedure throughout each of their experiments. At the start of a trial, pigeons were initially presented with illumination of the centre key with white light. A peck to the white key initiated the trial, and the centre key would change to the colour red, signalling that s had begun. After a given duration, which varied from trial to trial the red key would change to green indicating that c had begun. The green key would also remain on for a given duration, which varied from trial to trial. Once c had elapsed the centre key would become dark and the subject would be presented with yellow on the two side keys. A peck to the left key indicated that $c < s$, which would be reinforced if correct. On the other hand, a peck to the right key indicated that $c > s$, which would also be reinforced if correct. Incorrect responses would result in a time-out.

Fetterman and Dreyfus (1986) first demonstrated that pigeons were capable of indicating when $c < s$ and $c > s$ in a duration comparison procedure. When tested with unequal duration pair probe trials at various $s - c$ delays (0, 2, 5, 10, & 30 s), accuracy on extreme duration pairs (e.g., 2 vs. 16 s) remained relatively high even at the longest $s - c$ delays. However, accuracy on the more intermediate duration pairs (e.g., 4 vs. 8 s) decreased to chance levels as a function of $s - c$ delay length. Fetterman and Dreyfus (1986) also found that pigeons generalized relatively accurately to novel unequal duration pairs, particularly when the difference between s and c was larger (e.g., 2 vs 6 s) compared to when the difference between s and c was smaller (e.g., 3 vs 4 s). Although the pigeons were not tested with equal duration pairs using an $s - c$ delay, testing with equal duration pairs at the baseline 0-s $s - c$ delay produced predominantly $c > s$ responding. Interestingly, the observed increase in responding $c > s$ may have been the product of subjective shortening, which would represent a decrease in the remembered duration of s . In the duration comparison procedure, the representation of s would have to be maintained in working memory during the presentation of c . Thus, the longer c was, the greater the chance that s would have to subjectively shorten.

In a variant of the duration comparison task, Fetterman (1987) trained pigeons to make one response when s and c were of the same duration and another response when they were different. Compared to the previous work by Fetterman and Dreyfus (1986), Fetterman found that the pigeons were much less successful in learning the task. It was suggested that the pigeons could not classify the two different trial types (i.e., $c < s$, $c > s$) as requiring the same response (i.e., that they were different). Accuracy was higher on the equal duration pairs with a shorter total duration (e.g., 1-1 & 2-2) compared to the equal duration pairs with a longer total duration (e.g., 4-4 & 8-8), which again may have been indicative of the effects of subjective shortening

similar to those observed in Fetterman and Dreyfus (1986). Fetterman's previous research had also shown that when testing pigeons in the duration comparison design, c may gain more control over responding due to its proximity to the opportunity to gain reinforcement as well as the fact that compared to s , it was relatively "fresh" in memory when making a decision. Fetterman (1987) then attempted to improve performance by making c less than that of s , which would make control of responding on the absolute duration of c far more difficult. Although fewer errors were made, Fetterman suggested that discriminative responding was controlled by the relational properties of the two durations in some cases but also by the absolute value of c in other instances.

Dreyfus, Fetterman, Smith, and Stubbs (1988) examined to what lengths pigeons could make relational discriminations. It was found that pigeons were able to discriminate duration pairs which were largely different in duration, particularly duration ratios of either 1:4 or 4:1. However, accuracy had decreased as the duration ratio became smaller, decreasing the relative difference between s and c . The pigeons were also more likely to make an error where they were more likely to report $c > s$ when both durations were of equal length (e.g., 1:1). Dreyfus et al. (1988) further ruled out the possibility that pigeons were using spatial mediation to solve the task since training pigeons in a duration comparison task with non-spatial response choices revealed similar performance to the spatial response choices that had previously been used. It was suggested, though, that since there was variability in the way in which the subjects were responding that on some trials the pigeons were again making use of the predictable relation between s and c but also did not rule out the fact that they could be using the absolute value of a single duration as well, particularly with respect to extreme duration pairs.

In an unpublished manuscript, Fetterman et al. (1988) proposed a critical question regarding how an $s - c$ delay, post- c delay, or simply the length of the duration pairs would impact the control which c gained in discriminative responding. When the comparison duration belonged to an extreme category (i.e., 0.5 – 2 s; 8.5 – 16 s), pigeons' accuracy remained above chance as the $s - c$ delay increased. However, when the comparison duration belonged to an intermediate duration (i.e., 2.5 – 4 s; 4.5 – 8 s) pigeons' accuracy was closer to chance performance as the $s - c$ delay increased. With respect to the types of errors that pigeons were making, there was an increasing likelihood to respond $c > s$ following long $s - c$ delays, post- c delays, and an even greater tendency to report $c > s$ when tested with both an $s - c$ and post- c delay. At the longest $s - c$ delays it was suggested that c may have gained absolute control over discriminative responding while at shorter $s - c$ delays the relation between s and c may have had more control over responding, which was reflected in the differences in accuracy for the extreme and intermediate categories of the comparison duration. Fetterman et al. suggested two potential explanations for pigeons' tendencies to report $c > s$: the first being that the pigeons may have added the duration of the $s - c$ and post- c delays to the remembered duration of c ; and the second being the process of subjective shortening whereby the remembered duration of s is shortened over an $s - c$ delay and compared to an un-shortened memory of c .

It is evident that whether pigeons make a temporal discrimination on a relational basis had become the focus of duration comparison research. Regardless of whether pigeons were trained with a limited range of duration pairs (Fetterman & Dreyfus, 1986) or with a large range of duration pairs (Dreyfus et al., 1988, 1992; Fetterman et al., 1988; Fetterman et al., 1989) responding was controlled by both absolute and relational properties of the duration pairs. Dreyfus et al. (1992) noted that c may gain more control over responding due to its proximity to

the pigeons' ability to make a choice and gain reinforcement. Similar to a signal detection framework of timing (Gaitan & Wixted, 2000; Wixted & Gaitan, 2004), rather than basing salience on stimulus length, proximity to reinforcement may make c the more salient duration in the pair. While the bulk of duration comparison research has focused more on pigeons' perception of time and their ability to make relational discriminations, very few have examined pigeons' memory for time using $s - c$ delays (Fetterman & Dreyfus, 1986; Fetterman et al., 1988). When testing pigeons' memory for time in a duration comparison procedure, it is evident that as a delay is interposed between s and c , there is an increasing reliance on c . This change in how pigeons respond over an $s - c$ delay is interesting because of how this change in responding can be explained. As previously noted, Fetterman et al. (1988) had described the increase in long responding as a function of $s - c$ delay length as an effect of the subjective shortening of s , resulting in c being perceived as being longer than s . Fetterman et al. also suggested that pigeons may actually add the delay to c , biasing responses to indicate that $c > s$. However, Fetterman et al. did not entertain the possibility that some kind of confusion between the $s - c$ delay or post- c delay, may have resulted in some form of instructional ambiguity/confusion. Although previous research has shown that pigeons can learn a duration comparison procedure, the process behind the increase in long responding is not certain, particularly when other explanations such as instructional ambiguity/confusion as seen in the DMTS procedure has not been ruled out. Although the human timing literature has taken a somewhat different approach to the duration comparison procedure, more recently the same processes have been used to explain memory biases observed in the duration comparison procedure.

Humans' Memory for Time using a Duration Comparison Procedure

As noted earlier, in the duration comparison task, on a given trial the subject is presented with a standard duration (s) followed by a comparison duration (c). Allan (1979) identified two central variations of the typical duration discrimination task. The first being a forced-choice (FC) task using a "roving standard", whereby s and c both vary from trial to trial. The second being the more commonly encountered DMTS paradigm, where a subject is presented with only a single duration from either a pair or small range of durations on a given trial, and typically the subject must respond with one of two choices such as short or long. In addition, in the majority of human studies using the duration comparison procedure, duration pairs typically range on the order of milliseconds to prevent chronometric counting (i.e., 350 vs 500 ms). Response biases that arise in the human timing literature have been explained by time-order errors (TOEs). A positive time-order error (+TOE) occurs when s is incorrectly judged to be longer than c , and inversely, a negative time-order error (-TOE) occurs when s is incorrectly judged to be shorter than c . Research in humans has demonstrated that like pigeons, the length of a duration pair influences the likelihood of reporting that $c > s$. Allan (1977) asked her participants to report whether $c < s$ or $c > s$ when s and c consisted of flashes of light. One group of subjects were tested with duration pairs which ranged from 70 to 160 ms and another group of subjects were tested with duration pairs which ranged from 900 to 1200 ms. Within each group, on some trials s and c were of the same length. As the length of the duration pair increased in each group, especially on equal duration pairs, subjects were more likely to make a -TOE (i.e., report $c > s$). Although in Allan's (1977) study, subjects were tested with a 1-s baseline $s - c$ delay, the length of the $s - c$ delay has also been linked to an increase in responding $c > s$ in human studies using the duration comparison task. Even early studies have demonstrated that the probability of

obtaining a $-TOE$ increases as a function of $s - c$ delay length (Stott, 1936; Woodrow, 1936) and have also been reported to be present in other cognitive processes such as pain perception (Geertsma, 1958). There has been some investigation into whether a $-TOE$ and subjective shortening are the same process, as well as whether subjective shortening is a phenomenon solely encountered in animals (Wearden & Ferrera, 1993; Wearden et al., 2007).

Recent research using the duration comparison procedure to study memory for temporal durations in humans has suggested similar processes to explain the increase in long responding that is observed in pigeons. Human research has been characterized by duration pairs on the order of milliseconds to prevent chronometric counting and the use of a constant rather than variable difference between s and c . Similar to Fetterman (1987), Wearden and Ferrera (1993) asked their participants to indicate whether c was either the same or different from s . It was found that participants showed an increase in reporting duration pairs of equal length (e.g., 0.5 s followed by 0.5 s) as being different, suggesting that the representations of s and c in working memory were not stable over time. This finding was further corroborated by the fact that when given the opportunity in another experiment to report whether c was shorter, longer, or equal to s , the likelihood of reporting $c > s$ increased as a function of $s - c$ delay length. Wearden and Ferrara (1993) suggested that the increase in long responding occurred because of subjective shortening, which had previously been used to explain biases in pigeons' memory for temporal durations (e.g., Spetch & Wilkie, 1983). However, Wearden and Ferrara also noted that at short $s - c$ delays participants were also making a $+TOE$. Wearden, Parry, and Stamp (2002) found similar results to Wearden and Ferrara (1993) in that the likelihood of responding $c > s$ increased as a function of $s - c$ delay length. Wearden et al. further found evidence for subjective shortening in humans but also tested whether subjective shortening could be applied to a

dimension outside of time, such as the physical length of stimuli. It was found that subjective shortening-like effects did not occur for length judgments and may be specific to temporal judgments.

In a further test of whether subjective shortening was responsible for the increase in long responding, Wearden et al. (2007) tested subjects with filled and unfilled auditory and visual intervals. Filled intervals consisted of the presentation of continuous tones or visual stimuli as s and c , while unfilled intervals consisted of the presentation of very brief clicks or lines that defined the lengths of s and c . When subjects were required to indicate whether c had been shorter, longer, or equal to s , subjective shortening-like effects were observed at long $s - c$ delays for filled and unfilled visual stimuli, filled auditory stimuli, but not unfilled auditory stimuli. As opposed to also having the option to indicate when a duration pair was equal, when participants were only given the opportunity to respond either $c > s$ or $c < s$, Wearden et al. found that long responding on equal duration pairs increased as a function of $s - c$ delay length for all trial types. Responding was also characterized by a +TOE at short $s - c$ delays. It was suggested that this +TOE arose from prospective interference from timing s and c when they occurred close together in time (i.e., a very short $s - c$ delay). Wearden et al. offered an explanation using the Information Processing Model of animal timing in that the process of timing s and storing that duration in working memory is not an instantaneous process. Therefore, using the Information Processing Model, when the switch of the internal clock opens at the end of the sample presentation period and the timed duration is being transferred to working memory, by the time c is presented the process of storing s in working memory may not yet be finished, causing pulses to be missed when timing c . In conclusion, the data obtained by Wearden et al. (2007) were consistent with past research (Wearden & Ferrara, 1993), which indicated that the way in which

humans remember time in a duration comparison procedure is characterized by a +TOE at short $s - c$ delays and a -TOE at long $s - c$ delays.

Although research using the duration comparison procedure with humans and pigeons has used similar mechanisms to explain how response choices change with increasing $s - c$ delay, the differences in forming the duration values in the respective studies have been inherently different. For instance, Wearden and colleagues' experiments with humans had used significantly smaller duration ranges on the order of milliseconds (e.g., 250 – 550 ms), while Fetterman and colleagues' experiments with pigeons had used much larger differences between duration pairs and even used huge ranges of duration pairs (e.g., 1.0 – 32.0 s). The current experiments will make use of Fetterman and colleagues' adaptation of the duration comparison design in studying temporal perception and memory in pigeons. However, the duration pairs used are much more similar to Wearden and colleagues' research, where the range of duration pairs are far more limited and even overlap to some degree. One of the obvious benefits of designing the current experiment using Wearden's design as a template is that the potential for relying solely on c is far less likely since the range of duration values are much smaller and separated by a constant value compared to a variable difference between s and c as seen in the studies of Fetterman and colleagues.

Experiment 1

The goal of the first experiment was to examine the role of subjective shortening in the duration comparison task when the $s - c$ delay and ITI share similar illumination conditions. Although previous research in both pigeons (Fetterman et al., 1988) and humans (Wearden & Ferrara, 1993; Wearden et al., 2002, 2007) have suggested a role for subjective shortening in explaining the increase in long responding at lengthy $s - c$ delays in the duration comparison

procedure, whether similarities in the stimulus conditions during the $s - c$ delay and the ITI result in an increase in long responding as a function of $s - c$ delay length is unknown. In the DMTS procedure, research has shown that when the DI and ITI share similar illumination conditions, a choose-short bias is observed (Sherburne et al., 1998). Fetterman et al. (1988) had differentiated between the $s - c$ delay and ITI by training pigeons with a dark ITI and the houselight on during the trial presentation period and had observed an increase in long responding as a function of $s - c$ delay length.

Instructional ambiguity/confusion, however, may work much differently in the duration comparison procedure, since the absolute duration of c may provide sufficient information for correct responding (Fetterman & Dreyfus, 1986; Fetterman et al., 1988). If confusion between the $s - c$ delay and the ITI can account for the data one would predict an increase in long responding since pigeons may reset their internal clocks upon confusion of the $s - c$ delay with the ITI and compare c to a memory of no standard being presented. In the current study, instructional ambiguity/confusion was assessed by training pigeons in a duration comparison task that did not differentiate between the $s - c$ delay and ITI. In the duration comparison procedure, however, instructional ambiguity/confusion may not altogether occur since pigeons may develop an expectation of being presented with s and c on each trial. In the current study, by training pigeons with a 1-s baseline $s - c$ delay, the potential for $s - c$ delay and ITI confusion (Sherburne et al., 1998) or even test trial ambiguity (Dorrance et al., 2000) may be reduced.

In Experiment 1, pigeons were trained to make one response if c was 1 s shorter than s and another response if c was 1 s longer than s . The duration of s consisted of red presented on all three keys of the operant chamber, followed by a 1-s $s - c$ delay, which was then immediately followed by c , which consisted of green presented on all three keys. On $c < s$ trials, s ranged

from 2.0 to 4.0 s in 0.5-s increments and c was 1.0 s shorter than s . On $c > s$ trials, s ranged from 1.0 to 3.0 s in 0.5-s increments and c was 1.0 s longer than s . Following training, subjects were tested with equal duration pairs at various $s - c$ delays. It was hypothesized that as the $s - c$ delay was increased beyond 1 s the number of long responses would increase. Although subjective shortening has been proposed to account for the increase in long responding observed in humans (Wearden & Ferrera, 1993; Wearden et al., 2002, 2007), the process responsible for the increase in long responding observed in pigeons has remained somewhat unclear. Although Fetterman et al. (1988) had noted that subjective shortening may account for their data; it was also suggested that an increase in long responding could be attributed to pigeons adding the $s - c$ delay to c . In addition, whether similarities in the stimulus conditions between the $s - c$ delay and the ITI produce instructional/ambiguity confusion in the duration comparison procedure has yet to be investigated. Thus, the main objectives of Experiment 1 were twofold: 1) to observe whether pigeons demonstrate an increase in long responding as a function of $s - c$ delay length when the total duration of s and c was controlled for, and 2) to elucidate whether an increase in long responding at extended $s - c$ delays is observed when the $s - c$ delay and ITI share similar ambient illumination conditions.

Method

Subjects

Eight adult Silver-King pigeons were individually housed and maintained at 80% of their adult free-feeding body weights. Constant access to grit and fresh water was provided and the subjects were given post-session feedings of Purina Pigeon Chow to maintain their reduced bodyweights. The colony room was kept on a 12:12 light/dark schedule, with the lights turning on at 7:00 am each morning. Testing was conducted five days per week between 8:00 am and

1:00 pm. Five of the eight birds (# 34, 35, 37, 13, & 22) had previously served in a symbol summation study (Olthof & Santi, 2007) and the three remaining birds (# 14, 15, & 18) had previous experience in a study examining perception of filled and empty intervals (Santi, Keough, Gagne, & Van Rooyen, 2007). Although the previous experience of the subjects differed, discrimination accuracy on the duration comparison task was equivalent in both groups at the end of training (data not reported).

Apparatus

Four Coulbourn Instruments (Allentown, PA) modular operant test chambers (Model #E10-10), each housed within individual isolation cubicles (Model #E10-20) were used. Each cubicle was equipped with a baffled air-intake system and ventilation fan. Each test chamber was equipped with three circular translucent keys that were horizontally aligned approximately at a pigeon's standing sight line. Behind each of the keys was a projector which displayed red, green, and yellow onto a frosted rear projector screen (Model #E21-18). Directly below the centre key was a 5.7 x 5 cm opening, which during reinforcement provided access to a food hopper containing mixed grain. During reinforcement a light inside the opening was illuminated (Model #E14-10 with bulb #S11819X). Located 6.5 cm above the centre key was a houselight (Model #E14-10) capable of directing light upward to reflect off of the top of the cage but was not used in the current series of experiments. The organization and recording of all experimental events and responses were performed by a microcomputer system within the same room.

Procedure

Discrimination Training. Figure 1 illustrates the duration comparison procedure used in the current experiment. A given trial began with the presentation of *s*, which consisted of red presented on all three keys. Following the presentation of *s*, there was a 1-s *s* – *c* delay where all

three of the keys went dark. Once the 1-s dark $s - c$ delay terminated c was presented, which consisted of green presented on all three keys of the operant chamber. Both s and c were presented on all three keys of the operant chamber to increase the salience of the sample presentation phase. Following a 0.5-s dark delay, yellow was presented on both of the side keys. The short 0.5-s delay between c and the presentation of the choice stimuli was used to prevent pigeons from responding instantaneously if pecking one of the side keys during the presentation of c . For half of the subjects, if $c < s$ a peck to the right key was correct, while if $c > s$ a peck to the left key was correct. Assignment of the correct response for the other half of the subjects was reversed. Spatial response alternatives were used since previous research in pigeons had shown that spatial or non-spatial response alternatives in a duration discrimination task yield very similar performance (Dreyfus et al., 1988). If the pigeon made the correct response, it was rewarded with access to mixed grain for 4 s followed by a dark ITI of variable length (4, 8, 16, or 32 s). If incorrect, the pigeon was given a 4-s timeout, followed by a correction trial consisting of the same duration pair as the previous trial. Correction trials continued until the subject made the correct response, which was followed by the ITI and a novel trial configuration. Within each block of ten trials each of the five different duration pairs for $c < s$ and $c > s$ trials occurred once for a total of ten trials per block. The order for each subject in which the trials were presented was randomized and each session consisted of 160 trials. Each pigeon was trained on the duration comparison task for 75 sessions and then moved on to $s - c$ delay testing. On the 75th session of discrimination training subjects were making an average of 22.0% long responses on $c < s$ trials and an average of 68.4% long responses on $c > s$.

Duration Values. Table 1 illustrates the ten duration pairs used during 1-s baseline $s - c$ delay training. The durations used in the current study were created in a similar fashion to the

procedure initially used by Wearden and Ferrara (1993). Previous studies in humans have shown that these types of trial configurations have produced data consistent with the subjective shortening hypothesis (Wearden & Ferrara, 1993; Wearden et al., 2007; Wearden et al., 2002). The range of the duration pairs used was 1.0 to 4.0 s in 0.5-s increments. Despite pigeons' ability to discriminate very short temporal durations of visual stimuli (Yamashita, 1986), this larger duration range was used to enhance the discriminability of the duration pairs. On $c < s$ trials, s ranged from 2.0 to 4.0 s in 0.5-s increments, and c was 1 s shorter. On $c > s$ trials, s ranged from 1.0 to 3.0 s in 0.5-s increments, and c was 1 s longer. The configuration of $c < s$ and $c > s$ trials prevented subjects from relying on the total duration of s and c combined across all trial types. The total duration of a given trial including s , c , and the 1-s $s - c$ delay ranged from 4.0 to 8.0 s in 1.0-s increments for both $c < s$ and $c > s$ trials. Therefore, the total duration of an individual trial could not serve as a discriminative cue for correct responding during training as well as during extended $s - c$ delay testing. However, duration pairs which had unique comparison durations for each trial type made it possible for pigeons to make a correct response based on the absolute duration of c : on two of the $c < s$ trials, the duration pairs 2.0 – 1.0 and 2.5 – 1.5; and on two of the $c > s$ trials, the duration pairs 2.5 – 3.5 and 3.0 – 4.0. The three remaining duration pairs shared a common duration of c (2.0, 2.5, & 3.0), preventing subjects from responding solely on the basis of the absolute duration of c on these trials. Duration pairs used for equal duration pair probe testing were sampled from the entire 1.0 – 4.0-s range and were presented in increments of 0.5 s for a total of seven equal duration pairs.

Probe Testing with Equal Durations. Probe testing with equal duration pairs was conducted for 20 sessions consisting of 168 trials each. Within each session 70 trials occurred at the 1-s baseline $s - c$ delay for both $c < s$ and $c > s$ trials for a total of 140 baseline trials per

session. On a given session, subjects received one trial of every equal duration pair in increments of 0.5 s from 1.0 to 4.0 s occurring at the baseline 1-s $s - c$ delay as well as three extended $s - c$ delays (2, 4, & 8 s) for a total of 28 probe trials per session. During all probe trials the $s - c$ delay was spent in darkness. During probe testing correct responses were reinforced only on baseline $c < s$ and $c > s$ trials. On equal duration pair probe trials subjects were not reinforced for their responses and a response to either key led to a variable length dark ITI of 4, 8, 16, or 32 s. The correction procedure remained in use only on baseline $c < s$ and $c > s$ trials. All statistical analyses reported in this study were performed using Biomedical Data Package 7.0 (BMDP) or SPSS v 15.0 statistical software and used a rejection region of $p < 0.05$.

Results

Figure 2 illustrates the mean percent long responding during acquisition training across blocks of five sessions. The data are broken down into $c < s$ and $c > s$ trials and further subdivided by comparison unique and comparison common durations of c for each trial type. The acquisition data was subjected to a 2 (trial type) x 2 (comparison type) x 15 (blocks of five sessions) repeated measures ANOVA. The trial type variable consisted of two levels: $c < s$ trials and $c > s$ trials; the comparison type variable consisted of two levels as well: comparison common trials where pigeons could not base their response decisions on the absolute duration of c and comparison unique trials where pigeons could base their response decisions on the absolute duration of c ; and the blocks of five sessions variable had fifteen levels. A main effect of trial type was found which indicated that the pigeons were making significantly more long responses on $c > s$ trials compared to $c < s$ trials during discrimination training [$F(1,7) = 60.92, p < 0.001$].

The ANOVA also revealed a significant trial type x comparison type interaction [$F(1,7) = 9.97, p < 0.05$]. A simple main effects analysis performed on the significant trial type x

comparison type interaction revealed that the number of long responses on $c > s$ unique trials was significantly higher than $c > s$ common trials [$F(1,7) = 7.85, p < 0.05$]. In addition, the number of long responses on $c < s$ unique trials was significantly lower than $c < s$ common trials [$F(1,7) = 9.84, p < 0.05$]. The number of long responses had also significantly increased on $c > s$ trials [$F(14,98) = 2.29, p < 0.05$] and significantly decreased on $c < s$ trials [$F(14,98) = 15.65, p < 0.001$] as a function of blocks of sessions as revealed by a significant trial type x block interaction [$F(14,98) = 16.78, p < 0.001$]. Overall, the analysis revealed that accuracy on both $c < s$ and $c > s$ trial types significantly increased during training and accuracy was higher on comparison unique durations of c for both trial types.

Figure 3 presents the mean percent long responding on baseline trials during the last five sessions of discrimination training compared to $s - c$ delay testing. The data presented are broken down into $c < s$ and $c > s$ trials and subdivided into comparison unique and comparison common durations of c . The data were subjected to a 2 (trial type) x 2 (comparison type) x 2 (phase) repeated measures ANOVA. The trial type variable consisted of two levels: $c < s$ and $c > s$ trials; the comparison type variable consisted of two levels: comparison unique and comparison common; and the phase variable consisted of two levels: training and $s - c$ delay testing. The analysis revealed a significant main effect of trial type [$F(1,7) = 61.21, p < 0.01$] indicating that there was greater long responding on $c > s$ trials than on $c < s$ trials.

Although the analysis revealed that the trial type x comparison type interaction was not significant [$F(1,7) = 5.11, p = 0.06$], long responding on $c > s$ trials did not differ as a function of comparison type [$F(1,7) = 1.73, p > 0.05$] but on $c < s$ trials there was significantly more long responding on comparison common trials than on comparison unique trials [$F(1,7) = 11.92, p < 0.05$]. The analysis also revealed a significant comparison type x phase interaction [$F(1,7) =$

7.96, $p < 0.05$]. Long responding on comparison unique trials did not differ between training and $s - c$ delay testing [$F < 1$]. Although there was more long responding on comparison common trials during training than during $s - c$ delay testing, this difference was not statistically significant [$F(1,7) = 4.29, p = 0.07$]. Furthermore, during training although the difference was also not statistically significant, there was more long responding on comparison common than comparison unique trials [$F(1,7) = 4.96, p = 0.06$]. However, there was no difference in long responding during $s - c$ delay testing as a function of comparison type [$F < 1$]. The slight difference observed between long responding during training and $s - c$ delay testing was due to an increase in accuracy on $c < s$ common trials during $s - c$ delay testing. Besides the slight increase in accuracy on $c < s$ common trials, the data indicate that accuracy between training and testing was relatively similar on 1-s baseline $s - c$ delay trials.

Figure 4 displays the mean percent long responding during $s - c$ delay testing with equal duration pair probe trials. The data are presented collapsed across comparison common durations of c (2.0, 2.5, & 3.0 s) as well as the comparison unique durations of c for both $c < s$ (1.0 & 1.5 s) and $c > s$ (3.5 & 4.0 s) trial types. The data were subjected to a 3 (comparison type) x 4 ($s - c$ delay) repeated measures ANOVA. The comparison type variable had three levels: $c < s$ unique trials, comparison common trials, and $c > s$ unique trials and the $s - c$ delay variable consisted of four levels: 1, 2, 4, and 8 s. The data revealed a significant main effect of comparison type [$F(2,14) = 29.97, p < 0.01$], $s - c$ delay [$F(3,21) = 14.37, p < 0.01$], and a significant comparison type x $s - c$ delay interaction [$F(6,42) = 2.42, p < 0.05$]. A simple main effects analysis performed on the significant comparison type x $s - c$ delay interaction revealed that the number of long responses significantly increased as a function of $s - c$ delay length on comparison common [$F(3,21) = 10.46, p < 0.001$] and $c > s$ unique trials [$F(3,21) = 10.84, p < 0.01$] but not

on $c < s$ unique trials [$F(3,21) = 1.93, p > 0.05$]. Single sample t -tests were used to assess whether the mean percent long responses were actually significantly above or below 50% indicative of a -TOE or +TOE respectively. On $c < s$ unique trials, a +TOE was observed at the 1- and 4-s $s - c$ delays [$t(7) = 2.19, 3.22$, respectively, $ps < 0.05$]. On $c > s$ unique trials, a -TOE occurred at all of the $s - c$ delays except 1 s [$t(7) = 4.09, 13.28, 19.84$, $ps < 0.01$]. On comparison common trials, although a +TOE was observed at the 1-s $s - c$ delay [$t(7) = 3.40, p < 0.05$], the mean percent long responses was significantly above 50% at the 4- and 8-s $s - c$ delay indicative of a -TOE [$t(7) = 2.73, 5.06$, respectively, $ps < 0.05$]. The analysis illustrates that long responding was influenced by the both the length of the comparison duration as well as the length of the $s - c$ delay.

Discussion

Experiment 1 demonstrated that pigeons were capable of learning the duration comparison discrimination with a 1-s baseline $s - c$ delay. During subsequent $s - c$ delay testing with equal duration pairs, pigeons demonstrated a very similar pattern of responding on comparison common trials compared to humans. The $s - c$ delay function for comparison common durations of c was characterized by an increased likelihood to respond $c < s$ at the 1-s $s - c$ delay (i.e., +TOE) and $c > s$ at the 4- and 8-s $s - c$ delay (i.e., a -TOE; Wearden & Ferrara, 1993; Wearden et al., 2007). However, on comparison unique trials, responding appeared to be primarily controlled by the absolute duration of c . These results were also similar to those obtained by Fetterman et al. (1988), in that when available, pigeons relied on the absolute duration of c , and long responding increased as a function of $s - c$ delay length.

Similar to past research, the discrimination training data suggested that pigeons were influenced more by the absolute duration of c on some trials and by the relation of c to s on other

trials as demonstrated by the differences observed between comparison unique and comparison common trials (Dreyfus et al., 1988, 1992; Fetterman and Dreyfus, 1986; Fetterman, 1987; Fetterman et al., 1988). However, this may not have necessarily been related to the difference between s and c as found by Fetterman and Dreyfus (1986) or Fetterman et al. (1988) who used duration pairs with larger differences between s and c , which could have been more easily discriminated by the absolute duration of s or c . For example, in Fetterman et al.'s (1988) data, an extreme duration pair such as 2 vs 16 s would provide enough information from s or c alone to respond correctly, while an intermediate duration pair such as 4 vs 6 s would be far more difficult to rely on the absolute duration of s or c . Furthermore, during discrimination training the differences observed between pigeons' accuracy on comparison unique trials was related to the discriminability of the duration pairs. On the last block of five sessions during training, the mean percent long responding on $c < s$ unique trials was 17.6% (i.e., 82.3% accurate), while the mean percent long responding on $c > s$ unique trials was 72.8%. According to Weber's Law, the $c < s$ unique duration pairs 2.0 – 1.0 and 2.5 – 1.5 would be easier to discriminate than the $c > s$ unique duration pairs 2.5 – 3.5 and 3.0 – 4.0. However, on the last block of five sessions accuracy was 69.0% and 67.3% on $c < s$ and $c > s$ comparison common trials respectively.

Fetterman et al. (1988) had suggested that pigeons may time from the offset of s until the presentation of the comparison stimuli following post- c delays (i.e., adding $c +$ post- c delay), which would result in the length of c being considerably longer than s and account for the increase in reporting $c > s$ as the $s - c$ delay increased. In the current study, if pigeons had been adding the $s - c$ delay to s (i.e., timing until the onset of c), then there should be predominantly more short responses made at the long $s - c$ delays. Alternatively, if the pigeons had been adding the $s - c$ delay to c (i.e., timing from the offset of s), then there should be predominantly more

long responses made at the long $s - c$ delays since c would always be longer than s . However, as illustrated in Figure 4, on comparison common trials the number of long responses did not dramatically increase or decrease with longer $s - c$ delays as would be expected if the pigeons were adding the $s - c$ delay to c or s respectively. For example, during $s - c$ delay testing on baseline 1-s $s - c$ delay trials pigeons were making a mean of 65.4% long responses on the 1.0 – 2.0 s duration pair. If the pigeons were adding the $s - c$ delay to c (i.e., timing from the offset of s) the durations being compared would be 1.0 vs. 3.0 s. During $s - c$ delay testing, when faced with a 1.0 – 1.0 s equal duration pair at a 2-s $s - c$ delay, if pigeons were timing from the offset of s , the durations being compared would be the same as a 1.0 – 2.0 s baseline duration pair (i.e., 1.0 vs. 3.0 s). Thus, one would expect that a relatively similar number of long responses would be made at the 2-s $s - c$ delay on a 1.0 – 1.0 s equal duration pair if the pigeons were timing from the offset of s . However, during $s - c$ delay testing the number of long responses following the 1.0 – 1.0 s equal duration pair at the 2-s $s - c$ delay was 38.1%. Another example such as the 2.0 – 3.0 s baseline duration pair would result in comparison of 2.0 vs. 4.0 s if timing from the offset of s . Again at the 2-s $s - c$ delay, a 2.0 – 2.0 equal duration pair would yield the same comparison of 2.0 vs. 4.0 s (45.6% long responses), but again long responding was much higher during baseline trials (66.2%) where the same temporal comparison would be made, suggesting that pigeons were not adding the $s - c$ delay to c .

Since pigeons appeared not to time the $s - c$ delay and add it to c , two different explanations may account for the $s - c$ delay data: subjective shortening or instructional ambiguity/confusion between the dark $s - c$ delay and the dark ITI. Since it would be expected that pigeons would confuse a dark $s - c$ delay with a dark ITI, the confusion explanation may better explain the observed increase in long responding. Consistent with past research with

pigeons that indicates that c may have more control over discriminative responding (i.e., Dreyfus et al., 1992), the pigeons may have confused the dark $s - c$ delay with the dark ITI and reset their internal clocks. If pigeons confused the $s - c$ delay with the ITI, they may expect s to be presented representing the start of a new trial. When the pigeon is presented with c , it is then forced to make a decision based on the temporal information that c alone provided. As illustrated by the $s - c$ delay data, the duration of c significantly influenced long responding. At the 8-s $s - c$ delay, an ordinal relationship existed between the mean percent of long responding and the length of the comparison duration (42.5, 49.4, 55.6, 62.5, 75.6, 82.5, and 92.5%, for equal duration pairs 1.0 – 4.0 respectively). On comparison unique trials, it is logical to assume that pigeons would resort to a response strategy, which they used during training, where c gained more control of discriminative responding. However, on comparison common trials the same strategy would be useless since the absolute duration of c did not provide enough information to make a correct response decision during training. Therefore, at long $s - c$ delays, pigeons may have generalized the comparison common durations (2.0, 2.5, & 3.0 s) into the comparison unique categories used to respond on $c < s$ trials (i.e., if c equals 1.0 or 1.5 s respond short) and $c > s$ trials (i.e., if c equals 3.5 or 4.0 s respond long). In addition, beyond the 1-s baseline $s - c$ delay, the $s - c$ delay functions for all comparison types did not vary greatly, potentially suggesting that the length of c rather than the $s - c$ delay had more influence over long responding.

The alternative explanation of the increase in long responding is based on the subjective shortening of s over the $s - c$ delay. However, this explanation rests on the assumption that the pigeons did not confuse the dark $s - c$ delay with the dark ITI. As previously mentioned in the introduction to Experiment 1, it may be possible that the expectation of experiencing s and c on a

given trial and training pigeons with a nonzero baseline $s - c$ delay (e.g., 1 s) may altogether prevent confusion from occurring. Yet, the fact that instructional ambiguity/confusion predicts that the dark $s - c$ delay should be confused with the dark ITI and a strong ordinal relationship based on the length of the comparison duration existed at the 8-s $s - c$ delay, the data seem to suggest that confusion accounts for the increase in long responding during $s - c$ delay testing. However, which explanation can account for the data is difficult to discern since both explanations would theoretically produce an increase in long responding. Subjective shortening would presumably produce an increase in long responding for every equal duration pair as a function of $s - c$ delay length. An increase in long responding would also occur if the pigeons had confused the $s - c$ delay with the ITI, since a fresh memory of c would be compared to no memory of s . Regardless, it appears that further tests are required to elucidate whether confusion or subjective shortening was responsible for the increase in long responding on comparison common trials.

Experiment 2

Previous research in pigeons' memory for temporal durations using a duration comparison procedure has addressed the role of both absolute and relational properties of duration pairs controlling discriminative responding (Dreyfus et al., 1988; Dreyfus et al., 1992; Fetterman, 1987; Fetterman & Dreyfus, 1986; Fetterman et al., 1988). In the duration comparison procedure there is an increased probability of pigeons relying on c , since it is the duration closest to the opportunity to gain reinforcement (Dreyfus et al., 1992). When using an $s - c$ delay, the remembered duration of s is further back in time from the opportunity to emit a response and inherently changes the remembered duration of s , which may be required to make the correct response. Past research has shown that there is an increasing tendency to report $c > s$

as a function of both the length of the $s - c$ delay as well as the length of the duration pair in both the human (Allan, 1977; Wearden & Ferrera, 1993; Wearden et al., 2007; Wearden et al., 2002) and pigeon duration comparison literature (Fetterman & Dreyfus, 1986; Fetterman et al., 1988). Naturally, the question that arises from this change in responding as a function of $s - c$ delay length is whether responding at lengthy $s - c$ delays is based on the relation of c to s or on the absolute duration of c ? If subjective shortening was responsible for the increase in long responding in Experiment 1, it would suggest that the pigeons were making a relational judgment between a "fresh" un-shortened memory of c and a memory of s that has been subjectively shortened over an $s - c$ delay. However, the data obtained at the 8-s $s - c$ delay in Experiment 1 are of particular interest since they suggest that the pigeons may have confused the $s - c$ delay with the ITI.

Determining whether instructional ambiguity/confusion can account for the $s - c$ delay data in Experiment 1 would require that the pigeons be tested with probe trials consisting solely of c . This would be used to assess whether the long responding to c alone differs from when presented with both s and c during $s - c$ delay testing. In a matching-to-sample task, Kraemer (1990) presented pigeons with a standard duration immediately followed by a comparison duration on the centre key of an operant chamber, which was counterbalanced across stimulus colour (red, green) and duration (2, 8 s) for a total of eight trial configurations. One group of pigeons was reinforced for matching the 2 s duration to either a red or green side key that corresponded to the 2 s duration, while a second group of pigeons was reinforced for matching the 8 s duration to either a red or green side key that corresponded to the 8 s duration. Once the pigeons successfully learned the task where both s and c were presented, Kraemer administered probe trials where only s or c was presented on a given trial. It was found that following long

duration probe trials (e.g., just 8 s), regardless of the colour in which they were presented pigeons were as accurate as they were on normal trials where they received both *s* and *c*. On the other hand, following short duration probe trials (e.g., 2 s), regardless of the colour in which they were presented pigeons' accuracy was significantly below chance. Kraemer concluded that the pigeons in his study were not making a relational discrimination, but instead were using the presence or absence of the 8-s duration as a discriminative cue for responding. Although Kraemer's study did not use a large enough range of duration pairs to promote relational responding, Kraemer did note the importance of probe testing the pigeons with *s* and *c* alone to determine the extent of responding based on the absolute properties of the durations that were used. Not in any of the previous studies by Fetterman and colleagues had this method been used for determining whether their pigeons had been responding on an absolute or relational basis. The current study will be the first besides Kraemer (1990) to use this method to elucidate whether pigeons were responding on an absolute or relational basis in a duration comparison task. In addition, using this method to assess whether pigeons were responding on an absolute or relational basis will also serve as a means to assess whether subjective shortening or instructional ambiguity/confusion was responsible for the increase in long responding at long *s* – *c* delays.

According to signal detection theory (Gaitan & Wixted, 2000), in the DMTS procedure the longer of two samples is treated as the more salient of the two durations, and when presented with comparison stimuli after a delay interval, the pigeon searches its memory for the long sample. With respect to the signal detection theory (Gaitan & Wixted, 2000; Wixted & Gaitan, 2004), in the duration comparison procedure *c* is the more salient of the two durations chiefly because *s* is more prone to subjective shortening over an *s* – *c* delay and that *c* also occurs much more closely to the opportunity to respond and obtain food reinforcement (Dreyfus et al., 1992).

When faced with having to make a decision at a lengthy $s - c$ delay such as 8 s, the pigeon may search its memory for the remembered duration of s that was presented and when no memory of s is recalled, the pigeon will respond as if $c > s$.

Using a procedure somewhat similar to that of Kraemer (1990), in the current experiment pigeons were presented with random probe trials that consisted only of c . It was predicted that if the 8-s $s - c$ delay data from Experiment 1 can be explained in terms of the pigeons confusing the $s - c$ delay with the ITI, then the mean percent long responding on no-standard probe tests should not significantly differ from that of 8-s $s - c$ delay testing in Experiment 1. If there is no significant difference, this would suggest that the pigeons were responding as if they did not have a memory of s being presented. However, if long responding at the 8-s $s - c$ delay is significantly lower than the no-standard probe testing, this would suggest that the pigeons may still have some kind of memory for s even at the 8-s $s - c$ delay.

Method

Subjects and Apparatus

The same pigeons and apparatus from Experiment 1 were used in the current experiment.

Procedure

No-Standard Probe Testing. Following Experiment 1, each pigeon received a minimum of 3 sessions of 1-s baseline $s - c$ delay training before being moved on to the current experiment. The pigeons were given five sessions of no-standard testing, which were similar to baseline training sessions except that they received 140 baseline trials and an additional 28 trials per session where s was not presented. One block of twelve trials consisted of one of each of the ten baseline $c < s$ and $c > s$ trials and two no-standard trials. Baseline trials occurred with a probability of approximately 83% and no-standard trials occurred with a probability of

approximately 17%. On no-standard trials, subjects experienced only c (three green keys) following a variable length dark ITI of 8, 16, 32, or 64 s. The no-standard probe trials consisted of the presentation of each of the comparison durations ranging from 1.0 to 4.0 s in 0.5-s increments. On the no-standard trials, whether or not the subject made the long response was recorded but subjects were not reinforced and once a response was made the subject proceeded to a new trial. Following testing, planned comparisons were used to assess whether long responding significantly differed between 8-s $s - c$ delay testing and no-standard testing for each of the individual comparison duration categories. All statistical analyses reported in this study were performed using Biomedical Data Package 7.0 (BMDP) or SPSS v 15.0 statistical software and used a rejection region of $p < 0.05$.

Results

Figure 5 illustrates the mean percent long responding during 8-s $s - c$ delay testing in Experiment 1 compared to no-standard probe testing in Experiment 2. The data are represented by $c < s$ unique, comparison common, and $c > s$ unique durations of c . The data were subjected to a 3 (comparison type) x 2 (phase) repeated measures ANOVA. The comparison type variable consisted of three levels: $c < s$ unique (1.0, 1.5 s), comparison common (2.0, 2.5, 3.0 s), and $c > s$ unique (3.5, 4.0 s); and the phase variable consisted of two levels: 8-s $s - c$ delay testing and no-standard testing. There was a significant main effect of comparison type [$F(1,7) = 125.78, p < 0.01$] indicating that long responding increased as a function of the length of c . The comparison type x phase interaction was not significant [$F(2,14) = 2.62, p > 0.05$]. Planned comparisons between the 8-s $s - c$ delay and no-standard probe testing data revealed very similar levels of long responding on both $c < s$ unique trials [$t(7) = 0.86, p > 0.05$] and $c > s$ unique trials [$t(7) = 0.27, p > 0.05$]. However, on comparison common unique trials there were significantly more

long responses being made during no-standard probe testing compared to the 8-s $s - c$ delay data [$t(7) = 2.62, p < 0.05$]. Since the 8-s $s - c$ delay would be the $s - c$ delay most likely to be confused with the ITI and there was significantly less long responding (64.6%) compared to no-standard testing (73.6%), this suggests that s still had an impact on long responding even at the 8-s $s - c$ delay on comparison common trials.

Discussion

The data suggest that there must have been some memory of s still influencing long responding at the 8-s $s - c$ delay since significantly more long responding was observed during no-standard testing on comparison common durations of c . In addition, long responding was not significantly different when c was a comparison unique duration, which may be expected since as previously suggested in Experiment 1, the pigeons were using the same response strategy learned on comparison unique trials in training during $s - c$ delay testing. These results also reflect the fact that subjective shortening, rather than confusion, may account for the data on comparison common trials in Experiment 1 and that on these trials pigeons were making a relational judgment. As suggested in Experiment 1, if pigeons were confusing the $s - c$ delay with the ITI and they reset their clocks and rapidly erased s from working memory, the pigeons would always be comparing c to a value of 0. If confusion between the $s - c$ delay and ITI had indeed occurred and pigeons were comparing the memory of c to that of nothing (i.e., an s of 0) then there should have been no differences observed between no-standard and 8-s $s - c$ delay testing. However, one must also consider that if the pigeons confused the $s - c$ delay with the ITI in Experiment 1, then the pigeons may have adopted a strategy of responding on comparison common trials based on how well the comparison common durations generalized to comparison unique categories. At the 8-s $s - c$ delay, it may have be plausible that the pigeons generalized

the 2.5 s and 3.0 s comparison common durations of c (62.5 % and 75.6% long responding respectively) into the $c > s$ unique category. The 2.0 s comparison common duration of c may have been more difficult to classify into either the $c < s$ or $c > s$ unique categories resulting in closer to chance performance (55.6% long responding). Although the no-standard testing data suggest that pigeons were not confusing the $s - c$ delay with the ITI, by training the pigeons with an ITI that is distinct from the $s - c$ delay, it may be possible to rule out whether the increase in long responding on comparison common trials in Experiment 1 was caused by the pigeons confusing the $s - c$ delay with the ITI.

Experiment 3

In Experiments 1 and 2, during an entire session the houselight had remained off, which according to the instructional ambiguity/confusion hypothesis should have made the $s - c$ delay confusable with the ITI. Several studies using the DMTS procedure have demonstrated that if the ambient illumination conditions in the ITI are different from that of the DI, then the choose-short effect does not occur, and a symmetrical decline in accuracy as a function of DI length is observed for both short- and long-sample trials (Dorrance et al., 2000; Sherburne et al., 1998; Spetch & Rusak, 1992). Since the results of Experiment 2 suggest that confusion did not occur, whether instructional ambiguity/confusion can occur in the duration comparison procedure is an important question. As previously noted, Fetterman et al. (1988) also observed an increase in long responding as a function of $s - c$ delay length, but right from training the entire trial presentation phase had been made distinct from the ITI by using houselight illumination. Since a similar increase in long responding was observed on comparison common trials in Experiment 1, making the $s - c$ delay distinct from the ITI may not necessarily be critical for avoiding confusion in the duration comparison procedure. In addition, as illustrated by Kelly and Spetch

(2000), simply differentiating the ITI from the DI in the DMTS procedure may not necessarily eliminate any response biases. Past research has also shown that by simply illuminating the $s - c$ delay, the presentation of another visual stimulus may also degrade, distort, or even erase the memory of s from working memory during the $s - c$ delay (Grant & Roberts, 1976; Grant, 1988; Harper & White, 1997). Rather than using ambient houselight illumination as a means to distinguish the $s - c$ delay from the ITI (Fetterman et al., 1988), the current experiment attempted to make the $s - c$ delay distinct from the ITI by adding white vertical lines to the keys of the operant chamber throughout the entire trial presentation period.

In the current experiment, pigeons were trained similarly to Experiment 1 in that they were required to indicate whether c was 1 s shorter than or 1 s longer than s . The duration of s consisted of red presented on all three keys of the operant chamber, followed by a 1-s $s - c$ delay, which was then immediately followed by c consisting of green presented on all three keys. However, during the presentation of s , the $s - c$ delay, c , and presentation of the choice stimuli the pigeons were presented with a white vertical line superimposed on all three keys of the operant chamber. Pigeons were then tested with equal duration pairs at $s - c$ delays of 1, 2, 4, and 8 s. During one type of test session, the white vertical lines remained on during s , the $s - c$ delay, c , and the presentation of the choice stimuli. During the other type of test session the vertical lines remained on during s , c , and the presentation of the choice stimuli but *not* during the $s - c$ delay. It was hypothesized that when the white vertical lines were present through s , the $s - c$ delay, c , and presentation of the choice stimuli that pigeons would learn not to confuse the distinct trial period with the ITI. If the data obtained in Experiment 1 were due to confusion between the $s - c$ delay and the ITI, it was predicted that line-present test sessions should produce $s - c$ delay functions that are dissimilar from Experiment 1. In particular, it was

expected that there should be no effect of $s - c$ delay on the percent long responding for equal duration pair trials. However, on alternate sessions where the white vertical lines were *not* present during the $s - c$ delay on equal duration test trials, it was predicted that pigeons should confuse the $s - c$ delay and ITI. If the data obtained in Experiment 1 were due to confusion between the $s - c$ delay and the ITI, it was predicted that line-absent test sessions should produce $s - c$ delay functions similar to those obtained in Experiment 1.

Method

Subjects and Apparatus

The same pigeons and apparatus from Experiment 1 and 2 were used in this study.

Procedure

Discrimination Training. Following Experiment 2, each pigeon received a minimum of 1 session of 1-s baseline $s - c$ delay training before being moved on to the current experiment. The same discrimination training procedure used in Experiment 1 was used in the current experiment except that a white vertical line (6 mm width) was superimposed on the centre of each of the three keys of the operant chamber during the presentation of s , the $s - c$ delay, c , and presentation of the choice stimuli. The white vertical line stimuli also remained on for the 0.5-s delay between the presentation of c and the choice stimuli. The duration pairs used during baseline $s - c$ delay training in Experiment 1 also remained the same and sessions consisted of 160 trials. The criterion used to determine whether a pigeon was ready to be moved on to $s - c$ delay testing was a minimum difference of 25% on $c < s$ and $c > s$ comparison common trials in a block of five sessions. After 30 sessions of discrimination training six of the eight pigeons were moved on to equal duration pair testing at various $s - c$ delays, while two birds were dropped from the study due to poor discrimination accuracy. On the last block of five sessions (sessions

26 to 30), the six pigeons that proceeded to $s - c$ delay testing were making a mean of 20.8% and 24.3% long responses on unique and common $c < s$ trials, respectively, and a mean of 68.0% and 61.8% long responses on unique and common $c > s$ longer trials, respectively. The mean difference between $c < s$ and $c > s$ comparison common trials was 37.50% on the last block of five sessions.

Equal Duration Probe Testing. During equal duration pair probe testing, pigeons were tested in alternating sessions where the white vertical line stimuli were either present or absent on all three keys of the operant chamber. During odd numbered test sessions (e.g., 1, 3, 5, etc.) the white vertical line stimuli used during discrimination training were present during s , the $s - c$ delay, c , and the presentation of the choice stimuli. Figure 6 provides an illustration of a line-present test trial. During even numbered test sessions (e.g., 2, 4, 6, etc.) the white vertical line stimuli used during discrimination training were present during s , c , and the presentation of the choice stimuli, but *not* during the $s - c$ delay. Figure 7 provides an illustration of a line-absent test trial. Similar to Experiment 1, during the alternating line-present and line-absent test sessions, pigeons received one trial of every equal duration pair in increments of 0.5 s from 1.0 to 4.0 s occurring at the baseline 1-s $s - c$ delay as well as three extended $s - c$ delays (2, 4, & 8 s) for a total of 28 probe trials per session. In addition, during both odd (i.e., line-present) and even (i.e., line-absent) numbered test sessions pigeons received 140 baseline trials for a total of 168 trials per session. In both test conditions, the equal duration pair probe trials occurred randomly, one in every sixth trial. Each pigeon received 20 alternating sessions of line-present and line-absent $s - c$ delay testing for a total of 40 test sessions. All statistical analyses reported in this study were performed using Biomedical Data Package 7.0 (BMDP) or SPSS v.15.0 statistical software and used a rejection region of $p < 0.05$.

Results

Figure 8 presents the mean percent long responding for all eight birds during the last session of baseline training following Experiment 2 compared to the first session of baseline training in Experiment 3. The data were subjected to a 2 (trial type) x 2 (comparison type) x 2 (experiment) repeated measures ANOVA. The trial type variable consisted of two levels: $c < s$ and $c > s$ trials; the comparison type variable consisted of two levels as well: comparison common trials where pigeons could not base their response decisions on the absolute duration of c and comparison unique trials where pigeons could base their response decisions on the absolute duration of c ; and the experiment variable also consisted of two levels: representing the last session of baseline training following Experiment 2 and the first session from Experiment 3. The mean number of long responses was significantly higher on $c > s$ trials compared to $c < s$ trials, as illustrated by the main effect of trial type [$F(1,7) = 193.42, p < 0.01$]. There was also a significant trial type x comparison type interaction [$F(1,7) = 8.43, p < 0.05$]. A simple main effects analysis performed on this interaction indicated that the pigeons were less accurate (i.e., making more long responses) on $c < s$ trials when the comparison was common than when it was unique [$F(1,7) = 22.30, p < 0.01$], but there was no significant difference observed in accuracy on $c > s$ trials between comparison common and comparison unique durations of c [$F(1,7) = 4.09, p > 0.05$]. In addition, there was also a significant trial type x experiment interaction [$F(1,7) = 25.23, p < 0.01$] and a simple main effects analysis revealed that accuracy decreased more on $c < s$ unique [$F(1,7) = 17.63, p < 0.01$] than on $c > s$ unique [$F(1,7) = 8.60, p < 0.05$] trial types from the last day of baseline training following Experiment 2 to the first day of baseline training in Experiment 3. Thus, the analysis revealed that there was some disruption in discrimination accuracy during the switch to training the pigeons with the white vertical lines

present throughout the entire trial presentation period. Since the pigeons had originally been trained without the lines present during the trial presentation phase, the addition of the line stimuli resulted in a generalization decrement. In addition, a similar analysis performed only on the data for the six birds that proceeded to $s - c$ delay testing found similar results.

Figure 9 displays the mean percent long responding during acquisition training for all eight birds in Experiment 3 across blocks of five sessions. The data presented are broken down into $c < s$ and $c > s$ trials and further subdivided by comparison unique and comparison common durations of c for each trial type. The acquisition data were subjected to a 2 (trial type) x 2 (comparison type) x 6 (blocks of five sessions) repeated measures ANOVA. The trial type variable consisted of two levels: $c < s$ and $c > s$ trials; the comparison type variable consisted of two levels as well: comparison common trials and comparison unique trials; and the blocks of five sessions variable had six levels. A main effect of trial type was found, which indicated that the pigeons were making significantly more long responses on $c > s$ trials compared to $c < s$ trials [$F(1,7) = 116.31, p < 0.001$]. There was also a significant trial type x block interaction [$F(5,35) = 10.43, p < 0.001$]. A simple main effects analysis performed on this interaction revealed that accuracy on $c > s$ trials did not significantly improve during training [$F < 1$], however, accuracy did significantly improve on $c < s$ trials as illustrated by the decrease in the mean number of long responses made on $c < s$ trials across blocks of sessions [$F(5,35) = 5.90, p < 0.001$]. This analysis illustrates that pigeons accuracy on $c < s$ trials, but not $c > s$ trials, had significantly increased across training sessions.

Figure 10 illustrates the mean percent long responding for the six pigeons that proceeded to $s - c$ delay testing during their last five discrimination training sessions before $s - c$ delay testing in Experiments 1 and 3. The data from Experiment 1 are presented in the top panel of the

figure and the data from Experiment 3 are presented in the bottom panel of the figure. The data presented are broken down into $c < s$ and $c > s$ trials and further subdivided by comparison unique and comparison common durations for each trial type. The data were subjected to a 2 (experiment) x 2 (trial type) x 2 (comparison type) x 5 (session) repeated measures ANOVA. The levels from all of the variables were the same as the previous analysis except for the experiment variable, which consisted of two levels: Experiment 1 and Experiment 3. A main effect of trial type was found which indicated that the pigeons were making significantly more long responses on $c > s$ trials compared to $c < s$ trials [$F(1,5) = 63.88, p < 0.001$]. A significant experiment x comparison type interaction was also found [$F(1,5) = 11.81, p < 0.05$]. A simple main effects analysis performed on the significant experiment x comparison type interaction indicated that in the last five sessions of discrimination training pigeons were making significantly more long responses on comparison common trials in Experiment 1 (49.2%) than in Experiment 3 (42.5%) [$F(1,5) = 8.89, p < 0.05$], which reflected the increase in accuracy on $c < s$ trials but not on $c > s$ trials during baseline training in Experiment 3. However, pigeons were making an equivalent number of long responses on comparison unique trials [$F < 1$] indicating that accuracy was equivalent on these trial types during the last five sessions of baseline training in both Experiments 1 and 3.

Figure 11 presents the mean percent long responding during baseline trials on the last five sessions of discrimination training in Experiment 3 compared to line-present and line absent $s - c$ delay testing sessions for the six pigeons that proceeded to $s - c$ delay testing. The data presented are broken down into $c < s$ and $c > s$ trials and subdivided into comparison unique and comparison common durations of c . The data were subjected to a 2 (trial type) x 2 (comparison type) x 3 (phase) repeated measures ANOVA. The trial type variable consisted of two levels: $c <$

s and $c > s$ trials; the comparison type variable consisted of two levels: comparison unique and comparison common; and the phase variable consisted of three levels: training, line-present, and line-absent $s - c$ delay testing. The analysis revealed a significant main effect of trial type [$F(1,5) = 140.23, p < 0.01$] indicating that there was greater long responding on $c > s$ compared to $c < s$ trials. There was also a significant trial type x comparison type interaction [$F(1,5) = 9.39, p < 0.05$], which revealed that long responding on $c < s$ trials did not significantly differ as a function of comparison type [$F(1,5) = 3.46, p > 0.05$] but on $c > s$ trials long responding was significantly higher on comparison unique than comparison common trial types [$F(1,5) = 9.55, p < 0.05$]. Overall, the data demonstrated that a similar pattern of responding was observed on baseline 1-s $s - c$ delay trials during training and both line-present and line-absent $s - c$ delay testing sessions. This suggests that probe testing at extended $s - c$ delays did not significantly disrupt accuracy on baseline 1-s $s - c$ delay trials.

Figure 12 displays the mean percent long responding during line-present $s - c$ delay testing. The data are represented by $c < s$ unique, comparison common, and $c > s$ unique durations of c . The data were subjected to a 3 (comparison type) x 4 ($s - c$ delay) repeated measures ANOVA. The analysis revealed a significant main effect of comparison type [$F(2,10) = 28.66, p < 0.01$], which indicated that long responding increased as a function of the length of the duration of c . Long responding also increased as a function of the length of the $s - c$ delay as illustrated by a significant main effect of $s - c$ delay [$F(3,15) = 4.47, p < 0.05$]. The $s - c$ delay x comparison type interaction was not significant [$F(6,30) = 1.55, p > 0.05$] but a simple main effects analysis revealed that long responding had significantly increased as a function of $s - c$ delay length on comparison common trials [$F(3,15) = 7.73, p < 0.05$] but not on $c < s$ or $c > s$ unique trials [$F_s(3,15) = 2.25, 1.65$, respectively, $p_s > 0.05$]. Additional single sample t -tests

were used to identify where the mean percent long responding significantly deviated from chance (50% long responses): $c < s$ unique trials demonstrated a +TOE at the 1- and 2-s $s - c$ delays [$t(5) = 2.57, 2.01, ps < 0.05$]; a +TOE was observed on comparison common trials at the 1-s $s - c$ delay [$t(5) = 3.63, p < 0.05$], but as the $s - c$ delay increased, although it was not significantly above 50%, long responding increased at the 8-s $s - c$ delay [$t(5) = 1.99, p = 0.052$]; and lastly, on $c > s$ unique trials, the mean percent long responding was significantly above 50% at all $s - c$ delays [$t(5) = 2.96, 4.06, 3.69, 3.28, all ps < 0.05$]. Similar to Experiment 1, comparison common trials demonstrated an increase in long responding as function of $s - c$ delay length, which was characterized by a shift from a +TOE at the 1-s $s - c$ delay to a -TOE at the 8-s $s - c$ delay. Since it would be difficult for a pigeon to confuse a line-present test trial with the ITI, the similarities in the $s - c$ delay functions compared to Experiment 1 suggest that confusion between the $s - c$ delay and the ITI was not responsible for the increase in long responding in Experiment 1.

Figure 13 illustrates the mean percent long responding for comparison common trials during $s - c$ delay testing in Experiment 1 and the line-present $s - c$ delay testing in Experiment 3. The $s - c$ delay functions for both Experiment 1 and 3 demonstrated a similar increase in long responding on comparison common trials as a function of $s - c$ delay length. The data were subjected to a 2 (experiment) x 4 ($s - c$ delay) repeated measures ANOVA. The experiment variable consisted of two levels: $s - c$ delay testing in Experiment 1 and line-present $s - c$ delay testing in Experiment 3; and the $s - c$ delay variable consisted of four levels: 1, 2, 4, and 8 s. The analysis revealed a significant main effect of $s - c$ delay length [$F(3,15) = 11.66, p < 0.05$]. No other main or interaction effects were significant. The analysis highlights the equivalent increase in long responding between $s - c$ delay testing in Experiment 1 and line-present $s - c$ delay

testing in Experiment 3. This supports the hypothesis that subjective shortening, rather than confusion between the $s - c$ delay and ITI was responsible for the increase in long responding.

Figure 14 illustrates the mean percent long responding during line-absent $s - c$ delay testing. The data are represented by $c < s$ unique, comparison common, and $c > s$ unique durations of c . The data were subjected to a 3 (comparison type) x 4 ($s - c$ delay) repeated measures ANOVA. The analysis revealed a significant main effect of comparison type [$F(2,10) = 28.66, p < 0.01$] which indicated that long responding was influenced by the length of the comparison duration. No main effect of $s - c$ delay length or significant $s - c$ delay length x comparison type interaction was found. Thus, the analysis makes it clear that during line-absent test sessions, the length of the $s - c$ delay had no bearing on long responding for any of the comparison types. Long responding was only influenced by the length of the equal duration pairs. The only significant deviations from chance were a +TOE at the 2- and 4-s $s - c$ delay on $c < s$ unique trials [$t(5) = 2.22, 2.76, ps < 0.05$]. The line-absent $s - c$ delay testing data were completely dissimilar from the pattern of data observed in Experiment 1 and the line-present $s - c$ delay data, which suggests that confusion between the $s - c$ delay and the ITI was not responsible for the data obtained in Experiment 1.

Discussion

On comparison common trials, during line-present test sessions $s - c$ delay functions similar to Experiment 1 were obtained. Since it would be very difficult to confuse the $s - c$ delay with the ITI on these test trials, this suggests that the data obtained in both Experiment 1 and the line-present test sessions were not produced by the pigeons confusing the $s - c$ delay with the ITI. On comparison common trials, similar to Experiment 1 an increase in long responding as a function of $s - c$ delay length was found and on comparison unique trials responding was

influenced more by the absolute duration of c . On the other hand, the $s - c$ delay functions obtained following line-absent test sessions indicated that the novelty of the dark $s - c$ delay resulted in a generalization decrement. Line-absent test trials were only influenced by the length of the equal duration pair and remained relatively unaffected by the length of the $s - c$ delay. On comparison common trials, responding was at chance and even on comparison unique trials long responding did not reliably differ from chance. In Experiment 1 and line-present testing in Experiment 3, this type of confusion may have been averted because extended $s - c$ delay trials were still similar to the 1-s baseline $s - c$ delay trials.

Grant and Roberts (1976) had noted that pigeons attend strongly to novel stimuli, which can interfere with the maintenance of the original discrimination on which they were trained. Although the temporal basis for the discrimination had remained the same between Experiments 2 and 3, the initial presentation of white vertical lines throughout s , the $s - c$ delay, c , and the presentation of the choice stimuli resulted in a decrease in pigeons' accuracy. This decrease in accuracy was characteristic of a generalization decrement caused by the addition of the white vertical lines to all three keys during the trial presentation period. After some initial disruption in discrimination accuracy, the six pigeons that progressed to $s - c$ delay testing were performing at very similar levels during the last five sessions of discrimination training before $s - c$ delay testing compared to Experiment 1. During training the mean percent long responding decreased significantly as a function of blocks of five sessions on $c < s$ trials (i.e., indicative of an increase in accuracy). Although there was a trend in the data that shows the number of long responses on $c > s$ trials increased across blocks of five sessions, this increase was not significant. Similar to Experiment 1, however, the training data suggest that pigeons were influenced more by the absolute duration of c on some trials as demonstrated by the fact that accuracy was once again

lower on comparison common trials compared to comparison unique trials (Dreyfus et al., 1988, 1992; Fetterman, 1987; Fetterman & Dreyfus, 1986; Fetterman et al., 1988). In addition, during $s - c$ delay testing there was also evidence that baseline performance on line-present and line-absent test sessions was similar suggesting that alternating test sessions did not significantly affect accuracy on baseline trials during $s - c$ delay testing. However, there appeared to be more influence of the length of c during baseline trials during $s - c$ delay testing compared to discrimination training. During line-present and line-absent test sessions, the number of long responses made to $c < s$ common trials as well as $c > s$ unique trials had significantly increased as a function of the length of c . No such differences related to the length of c were observed during the last five sessions of discrimination training.

The increase in long responding as a function of $s - c$ delay length during line-present test sessions does not reflect instructional ambiguity/confusion for several reasons. Primarily, it would be very difficult or impossible for a pigeon to confuse the $s - c$ delay during a line-present test trial with the ITI since the pigeons had been trained with the white vertical lines as a continuing part of a trial. What in fact may have transpired during line-present extended $s - c$ delay testing was that the presence of the lines throughout the $s - c$ delay may have served as a cue which indicated that they would be presented with c following s . Since similar $s - c$ delay functions were obtained in Experiment 1, the similarity between baseline training trials and extended $s - c$ delay test trials (i.e., the baseline and extended $s - c$ delays were both dark) may have had a similar effect, and have actually led pigeons to perceive that they were to still expect c to be presented following the dark $s - c$ delay. Compared to line-absent test trials, rather than having baseline trials which were similar to extended $s - c$ delay test trials with equal duration pairs, the dark $s - c$ delay without the lines present may have been confused with the ITI.

Fetterman et al. (1988) did not use a nonzero baseline training delay (i.e., 1 s) and obtained a similar increase in long responding as a function of $s - c$ delay length. However, this may be explained by the fact that only a quarter of the trials during testing were baseline 0-s $s - c$ delay trials. Coupled with the fact that the houselight remained on throughout the entire trial presentation period, this may have prevented Fetterman et al. from observing an effect of test trial ambiguity or novelty on extended $s - c$ delay test trials. Similar to line-present test trials in the current study, through having the houselight present through the $s - c$ delay, Fetterman et al.'s pigeons may have developed the expectation that they were still in the trial presentation phase. Fetterman et al. may have found a similar effect to the line-absent test condition if the houselight had been turned off during the $s - c$ delay.

Furthermore, since the line-absent test sessions were different from baseline training in Experiment 3, this led to a generalization decrement on these novel trials. Thus, the original context in which the pigeons were trained in Experiment 3 had changed. The response strategies that the pigeons had used during baseline training may not have been as efficiently or as accurately remembered when tested with the dark key presented alone on a line-absent test trial (i.e., an element of the original training compound; Roberts, 1998). Although coding decrement has been more successful in explaining data in simpler matching-to-sample procedures, the line-absent data may represent an inability to recall the correct response strategies that the pigeons had used in training. Grant and MacDonald (1990) had trained pigeons to match colors or lines that were cued by either a triangle or black dot. Following probe tests using incorrectly-cued and no-cue trials, a decrement in matching accuracy was found. Compared to the current experiment, the novelty of the white lines being absent from the keys during the $s - c$ delay may in fact have acted as an incorrectly-cued or no-cue test trials since the pigeons had been trained with the lines

being present as a continual part of a trial from the onset of s and right to the choice stimuli. For example, $c > s$ unique trials prompted the highest number of long responses (59.0%) and $c < s$ unique trials prompted the lowest number of long responses (38.4%), which suggests that the absolute duration of c was still influencing long responding during line-absent test sessions. However, without additional information about s , long responding remained relatively at chance on comparison common trials (48.3%). Although line-absent test trials produced a generalization decrement, it suggests that pigeons were not simply comparing c to a memory of $s = 0$ in working memory. If the pigeons just compared c to an $s = 0$, one would expect significantly more long responding. Instead, pigeons were probably randomly guessing on comparison common trials since they did not have sufficient information to make a response decision.

General Discussion

In Experiment 1, long responding increased as a function of $s - c$ delay length on comparison common trials. Since the $s - c$ delay and ITI were both dark and a strong ordinal relationship based on the length of the equal duration pairs was observed at the 8-s $s - c$ delay, it was suggested that pigeons may have been confusing the $s - c$ delay with the ITI and using the absolute duration of c to decide whether to respond $c < s$ or $c > s$. In Experiment 2, during non-standard testing the number of long responses on comparison common trials was significantly higher than at the 8-s $s - c$ delay in Experiment 1. Therefore, there may have been some residual effect of s on the memory of c even at the 8-s $s - c$ delay on comparison common trials, suggesting that subjective shortening rather than confusion between the $s - c$ delay and the ITI was responsible for the increase in long responding on comparison common trials in Experiment 1. In Experiment 3, pigeons were trained with white line stimuli superimposed on the keys during s , the $s - c$ delay, c , and the presentation of the choice stimuli and then tested with the

lines either present or absent during extended $s - c$ delays. When the lines were present during the $s - c$ delay (similar to the baseline 1-s $s - c$ delay), similar $s - c$ delay functions to Experiment 1 were found. When the lines were absent during the $s - c$ delay (dissimilar from the baseline 1-s $s - c$ delay), relatively flat $s - c$ delay functions were found suggesting that the novelty of the line-absent test trials produced a generalization decrement. Since it would be impossible for pigeons to confuse the $s - c$ delay with the ITI during lines-present $s - c$ delay testing, these results suggest that subjective shortening was responsible for the increase in long responding on comparison common trials in Experiment 1.

A number of previous studies have shown that pigeons will develop response rules based on absolute values of a single duration when available and on the relation between two durations when the absolute value of a given duration does not provide sufficient information to make a response (Dreyfus et al., 1988, 1992; Fetterman, 1987; Fetterman & Dreyfus, 1986; Fetterman et al., 1988). In the current experiments, this was also true for the comparison unique and comparison common durations respectively. Fetterman et al. (1988) had observed a pattern in their data in that responding was based on either s or c in the case of the extreme categories of duration pairs. This effect, however, may be attributed to the larger range of duration pairs used (i.e., 0.5 – 16 s). However, if a pigeon made a decision based on an absolute duration, it does not necessarily mean that it only times either s or c independent of the other duration. In the current study, it appears that pigeons timed both s and c regardless of whether it was a comparison common or comparison unique trial type. The use of a constant 1-s difference between s and c as well as employing a more limited range of duration pairs (1.0 – 4.0 s) prevented pigeons from relying only on s or c .

Furthermore, Wearden et al. (2007) had found that following presentation of equal duration pairs, people were more likely to indicate $c < s$ at short $s - c$ delays and $c > s$ at long $s - c$ delays. Wearden et al.'s data were obtained using equal duration pairs ranging from 350 to 650 ms and collected in a very similar fashion in that participants were deliberately forced to make errors on equal duration pairs (i.e., there was no option to indicate that the duration pairs were equal). Interestingly, the data are very similar, especially with respect to comparison common trial types, which were impossible to respond to based on the absolute duration of c . In a comparison of pigeons' and humans' discrimination of duration ratios, Fetterman, Dreyfus, and Stubbs (1996) noted that although the scale in the dimension being compared across species may not be quantitatively similar, the cognitive demands of the task may still be qualitatively similar. The use of a constant difference of 1.0 s and such a limited range of durations in the current study may have been just as cognitively demanding to a pigeon as it was for human participants in Wearden et al.'s study, which employed duration pairs that ranged in milliseconds and used a constant difference of 100 ms between s and c .

In both the $s - c$ delay data from Experiment 1 as well as the lines-present condition in Experiment 3, a +TOE was observed at the 1-s $s - c$ delay on $c < s$ unique and comparison common trial types. Although this result may be expected in the case of the $c < s$ unique durations, the process behind this error on comparison common trial types is less clear. Research with humans has suggested that when the two durations are presented close together in time, the process of coding and storing s prospectively interferes with the accurate timing of c (Hellstrom & Rammsayer, 2004; Wearden et al., 2007). With adequate $s - c$ delay, there may not be any proactive interference. On comparison common trials, at the 1-s $s - c$ delay in both Experiment 1 and in the line-present test sessions in Experiment 3, pigeons were more likely to indicate $c < s$

(i.e., make a +TOE; 41.3 & 39.4%, respectively). However, at the 2-s $s - c$ delay in both Experiment 1 and in the line-present test sessions in Experiment 3, long responding did not significantly deviate from chance (58.9 & 49.3%, respectively). These results may reflect pigeons' accurate timing of both s and c and a true uncertainty in how to respond when faced with an equal duration pair.

Overall, the results are somewhat reflective of Fetterman's (1987) difficulty in training pigeons to report whether two durations in a pair were either the same or different. When response contingencies were reversed during a single probe session following training, Fetterman found that the reversal affected some but not all of the duration pairs indicating that the pigeons had learned response rules based on specific instances of duration pairs. In both experiments in the current study, despite experiencing equal duration pairs during $s - c$ delay testing the pigeons still used a response strategy that was based on the absolute duration of c learnt during training. Although the pigeons appeared to not have confused the $s - c$ delay with the ITI, they continued to make use of the absolute rule on comparison unique duration pairs. Considering, however, that the length of c and its proximity to reinforcement influences what is remembered about s , it is not surprising that the pigeons used these response rules on equal duration pairs that contained comparison unique durations of c (Dreyfus et al., 1992). What may have led pigeons to rely on this strategy is the fact that they were trained with a limited number and range of duration pairs. In many of Fetterman and colleagues' duration comparison experiments (Dreyfus et al., 1988, 1992; Fetterman et al., 1988; Fetterman et al., 1989) employing many different duration pairs (> 700 in some cases) may have had more of a facilitative effect on developing the use of relational judgements. Through employing a larger number and range of duration pairs during training, it

may have been possible for pigeons to be more likely to learn a relational rule and not employ the same strategy when faced with equal duration pairs during testing.

The results of the current study extend the original investigation of Fetterman et al. (1988) into pigeons' memory for time in a duration comparison task. The results do not perfectly mirror the processes of instructional ambiguity/confusion as seen in the DMTS procedure, but the current set of experiments do suggest that test trial novelty and the similarity between the $s - c$ delay and the ITI must be considered when designing duration comparison experiments. While these studies have provided another step in the understanding of pigeons' memory for time in a duration comparison procedure, future studies could consider the impact of other factors which may lead to confusion/ambiguity in the duration comparison procedure. For example, whether pigeons can learn a duration comparison task where s and c are the same colour or stimulus is an interesting question. The expectation that pigeons may have developed in experiencing both s and c on a given trial may have been based to some degree on the difference in colour between the duration pairs. If the same colours were used, it is unknown whether pigeons could even learn the discrimination. However, if they could, when tested with extended $s - c$ delays, pigeons may confuse c with s and the start of a new trial. Therefore, one may expect that pigeons may develop a strategy to choose-short (i.e., respond $c < s$) on these test trials since they would have no record of c when the $s - c$ delay is confused with the ITI. It may be possible though, that the duration comparison procedure may facilitate relational responding to a degree on all duration pairs, and a response choice may not be made until two durations have been presented irrespective of similarity of the stimuli used.

In conclusion, since similar $s - c$ delay functions were obtained during line-present $s - c$ delay testing in Experiment 3, instructional ambiguity/confusion between the $s - c$ delay and the

ITI cannot account for the increase in long responding on comparison common trials in Experiment 1. In addition, while it appears that the increase in long responding was not due to the pigeons adding the $s - c$ delay to c , subjective shortening must have been responsible for the increase in long responding on comparison common trials.

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Table 1

The values used, in seconds, for the standard durations (s), comparison durations (c), and total duration (td) across comparison shorter and comparison longer trials during duration discrimination training. In the comparison (c) columns, comparison common durations are denoted by bold numbers and comparison unique trials are denoted by italicized numbers.

Comparison Shorter Trials			Comparison Longer Trials		
<i>c</i> is 1 s shorter than <i>s</i>			<i>c</i> is 1 s longer than <i>s</i>		
<i>s</i>	<i>c</i>	<i>td</i>	<i>s</i>	<i>c</i>	<i>td</i>
			1.0	2.0	3.0
			1.5	2.5	4.0
2.0	<i>1.0</i>	3.0	2.0	3.0	5.0
2.5	<i>1.5</i>	4.0	2.5	3.5	6.0
3.0	2.0	5.0	3.0	<i>4.0</i>	7.0
3.5	2.5	6.0			
4.0	3.0	7.0			

Figure Captions

Figure 1. An illustration of the duration comparison procedure used in Experiment 1.

Figure 2. The mean percent long responding during discrimination training across blocks of five sessions for each of the trial ($c < s$, $c > s$) and comparison types (common, unique). Error bars represent the standard error of the mean.

Figure 3. The mean percent long responding during the last five sessions of baseline discrimination training compared to baseline trials during $s - c$ delay testing in Experiment 1. Error bars represent the standard error of the mean.

Figure 4. The mean percent long responding during $s - c$ delay testing with equal duration pairs collapsed across the three different types of comparison durations: $c < s$ unique (1.0, 1.5), comparison common (2.0, 2.5, 3.0), and $c > s$ unique (3.5, 4.0). Error bars represent the standard error of the mean.

Figure 5. The mean percent long responding during no-standard probe testing compared to $s - c$ delay testing collapsed across the three different types of comparison durations: $c < s$ unique (1.0, 1.5), comparison common (2.0, 2.5, 3.0), and $c > s$ unique (3.5, 4.0). Error bars represent the standard error of the mean.

Figure 6. An illustration representative of a line-present test trial in Experiment 3.

Figure 7. An illustration representative of a line-absent test trial in Experiment 3.

Figure 8. The mean percent long responding on the last session of baseline training for all eight birds in Experiment 1 compared to the first session of baseline training in Experiment 3. The data presented represent each of the trial ($c < s$, $c > s$) and comparison types (common, unique). Error bars represent the standard error of the mean.

Figure 9. The mean percent long responding for all eight birds during discrimination training in Experiment 3 across blocks of five sessions for each of the trial ($c < s$, $c > s$) and comparison types (common, unique). Error bars represent the standard error of the mean.

Figure 10. The mean percent long responding during the last five sessions of discrimination training for the six pigeons that proceeded to $s - c$ delay testing before $s - c$ delay testing. The data from Experiment 1 is represented in the top panel of the figure and the data from Experiment 3 is represented in the bottom panel of the figure. The data presented are broken down into $c < s$ and $c > s$ trials and further subdivided by comparison unique and comparison common durations of c for each trial type. Error bars represent the standard error of the mean.

Figure 11. The mean percent long responding for the six pigeons that proceeded to $s - c$ delay testing on baseline trials during discrimination training in Experiment 3 compared to baseline trials during subsequent line-present and line-absent $s - c$ delay testing. The data presented represent each of the trial ($c < s$, $c > s$) and comparison types (common, unique). Error bars represent the standard error of the mean.

Figure 12. The mean percent long responding during line-present $s - c$ delay testing sessions collapsed across the three different types of comparison durations: $c < s$ unique (1.0, 1.5), comparison common (2.0, 2.5, 3.0), and $c > s$ unique (3.5, 4.0). Error bars represent the standard error of the mean.

Figure 13. The mean percent long responding for the six pigeons that proceeded to $s - c$ delay testing on comparison common trials during $s - c$ delay testing in Experiment 1 and during line-present $s - c$ delay testing in Experiment 3. Error bars represent the standard error of the mean.

Figure 14. The mean percent long responding during line-absent $s - c$ delay testing sessions collapsed across the three different types of comparison durations: $c < s$ unique (1.0, 1.5),

comparison common (2.0, 2.5, 3.0), and $c > s$ unique (3.5, 4.0). Error bars represent the standard error of the mean.



























