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Perception of Empty and Filled Time Intervals In Pigeons:
An Attentional Allocation Explanation of the Empty Interval Illusion

by

Stephanie Hornyak

Bachelor of Science (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 (2004)

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Abstract

Studies with humans and non-human animals have established how stimulus properties play an important role in the subjective duration of time. A phenomenon referred to as the Filled Interval Illusion has been found with humans, which demonstrates that filled intervals are perceived to be longer than empty intervals of equivalent duration. Recently, it has been demonstrated that pigeons judge empty time intervals bounded by two 500-ms light markers to be longer than an equivalent filled interval of light. Experiment 1 was able to replicate the Empty Interval Illusion with pigeons. Experiment 2 attempted to determine whether the Empty Interval Illusion was due to decreased attentional resources being given to timing filled intervals of light by creating an equal opportunity for filled and empty intervals to be distracted away from timing. Results demonstrated an overall general decrease in matching accuracy for empty intervals during psychophysical testing. Experiment 3 changed the markers that bound empty intervals so that matching accuracy for anchor durations would improve. Results correspond to a memory mixing process with domination of filled intervals being present in reference memory.

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Perception of Empty and Filled Time Intervals in Pigeons:

An Attentional Allocation Explanation of the Empty Interval Illusion

Human beings and other non-human animals are adapted to a physical world that can be best described in terms of specific events that take place at a particular time in a particular location. These events can be explained as being some type of change in physical stimuli, for instance, the onset or termination of a loud noise, which can be restricted in time and space (Church, 2002).

The ability of humans and non-human animals to time short temporal intervals serves as an adaptive advantage. For humans, the awareness of elapsed time aids in the management of every day life such as boiling water, or running a bath. By keeping a temporal memory for the elapsing time since water was placed on the stove, or the time since water was turned on to fill a bathtub, humans can go about their day in a more efficient manner, engaging in other tasks while waiting for the first to conclude. In addition, for those animals that forage for food, searching in one location for a fixed interval of time serves to optimize the gathering of food, at the same time, minimizing their exposure to predators. With this timing capability taken into consideration, it is not surprising that experimental conditions in a laboratory have shown that humans and animals have the ability to time short intervals.

A variety of research has taken advantage of discrimination procedures such as the temporal bisection procedure, and production procedures such as the fixed interval schedule of reinforcement and the peak procedure. Both types of procedures have given rise to specific data, which have been the basis for several theories that have emerged in the timing literature.

According to the information-processing model of Scalar Timing Theory (STT) (Gibbon, Church, & Meck, 1984), the timing mechanism involves an internal clock that consists of three stages; a clock stage, memory stage, and a decision stage. This model has been able to explain such properties of timing such as the location of the point of subjective equality (PSE) being found at the geometric mean of two anchor durations. In addition, STT has been able to explain the occurrence of superimposition, which occurs when subjects are trained on more than one set of anchor durations. Details of the point of subjective equality and superimposition will be explained in detail afterward.

It must be recognized that each component of the internal clock model represents a source of variance that may occur when temporal intervals are being timed. These sources of variance come into play when considering the importance of stimulus properties on perceived duration. The assumption is made that subjects are able to process relevant information with respect to the sample stimulus being presented. Therefore, regardless of the modality (i.e., visual or auditory), type of interval (i.e., filled or empty), or some other manipulation (i.e., physical) placed on the stimulus, subjects are assumed to use any type of stimulus as a cue in the timing procedure as long as duration is the most relevant feature (Buhsu & Meck, 2000; 2002). However, research with humans and non-human animals has demonstrated that perception of time is strongly influenced by the stimulus properties mentioned above.

The Modality Effect (Behar & Bevan, 1961; Goldstone & Goldfarb, 1964a, 1964b; Goldstone & Lhamon, 1972, 1974; Wearden, Edwards, Fakhri, & Percival,

1998) and the Filled Interval Illusion (Goldfarb & Goldstone, 1963; Goldstone & Goldfarb, 1963; Thomas & Brown, 1974) are two important phenomena that have arisen through differential timing of temporal intervals, and have been explained in terms of STT. A model proposed by Penney, Allan, Meck, and Gibbon (2000) suggests that differential timing occurs due to a clock rate difference between two different stimuli, in addition to the presence of mixed distributions of values present in reference memory.

Most recently, an Empty Interval Illusion has been found in pigeons (Miki, 2001). Utilizing a temporal bisection procedure in a within-subjects design, pigeons perceived an interval bound by two markers (i.e., an empty interval) as being longer than a filled interval of equal duration. This experiment was conducted with three sets of anchor durations (i.e., 2 s and 8 s, 1 s and 4 s, and 4 s and 16 s), and the Empty Interval Illusion was present with all three sets. Considering the previous literature attempting to explain such phenomena as the Modality Effect and the Filled Interval Illusion, an Empty Interval Illusion is not only a surprising finding, but is also difficult to explain.

The present study investigated the Empty Interval Illusion with pigeons. The Empty Interval Illusion is a phenomenon that has never been found with either humans or other non-human animals and shows that pigeons perceive an empty interval to be longer than a filled interval of equal duration. In fact, an opposing Filled Interval Illusion has been found in humans. The purpose of this study was to attempt to replicate the Empty Interval Illusion with pigeons in order to examine its reliability. An additional purpose was to examine the Empty Interval Illusion in the

theoretical framework of STT and the Mixed Memory Model (Penney et al., 2000), incorporating an attentional component. This was to examine the possibility that the empty-filled timing difference found in pigeons is due to differential attention being placed on empty and filled intervals of light when timing these intervals.

Temporal Perception Procedures

1. The Temporal Bisection Procedure

First developed for the study of temporal perception in rats (Church & Deluty, 1977), the temporal bisection procedure utilizes a matching paradigm referred to as the symbolic matching-to-sample design. A trial is initiated by the presentation of a sample stimulus, which can be one of a variety of modalities (e.g. duration of light or a tone), or one of numerous stimuli that is physically modified (e.g. a flickering light or an intense tone). Subsequent to the presentation of the sample stimulus, two comparison stimuli are presented. In the case of rats and pigeons, the two comparison stimuli are either a left and a right lever, or a red and green key light respectively. The trial terminates when the subject makes a response to one of the two comparison stimuli. Within a symbolic matching-to-sample paradigm, the sample stimulus presented bears no physical resemblance to either of the comparison stimuli. The subject in turn learns the symbolic relationship between the sample stimulus being presented and the suitable comparison stimulus. An example of this would be if a pigeon was presented with one of two visual sample stimuli (e.g. a white square presented for either 2 s or 8 s), it could eventually learn to associate the shorter visual stimulus with responding to the red key light, and learn to associate the longer visual stimulus with responding to the green key light.

The temporal bisection procedure consists of two phases. The first phase is referred to as the training phase and involves the presentation of one of two sample stimuli, for instance a short or long duration of light. These two sample stimuli are referred to as the anchor durations and are temporally different from each other (e.g. 2 s vs. 8 s). Following the offset of the sample, the subject is presented with two choice key lights and must respond in terms of whether it perceived the sample stimulus to be the short stimulus or the long stimulus. Reinforcement is provided when the correct comparison stimulus is chosen. When the subject has the ability to accurately discriminate between the two anchor durations, the second phase, or testing phase is implemented. During the test phase, the subject is presented with the original anchor durations and intermediate durations. Those trials where the presentation of the intermediate durations occurs are referred to as probe trials. The response following the presentation of an intermediate duration is recorded but no reinforcement is given. After several testing sessions have been implemented, the proportion of long responses, or the average percentage of times the subject chose the comparison associated with the long anchor duration can be plotted as a function of signal duration. Figure 1 displays the resulting function known as a psychophysical function, which is characterized by its ogival shape. The beginning portion is flat, rises rapidly, and then flattens as it nears the longest signal duration. The important properties of the psychophysical function will be discussed at a later time.

2. The Fixed Interval (FI) Schedule of Reinforcement

The fixed interval (FI) schedule of reinforcement procedure is one example of a production procedure. In an FI schedule of reinforcement, a response generates a

reward after a fixed interval of time has elapsed since the prior reward. For example, a fixed interval schedule of 20 s (FI(20)) specifies that a subject will receive reinforcement for the first appropriate response following 20 s of time. Following several training sessions, the subject will display few responses during the initial part of the 20 s interval, but will accelerate responding during the latter part of the 20 s interval. Figure 2 displays a typical upwardly sloping response scallop for a fixed interval schedule of 20 s (Church, 1978; Gibbon, 1977; S. Roberts & Church, 1978). This display of accelerated responding near the end of the interval is advantageous for non-human animals due to the fact that it maximizes the rate of reinforcement. If non-human animals such as rats or pigeons were not sensitive to the passage of time like humans are, they would not avoid responding at the beginning of the interval to be timed, and they would not increase to rapid responding as the interval to-be-timed nears the end so that reinforcement can be obtained.

3. The Peak Procedure

The peak procedure is a second example of a production procedure. It involves the use of the fixed interval schedule of reinforcement, where reinforcement is provided for the first response that occurs after the interval has elapsed (Catania, 1970; S. Roberts, 1981). A subject is trained to time a stimulus under an FI schedule. For example, if a FI(20) schedule is applied, a house light may signal the onset of a trial and the animal is once again reinforced for its first response following 20 s. Infrequent nonreinforced probe trials that are longer in duration than the trained FI schedule are implemented in order to assess the response rate following the time that reinforcement would have occurred. Figure 3 shows a common Gaussian response-

rate function that peaks at around the time that reinforcement would originally have been given during training, and then slopes downwardly to a level of low responding (Kaiser, Zentall, & Neiman, 2002).

Important Properties of Temporal Intervals

Studies in the area of timing that have utilized such procedures as temporal bisection, fixed interval schedule of reinforcement and the peak procedure have discovered various significant properties of timing. The results from such procedures have shown that the psychological representation of time is accumulated in a linear fashion. Two important properties of timing have surfaced by utilizing the timing procedures discussed earlier. First, the temporal bisection procedure has the ability to estimate the point of subjective equality (PSE). Secondly, both the temporal bisection procedure as well as the peak procedure, produces timing data that display the property of superimposition. Both of these timing properties have strong implications for theories that attempt to explain the process that is occurring when humans and non-human animals time specific durations. These theories will be discussed in more detail later.

1. The Point of Subjective Equality (PSE)

A main property of the psychophysical function obtained by the temporal bisection procedure is that it has the ability to estimate the point of subjective equality (PSE) or the bisection point. At the bisection point, a subject illustrates indifference to responding short or long. In other words, the probability of responding short or long is fifty percent. A commonly accepted characteristic of the PSE is that it can be found at the geometric mean (i.e., the square root of the product of the two anchor

durations). This has been found in studies using human adults (Allan & Gibbon, 1991; Wearden & Ferrara, 1996), human children (Droit-Volet & Wearden, 2001) pigeons, (Gibbon, 1986; Platt & Davis, 1983; Stubbs, 1968, 1976), and rats (Church & Deluty, 1977; Meck, 1983). Although it is widely accepted that the PSE is generally found at the geometric mean of the two anchor durations during temporal bisection, contrasting research has shown that on several occasions, the PSE has been found to be closer to the arithmetic mean (Wearden, 1991; Wearden & Ferrara, 1995, 1996; Wearden, Rogers, & Thomas, 1997). Wearden and Ferrara (1995, 1996) were interested in identifying the conditions needed to obtain a PSE at the geometric mean and the conditions needed to obtain a PSE at the arithmetic mean. They concluded that the difference in PSE values was due to discriminability between the two anchor durations. When the discrimination between the short and long anchor durations is relatively difficult (i.e., as the short to long ratio approaches a value of one), the PSE was found at the geometric mean. In turn, when the discrimination between the short and long anchor durations is relatively easy, the PSE was generally found at the arithmetic mean (Allan, 1998)

The location of the PSE on the psychophysical function has been used to draw inferences with respect to the psychological representation of time. One of the first studies to explore the location of the PSE was conducted by Church & Deluty (1977). Rats were trained in a temporal bisection procedure using two time intervals of darkness for the anchor durations. The empirical aim of this study was to determine whether the PSE would be found at the geometric mean of the two anchor durations, or at some other location such as the arithmetic mean or the harmonic mean. It was

hypothesized that the PSE would indicate how the internal representation of time would be altered with the duration of an interval. As discussed by Church and Deluty (1977) when the anchor durations are 2 s and 8 s, various functions relating subjective time ($s(t)$) to physical time (t) make different predictions for the location of the bisection point. When examining Figure 4 taken from Church and Deluty's (1977) study, one would predict that time is scaled in linear units if the PSE is located at the arithmetic mean (left graph). If the PSE was found at the geometric mean, this would show that time is scaled in logarithmic units (middle graph). Lastly, if the PSE was found at the harmonic mean, this would show that time is scaled in reciprocal units (left graph). The results from Church and Deluty's (1977) temporal bisection procedure yielded a PSE at the geometric mean. Therefore, it was concluded that the psychological representation of time increases as a logarithmic function of time. However, further research with respect to the location of the PSE has shown conflicting results, demonstrating that time may perhaps be scaled as a linear function.

Gibbon and Church (1981) were able to provide evidence that refuted the assumption that the psychological representation of time was scaled logarithmically. By developing what was termed the Time Left Procedure, Gibbon and Church (1981) made the proposition that time is scaled in a linear fashion. Rats were given a choice between a standard fixed interval to reinforcement, and the time left to reinforcement in an elapsing comparison interval. Subjects were trained to respond on a comparison 60 s fixed interval schedule on one lever and a standard 30 s fixed interval schedule on a second lever. Upon acquisition, combined trials were applied with the entry of

the comparison 60 s lever, followed by the standard 30 s lever after 15, 30, or 45 s. Rats responded on the standard lever when it entered early in the trial, and they responded to the comparison lever when the standard entered late. They were indifferent between the two levers when the standard entered halfway through the comparison interval so that the remaining time to food was equal on both levers. If rats base their psychological representation of time logarithmically, the subjects should have preferred the standard lever when it was inserted after 15 s and preferred the comparison lever when the standard was inserted after 30 s and 45 s. However, subjects' demonstrated indifference when the standard was inserted after 30 s. Additionally, it was shown that the increase in preference for the standard when it entered at 15 s was equivalent to the decrease in preference for the standard when it entered at 45 s. Therefore, it can be stated that preference was symmetrical around indifference and provides strong evidence that the psychological representation of time is scaled in linear units (Gibbon & Church, 1981).

2. *Superimposition*

A second important property that has been found frequently in human timing literature with both the temporal bisection procedure as well as production procedures is proportionality (Allan & Gibbon, 1991; Penney et al., 1998; Wearden & Ferrara, 1995, 1996; Wearden et al., 1997). When subjects are trained with different anchor durations, the psychophysical functions have been found to superimpose when plotted in relative time (Allan & Gibbon, 1991). Similar results have been found when the curves generated from production procedures are plotted in relative time (Church, 1978; Gibbon, 1977; S. Roberts, 1981). The superimposition of both psychophysical

functions and production curves can justify two inferences. First, superimposition supports Weber's Law (i.e., Weber fractions (WFs) can be calculated) described in Allan (1998), Gibbon and Church (1981), Grondin (2001), and W. A. Roberts (1998) as being the spread or variability of the function being proportional to the length of the interval being timed. Therefore, functions for shorter anchor durations have less variability than functions for longer anchor durations. Correspondingly with respect to the peak procedure, longer FI schedules have greater variability than shorter FI schedules. Secondly, superimposition is an important characteristic of human and animal timing that demonstrates a scalar-based process known as the scalar property (Gibbon, 1977). The judgment of whether a particular sample stimulus is short or long is based on a computed ratio. This ratio is computed between the absolute time elapsed within an interval and the base time. To illustrate this, perhaps a rat has been trained on a FI (10) schedule, and during one trial 5 s has elapsed. According to the scalar process, the rat should respond at the same rate in this trial as it would after 10 s in a trial with a FI(20) because the ratio between the absolute time elapsed and the base time is 1:2 for both of these occasions.

Scalar Timing Theory

An information-processing model of STT was developed by Gibbon, Church and Meck (1984) and is shown in Figure 5. STT is based on a linear psychological representation of time (Gibbon & Church, 1981) and ratio computations as discussed above. STT relies on the properties of the internal clock model, which consists of three stages: a clock stage, a memory stage, and decision stage. When the internal clock model is fit to various timing data, it is able to account for occurrences

discussed previously, such as the ogival shape of the psychophysical function, the PSE being found at the geometric mean, peak responding at the fixed interval schedule of reinforcement, and superimposition.

The first stage of the internal clock model consists of a clock stage. The clock stage follows the psychophysical law for time in that the psychological representation of time is accumulated linearly (Gibbon & Church, 1981). It also consists of three parts referred to as a pacemaker, a switch, and an accumulator. The defining feature of the pacemaker is that it is the internal mechanism that generates pulses. These pulses are emitted randomly, though over time, this emission is a constant average rate. For instance, the pacemaker may emit ten pulses per second on average. Given that the psychological representation of time is accumulated in a linear fashion, the average number of pulses emitted after 2 s is twenty, after 3-s is thirty and so on.

The defining feature of the switch is that it gates pulses from the pacemaker to the accumulator. Over time, the onset of a particular stimulus (i.e., the onset of a bright visual stimulus) will prompt the switch to close so that pulses from the pacemaker can be transmitted to the accumulator. In turn, the offset of the stimulus prompts the switch to open once again and the total number of pulses in the accumulator represents the subjective length of the stimulus. In other words, animals time the stimulus when the stimulus is on, due to the switch being closed at the onset of the stimulus (Church, 1984).

The defining feature of the accumulator is that it holds the total sum of pulses emitted from the pacemaker that pass through the closed switch. As discussed previously, evidence for the linear accumulation of time comes from Gibbon and

Church's (1981) time-left procedure. When the time left in an interval was equal to the standard interval, rats were indifferent in making a choice between the two levers.

The second stage of the internal clock model is referred to as the memory stage and consists of two parts termed working memory and reference memory. The defining feature of working memory is that it stores information about the duration of the stimulus for the current trial in the absence of the sample. This can occur over the period of a delay. Grant, Spetch and Kelly (1997), as well as Spetch and Wilkie (1982) have found evidence that this value kept in working memory will subjectively shorten as a delay interval increases, resulting in what is termed the choose-short effect. Due to the fact that neither the temporal bisection procedure nor the peak procedure involves a delay component, the working memory part of the internal clock model is not needed in this discussion of STT.

The second part of the memory stage is referred to as reference memory. Its defining feature is that it permanently stores information about past-reinforced trials. More specifically, within the temporal bisection procedure, there are two distributions of reinforced values, one that represents the short anchor duration and a second that represents the long anchor duration. With respect to the FI schedule of reinforcement or the peak procedure, each fixed interval possesses its own distribution. Therefore, reference memory contains a separate distribution for every fixed interval previously reinforced. These distributions are normally distributed with the mean value representing the particular anchor duration or fixed interval schedule.

The third stage of the internal clock model is referred to as the decision stage and consists of the comparator. The defining feature of the comparator is that it

determines a response on the basis of a decision involving a ratio comparison between the value in the accumulator or working memory with the value from reference memory (Church, 1984). Within the temporal bisection procedure, one value sampled from the short distribution and one sampled from the long distribution held in reference memory are sent to the comparator following the offset of a sample stimulus. It is in the comparator where ratio computations take place as discussed previously. The ratio computations are based on the value present in the accumulator and the two values retrieved from the reference memory distributions, and are the basis for the instrumental response of choosing short or long. If the response is reinforced, the value in the accumulator is stored in the corresponding distribution in reference memory. Within the peak procedure, the values sent from the accumulator (ACC) and the corresponding FI distribution for the particular value in reference memory (RM) is sent to the comparator where a discrimination ratio (DR) is calculated. The discrimination ratio is calculated as follows: $(DR = |RM - ACC| / RM)$. A threshold is sampled from a similar distribution, and if the discrimination ratio meets or falls below this threshold, the subject should begin to produce operant responses that specify whether or not the subject is near or at the reinforced time interval. In turn, at the time that the response is reinforced, the value in the accumulator will be sent to reference memory.

Scalar Timing Theory Accounting for Important Timing Properties

As stated beforehand, the information-processing version of scalar timing theory can account for important timing properties such as the ogival shape of the

psychological function, in addition to the PSE being found at the geometric mean, as well as proportionality.

1. The Point of Subjective Equality (PSE)

As previously discussed, when a sample stimulus is presented, its accumulated pulse value is calculated as a ratio between a short value and a long value taken from reference memory. If the example previously stated in the discussion of the internal clock model is taken into consideration, the rate of pulses discharged from the pacemaker is, ten pulses per second on average, and the subject is required to discriminate between the anchor durations of 2 s and 8 s. Therefore following a 2 s sample, twenty pulses will exist in the accumulator, and following an 8 s sample; eighty pulses will exist in the accumulator. When another short sample is presented, a ratio of 20:20 is calculated from the short distribution and a second ratio of 20:80 is calculated from the long distribution. The instrumental response of the subject is based on the ratio that is closer to 1.00; therefore in the case of a presentation of another short sample, a short response will be made. On the other hand, if the 8 s sample is presented, the ratios will be reversed and the instrumental response will be in favour of the long response. What is most significant in the ratio calculation process is the instrumental response in the case of a probe duration that is equal to the geometric mean (i.e., 4 s duration). The ratios for the short and long response are equal; the short response ratio is 20:40 and the long response ratio is 40:80. This is extremely important due to the fact that it illustrates how STT successfully predicts the PSE to be at the geometric mean within the temporal bisection procedure, if the

psychological representation of time is accumulated linearly (Gibbon & Church, 1981).

When taking into consideration the response pattern of production procedures, STT can also account for the Gaussian curve with the peak of the curve present at the fixed interval schedule previously learned by the subject. In a peak procedure, the comparator calculates a discrimination ratio between the values from the accumulator (ACC) and reference memory (RM) over the duration of the trial. If the values present in the accumulator are equal to that in reference memory, the discrimination ratio would be equal to zero, therefore a decision to respond should increase as the discrimination ratio approaches zero ($(RM-ACC)/RM$). If the rate of the pacemaker is ten pulses per second on average, the reinforcement schedule is a FI(20), and the threshold is equal to 0.5, the average value sent to the accumulator is equal to 200 pulses. STT would predict in this case that responding should begin after 10 s, if the threshold is 0.5. This model also predicts that responding would peak at 20 s, and stop after 30 s, which corresponds to the function obtained within the peak procedure paradigm.

2. Superimposition

Suppose anchor durations of 1 s and 4 s were used in the temporal bisection procedure instead of 2 s and 8 s discussed previously. STT can calculate ratios that are identical to those calculated when 2 s and 8 s anchor durations were used. If the pacemaker emits ten pulses per second on average, and the subject is required to discriminate between the anchor durations of 1 s and 4 s, following a 1 s sample, ten pulses will exist in the accumulator. In addition, following a 4 s sample, 40 pulses

will exist in the accumulator. When another short sample is presented, a ratio of 10:10 is calculated from the short distribution and a second ratio of 10:40 is calculated from the long distribution. The instrumental response of the subject is based on that ratio that is closer to 1.00; therefore in the case of a presentation of another short sample, a short response will be made. On the other hand, if the 4 s sample is presented, the ratios will be reversed and the instrumental response will be in favour of the long response. As stated previously, when probe durations equal to the geometric mean are presented (i.e., 2 s), the ratios for the short and long response are equal; the short response ratio is 10:20 and the long response ratio is 20:40.

Likewise in the case of the peak procedure, identical discrimination ratios are calculated when a FI(10) schedule of reinforcement is implemented, compared to a FI(20) schedule of reinforcement discussed earlier. According to the discrimination ratio calculations, a subject trained on either the FI(10) or the FI(20) should commence responding, peak, and stop responding at identical points in relative time.

Sources of Variance in Scalar Timing Theory

Due to the fact that the components of the internal clock model are based on distributions of values, several of these components represent a potential source of variance. Two such potential sources of variance occur within the clock stage of the internal clock model and are termed clock stage effects for this reason. To begin, the pacemaker randomly emits pulses, but over time, the rate of the emitted pulses are similar to a normal distribution where the mean represents the average rate of pulses emitted. Due to the fact that sample values are based on a distribution of several values, on any occasion, the pacemaker may emit pulses that are greater or less than

the average value. If this occurs, ratio calculations will be less accurate when comparing the accumulator value to the reference memory value. Therefore, this potential source of variance occurs within the pacemaker.

A second potential source of variance that may occur in the clock stage may occur with the switch. The first study to demonstrate that the switch within the internal clock model is controlled by attention was by Meck (1984). Meck cued the modality of the sample stimulus in a temporal bisection procedure with rats. In the first phase of the experiment, a light or a tone marked the sample durations. Preceding the sample duration, a cue was presented which specified the modality of the sample to-be-presented (e.g., an auditory cue preceded an auditory sample). In the testing phase of the experiment, probe trials involved the cue and the sample being mismatched (e.g., an auditory cue preceded a visual sample). On these mismatched trials, the psychophysical function was shifted to the right, relative to the matched trials. Meck interpreted this as being the rats utilizing the cue to direct their attention to the corresponding modality. The switch component of the internal clock model shows variance in itself because the closure of the switch was delayed when the cue did not match the sample. If the switch is delayed in its closure, pulses in the beginning of the sample are lost, causing the perceived duration to be shorter than if the switch had been closed for the entire duration of the sample. If the sample captured attention easily, this would result in the switch being closed immediately upon onset of the sample. It would also result in greater maintenance of switch closure during the sample (i.e., less flicker in the switch from closed to open). On the other hand, if the sample does not capture attention easily, the switch would be

delayed in its closure, or produce a greater amount of flicker. Both of these occurrences would result in pulses being lost, directly influencing the subjective timing of the sample because a decreased number of pulses would be accumulated (Meck, 1984).

Stimulus Properties and Their Effect on Perceived Duration

Scalar timing theory makes the assumption that subjects are able to abstract the relevant information with respect to the sample stimulus being presented. Therefore, regardless of the modality (i.e., visual or auditory), type of interval (i.e., filled or empty), or some other manipulation (i.e., physical) placed on the stimulus, subjects are assumed to use any type of stimulus as a cue in the timing procedure as long as duration is the most relevant feature (Buhusi & Meck, 2000). However, research with humans and non-human animals have demonstrated that perception of time is strongly influenced by the stimulus properties mentioned above.

1. Physical Manipulation of Stimulus Properties

The importance of physically manipulating the properties of the sample stimuli has a large impact on the subjective judgment of temporal intervals in both humans (Berglund, Berglund, Ekman, & Frankenhaeuser, 1969; Brown, 1995; Burle & Casini, 2001; Droit-Volet & Wearden, 2002; Goldstone, Lhamon, & Sechzer, 1978; Lhamon & Goldstone, 1975; Penton-Voak et al., 1996) and animals (Fetterman, 2000; Miki & Santi, 2001). Some experimental procedures have been manipulated to look at the effect of various frequencies of repetitive stimulation prior to the presentation of the sample stimulus, or as a property of the stimulus itself. These repetitive stimulations have been either auditory (e.g., trains of clicks, see

Burle & Casini, 2001; Penton-Voak et al., 1996, or a naturalistic auditory stimulus, see Miki & Santi, 2001), or visual (e.g., visual flicker, see Droit-Volet & Wearden, 2002; Fetterman, 2000; Goldstone & Lhamon, 1976). Other experimental procedures have been manipulated to examine the difference in perception of time between a stimulus that is moving relative to a stimulus that remains stationary (Brown, 1995; Goldstone & Lhamon, 1974; Lhamon & Goldstone, 1975), and the difference in perception of time between a stimulus that is more intense than a second stimulus (e.g., brighter visual stimulus, see Goldstone, Lhamon & Sechzer, 1978; or higher pitch auditory stimulus, see Berglund et al., 1969; Goldstone & Goldfarb, 1964a).

The general conclusion that can be made when examining the results of these several studies is that more intense stimuli are perceived as longer than their counterpart of equivalent duration. Brighter visual stimuli are judged subjectively longer than dim stimuli. In addition, higher pitched auditory stimuli are judged subjectively longer than lower pitched stimuli. Thirdly, a moving stimulus is perceived to be longer than its stationary counterpart of equivalent duration. It has been reported in the past in both pigeons (Wilkie, 1987) and rats (Kraemer, Brown, & Randall, 1995) that more intense stimuli are judged to be longer than less intense stimuli of equivalent duration, though conflicting results have been obtained, which will be discussed later (Miki, 2001). They presumably drive the pacemaker at a faster rate or capture attention more easily so that the switch flickers less.

This explanation can be extended to studies where the effect of various frequencies of repetitive stimulation was considered. Droit-Volet and Wearden (2002) trained children on a temporal bisection task with anchor durations of either 2

s and 8 s or 4 s and 16 s of light. A 5 s white circle preceded these anchor durations. Following discrimination training, psychophysical testing was implemented with the white circle either constant or flickering. The flickering white circle increased the proportion of children perceiving the intermediate samples as longer relative to the constant white circle condition. The psychophysical function of the signal durations preceded by the flickering white circle was shifted to the left relative to the control condition, in turn, decreasing the PSE for this condition as well. The results were consistent with the idea that the flickering white circle increased the speed of the pacemaker, causing durations to be perceived as longer. The addition of a repetitive stimulus being presented preceding the presentation of the sample stimulus has been conducted with auditory click trains in humans (Burle & Casini, 2001; Penton-Voak et al., 1996). In both cases, the presence of auditory clicks preceding the sample stimulus caused subjects to perceive the sample stimulus as being longer than its sample stimulus of equivalent length without the auditory clicks.

2. Perceptual Differences in Timing Auditory and Visual Intervals

In a series of studies, Goldstone and Goldfarb (1964a, 1964b) reported that a filled auditory interval was judged to be longer than a filled visual interval of identical duration. This phenomenon has been termed the Modality Effect and has been demonstrated with human participants (Behar & Bevan, 1961; Goldstone & Lhamon, 1972, 1974; Wearden et al., 1998). However, other research in this area has failed to find such modality differences (Bobko, Thompson, & Schiffman, 1977; Brown & Hitchcock, 1965). These conflicting results are difficult to resolve because a variety of experimental procedures have been used. However, a common feature of

most of these studies resulting in a modality effect is that a within-subjects design has been used (e.g., Behar & Bevan, 1961), whereas most studies failing to find a modality effect used a between-subjects design (e.g., Walker & Scott, 1981; Wearden et al., 1998). Within-subject designs allow for the direct comparison of auditory and visual signals.

Within the framework of STT, an explanation of the timing differences between auditory and visual stimuli requires the examination of the sources of variance discussed earlier such as clock rate differences, and onset latency to close the switch (Penney et al., 2000).

One possible explanation of the Modality Effect is that the internal clock runs at a faster rate for auditory signals than for visual signals. Therefore, the accumulated clock value of a given sample duration will be larger when the signal is auditory as opposed to the visual signal. Consequently, when the auditory and visual values are compared to each other, the auditory values will be perceptually larger (Penney et al., 2000). The possibility that clock speed may be influenced by stimulus properties (i.e., modality of the stimulus) is consistent with a study discussed previously.

Humans demonstrated that expected target durations were approximated earlier when a duration was preceded by a series of auditory clicks, as compared to those target durations that were not preceded by anything (Penton-Voak et al., 1996). On the other hand, the clock speed for auditory signals may be higher relative to visual signals because the switch closes more readily for auditory signals than for visual. It is possible that the switch is flickering between an open and closed state, therefore when the switch is closed, pulses emitted from the pacemaker are accumulated in the

accumulator, but when the switch is open, pulses are not accumulated. If the sample being presented needs to be attended to in order for the switch to remain in its closed state, it is possible that auditory samples capture attention more readily than visual ones. In turn, the switch would flicker less for auditory, resulting in a larger accumulation of pulses for the auditory relative to visual.

A second possible explanation of the Modality Effect could be the possibility that auditory signals are more readily processed as compared to visual signals. This would mean that a latency difference between auditory and visual signals is present in the initiation of timing. This explanation of the auditory-visual difference has been shown in Meck's (1984) study with rats. As discussed previously, rats' onset latency can be manipulated by the presentation of a warning cue. A warning cue that was followed by the mismatched modality (i.e., a visual cue followed by an auditory stimulus) shifted the expected time of reinforcement later relative to the matched cued trials. This indicates an increased timing onset latency. Therefore, if the accumulation of pulses for visual signals begins later than auditory due to the onset latency to begin timing, a rightward displacement of the psychophysical function for visual signals would occur relative to auditory. Refer to Figure 6 to examine the onset latency explanation visually, where subjective time is plotted as a function of signal duration. The onset latency account is similar to the flickering switch account described above because they both incorporate an attentional component, however, a flickering switch explanation of the auditory-visual timing differences abides by the important property of interval timing; superimposition (Penney et al., 2000).

A more convincing explanation of the auditory-visual timing difference comes from an adaptation of STT proposed by Penney et al. (2000), which incorporates a clock rate difference and mixed distributions of values present in reference memory. A Mixed Memory Model results in a classification difference between auditory and visual samples (Figure 7). This model consists of two memory distributions, one for the short auditory and visual signals, and one for the long auditory and visual signals (as opposed to the four memory distributions that would originally have been present if mixed memories were not taken into account). The solid and dashed diagonal lines represent the subjective accumulation of time for the auditory and visual signals respectively. Making the assumption that the clock rate runs slower for visual stimuli, subjective time accumulation will be smaller. Due to the different clock rates for the two modalities, the mean of the combined memory distributions for each anchor duration is larger than the mean visual accumulation of pulses and smaller than the mean auditory accumulation of pulses. With this said, a visual duration will be perceived as shorter than the auditory signal of equal duration, when compared to the short and long memory distributions combined.

3. Perceptual Differences in Timing Filled and Empty Intervals

Previous studies have also demonstrated that whether the interval is filled (i.e., a continuous visual or auditory stimulus) or empty (i.e., the same duration as filled except visual or auditory markers signal the beginning and end of the duration to-be-timed) affects temporal perception in both humans (Abel, 1972a, 1972b; Grondin, 1993; Rammsayer & Lima, 1991) and pigeons (Mantanus, 1981). For instance, Mantanus (1981) found that pigeons discriminated filled and empty temporal

intervals differently; with filled intervals being discriminated more accurately than empty intervals of equivalent duration. Due to procedural problems, Kraemer, Randall, and Brown (1997) addressed their concerns with Mantanus' (1981) study by conducting an experiment where pigeons had to discriminate either filled or empty intervals represented by light present and light absent conditions respectively. Pigeons were found to judge the duration of a filled interval to be longer than an empty interval of equivalent duration. This timing difference has also been recorded in human literature and has been termed the Filled Interval Illusion (Goldfarb & Goldstone, 1963; Goldstone & Goldfarb, 1963; Thomas & Brown, 1974), though findings with pigeons have been based on between-subjects designs.

Recently, Miki (2001) conducted a study to assess the perception of filled and empty time intervals in pigeons by training them in a within-subjects design to discriminate durations of a filled interval and durations of an empty interval. Initial training was performed with anchor durations of 2 s and 8 s, and psychophysical functions for both the filled and empty time intervals were obtained by presenting subjects with intermediate time intervals. Subsequent training and psychophysical testing was conducted with anchor durations of 1 s and 4 s, and 4 s and 16 s. The results of this series of psychophysical tests demonstrated a reliable timing difference between filled and empty time intervals except, it was in the opposing direction of previous pigeon literature; three sets of anchor durations all showed pigeons to perceive empty intervals to be subjectively longer than the filled interval of equivalent duration (refer to Figure 8). Although the direction of the timing difference was opposite to that reported in other pigeon literature (Kraemer et al.,

1997; Mantanus, 1981), the experimental procedure of this study was stronger in many respects. Miki (2001) utilized a within-subjects design, as opposed to the between-subjects used previously with pigeons (Penney et al., 2000). In addition, the current study operationalized an empty interval in a similar way that has been used in human timing studies (Grondin, Ivry, Franz, Perreault & Metthe, 1996). Thirdly, psychophysical testing was conducted with three sets of anchor durations and the empty-filled timing difference was present in each of the three situations.

Taking the internal clock model with mixed memories into consideration, this Empty Interval Illusion can be assumed to be due to the accumulation of emitted pulses for empty intervals being greater than the accumulation of emitted pulses for filled intervals. In addition, the memory of the empty and filled intervals is mixed in the two reference memory distributions. As discussed beforehand, a clock rate difference predicts a proportional shift in the psychophysical functions, which is what occurred in the study between the filled and empty time intervals. This clock rate difference could be due to such sources of variance as differential pacemaker rate or an attentional difference in maintaining switch closure.

According to the internal clock model with mixed memories, if the empty and filled interval durations are equally represented in the reference memory distributions for short and long, the PSE for the empty intervals would be located below the geometric mean, and the PSE for the filled intervals would be located above the geometric mean by a comparable amount. Miki (2001) showed the PSEs for empty intervals to be below the geometric mean, while the PSEs for filled intervals to be at or above the geometric mean. This pattern of results does not follow the assumption

that empty and filled intervals are represented equally in the short and long reference memory distributions. Penney et al. (2000) can account for these results in terms of a reference memory process that mixes the filled and empty anchor durations with domination by the filled intervals. As a result, the PSEs for empty intervals would tend to be found below the geometric mean, and the PSEs for filled intervals would tend to be found at the geometric mean.

As discussed previously, it has been reported that more intense signals are perceived to be longer than less intense signals of equal duration (Kraemer et al., 1997; Wilkie, 1987). If this were the case, filled intervals being the more intense signal than empty intervals should have possessed the faster pacemaker rate. In addition, filled intervals being the more intense signal than empty intervals should be able to capture attention more easily so the flicker of the switch would be decreased relative to empty intervals. If either of these explanations were reliable, a Filled Interval Illusion would have been expected.

Attentional Allocation and Its Effect on the Perception of Time

Attention being paid to an elapsing interval of time has been suggested as an important source of variance in time perception. Attentional models predict that perceived duration is completely related to the amount of attention allocated to the processing of time intervals (Thomas & Weaver, 1975; Zakay, 1989). Attentional manipulation has been investigated using dual-task procedures, where subjects have to simultaneously perform a temporal and non-temporal task. These studies have revealed the more demanding the nontemporal task, the more inferior the performance is on the temporal task (Casini & Macar, 1997; Macar, Grondin, &

Casini, 1994). The two assumptions mentioned above can be best explained by attentional explanations of time estimation (Thomas & Weaver, 1975; Zakay, 1989).

Thomas and Weaver (1975) proposed the first attentional explanation for short durations less than 100-ms, which was then revised to include longer durations by Zakay (1989). The first assumption is that humans distribute attentional resources, which are drawn from the same pool, between all tasks being performed. Temporal processing needs attentional resources to be allocated to it in order to process the interval well. Therefore, if more attention is needed to perform a second nontemporal task, fewer resources will be available for the temporal task, weakening performance on the temporal task. The second assumption takes into consideration STT. Diverting attention away from timing an interval delays the closure of the switch or may induce switch opening during the course of the duration (i.e., flickering switch). Accumulated pulses are lost, which induces the underestimation of the duration. (Lejeune, Macar, & Zakay, 1999).

Studies with human participants performing dual-task procedures seem to reflect an attentional sharing between the timing of an interval and a second nontemporal task. However, the status of attention is not as clear in animal timing performance. As discussed previously, Meck (1984) manipulated rats' attention while they were timing temporal intervals by biasing their attention to either an auditory or a visual stimulus and then presenting the timing cue of the opposing modality. Both the peak procedure and the temporal bisection procedure showed an underestimation of the length of the visual stimulus when their bias was towards the auditory stimulus. In a more recent experiment concerning attentional allocation,

Sutton and Roberts (1998) investigated pigeons' ability to divide their attention between temporal and nontemporal tasks. One group of pigeons were trained to discriminate two anchor durations of 2 s and 10 s, but were also supposed to pay attention to the line orientation of the stimulus (i.e., vertical or horizontal). Another group of pigeons were also trained to discriminate two anchor durations of 2 s and 10 s, but were also supposed to pay attention to the location of the stimulus (i.e., right or left of the chamber). Pigeons were not cued with respect to which stimulus dimension (i.e. temporal or nontemporal) they would be tested on, but they responded accurately regardless of dimension. This indicated that pigeons were processing both types of information at the same time (Sutton & Roberts, 1998).

Another study conducted by Sutton and Roberts (2002) examined pigeons' ability to time a temporal interval while simultaneously being engaged on another nontemporal task in three separate experiments. Pigeons' were required to discriminate temporal samples of 2 s and 10 s while engaging in a line orientation task (Experiment 1), or a location task (Experiment 2). In Experiment 3, a distractor light was illuminated on some probe trials to determine the degree to which the distractor would affect time perception. Results displayed a general rightward shift of the psychophysical curve for those pigeons that had to simultaneously process the temporal interval as well the orientation of the sample (i.e., vertical or horizontal). Results for Experiment 2 displayed a general loss of timing ability across all probe durations when pigeons had to process the temporal intervals and the location of the stimulus (i.e., left or right). Shorter intervals seemed to be classified as long, and longer intervals seemed to be classified as short. Similar results were found for probe

trials including the distractor light. Sutton and Roberts (2002) were able to demonstrate that when attention was divided between timing and a nontemporal task, a general loss of timing ability was seen in the timing task. These results follow previous research with pigeons (Lejeune et al., 1999) and humans (Zakay & Block, 1997) that suggests timing is hindered when a second nontemporal task is being performed at the same time as the timing task. The attentional explanation of timing as discussed previously is the most convincing account of the results obtained in the divided attention studies. When attention is drawn away from timing, the switch flickers open and does not allow as many pulses from the pacemaker to reach the accumulator. Therefore, when the accumulated pulse count is compared to the values stored in reference memory, it will evidently be shorter than the remembered value, resulting in an underestimation of time (Sutton & Roberts, 2002).

The Present Study

The Empty Interval Illusion is a phenomenon that has only been demonstrated with pigeons. They have shown evidence for perceiving an empty interval bound by visual markers to be longer than a filled interval of light of equivalent duration. The purpose of the present study was to focus on the reliability of the Empty Interval Illusion with pigeons. An empty-filled timing difference was found to be reliable, therefore the present study attempted to determine whether it was a result of differential attentional resources being given to timing the empty and filled durations of light. A decreased level of attention may be given to timing filled intervals of light because filled intervals involve the presentation of a light source for a particular duration of time. This illumination provides the opportunity for the pigeons to be

distracted by its surroundings. Attention is pulled away from the elapsing interval being presented, resulting in a subjectively shorter filled interval than its empty interval of equivalent duration.

Attentional explanations of time estimation can account for the empty-filled timing difference in pigeons as a result of the differential stimulus properties between filled and empty time intervals if placed within the context of STT. Attentional manipulation has been investigated utilizing dual-task procedures. These procedures have revealed the more difficult the nontemporal task, the more performance on the temporal task suffers. Diverting attention away from timing an interval delays the closure of the switch or may induce switch opening during the course of the duration. When the attentional switch is open, pulses from the pacemaker are prevented from being accumulated, which results in an underestimation of the duration being timed.

This attentional interpretation used in dual-task procedures can be further extended when pigeons are timing empty and filled intervals of light within the same session. As opposed to an empty interval that consists of a duration of time being bound by two 500 ms visual markers, filled intervals consist of a visual stimulus present for the duration to-be-timed. In other words, an empty interval to-be-timed is a period of darkness between the visual markers, whereas, a filled interval to-be-timed is a period of light. This is similar to what occurs in a dual-task procedure when a subject is required to pay attention to the temporal interval in addition to some second non-temporal aspect of the experiment. When attention is diverted away from timing filled intervals on some trials, the attentional switch of the internal clock model will open, preventing pulses to be accumulated. A resulting underestimation

of time will occur on those trials, creating the illusion that those filled intervals are shorter than the empty intervals of equal duration, in turn, displaying the Empty Interval Illusion.

The present set of experiments took advantage of the temporal bisection procedure to investigate the Empty Interval Illusion. A group of pigeons was trained and tested with filled intervals of light and empty intervals bound by light markers in a within-subjects design. If the Empty Interval Illusion was a reliable phenomenon with pigeons, a timing difference between filled and empty intervals of light would be evident (i.e., Experiment 1). More specifically, intermediate empty intervals should have been judged as subjectively longer than filled intervals of equivalent duration. If the illumination of the operant chamber was the reason for filled intervals to be underestimated, creating a condition whereby empty intervals are timed with equivalent distraction would eliminate the Empty Interval Illusion. Therefore, pigeons were trained in the same temporal bisection procedure as described previously, however the video monitor was illuminated as opposed to the dark background it was previously (i.e., Experiment 2 and 3). This illumination of the operant chamber was present during the presentation of both filled and empty interval durations, and remained present during the entire session. If the illumination of the surrounding operant chamber due to the presentation of filled intervals was the reason for the empty-filled timing difference, then psychophysical testing should reveal the Empty Interval Illusion during dark-background sessions, but not during the illuminated-background sessions. An attentional explanation of time estimation predicts that illumination of the video monitor during the session would promote distraction during

timing. Due to the fact that this illumination is present for the entire session, distraction should occur equally for both empty and filled intervals. In other words, there should be no evidence of an empty-filled timing difference when the operant chamber is illuminated.

Experiment 1

The purpose of Experiment 1 was to replicate the Empty Interval Illusion using anchor durations of 2 s and 8 s; common anchor durations that have given this phenomenon in the past (Miki, 2001). The pigeons that were used in Miki's (2001) study were retrained in a within-subjects design to discriminate durations of a filled interval (2 s and 8 s of light), and durations of an empty interval (2 s and 8 s of an unfilled interval marked at the beginning and the end by 500 ms durations of light). During psychophysical testing, intermediate durations (2.6, 3.2, 4.0, 5.0, and 6.4 s) were presented along with the anchor durations. If the Empty Interval Illusion is characteristic of specific anchor durations, and is a strong phenomenon within pigeons, retraining the birds with anchor durations that have previously shown the phenomenon, should demonstrate evidence of the Empty Interval Illusion.

Method

Subjects

Seven White Carneaux pigeons, maintained at approximately 80% of their free-feeding weights, and housed individually with constant access to grit and water, served as subjects throughout the experiment. Home cages were kept in a colony room, which is kept at a constant temperature of 22°C and is illuminated on a 12:12 h light: dark cycle by fluorescent lights, with light onset at 6:00am. Testing was

conducted between 9:00am and 3:00pm for five days a week, with no more than a 30-min start time variation over all sessions. The pigeons were weighed before each experimental session, and when necessary were fed an appropriate amount of Purina Pigeon Chow to supplement any loss of weight during the experimental sessions, and on days when the birds were not run. This was to maintain their 80% free feeding weight. The Wilfrid Laurier Animal Care Committee authorized all aspects of the experimental sessions, in accordance with the guidelines set out by the Canadian Council on Animal Care (CCAC). All of the pigeons had prior experience in experiments that involved symbolic delayed matching-to-sample (DMTS) tasks with durations of time for both empty and filled intervals of light. In addition, the pigeons had previous training consisting of sessions that possessed both types of intervals randomly within the same session.

Apparatus

Three touchscreen testing stations located in individual test rooms were used. Each test station consisted of a clear Plexiglas cage (30 cm wide X 40 cm deep X 36 cm high) with a large opening cut into the one end wall, which was constructed of stainless steel. On both the left and the right sidewalls of the cage, adjacent to the end with the large opening, was a 5.7 X 5 cm opening that provides access to a hopper filled with mixed grain (Coulbourn Model E14-10). A colour SuperVGA monitor (Mitsubishi SD4311C) with an attached touch frame (Carrol Touch, Frame 8100-9583-01, Card 8200-3224-01) was placed against the opening in the stainless steel wall. An IBM-compatible microcomputer located in each of the individual rooms controlled the stimulus displays, recorded peck location, and operated the feeders.

Procedure

Baseline Training with 2 s and 8 s Anchor Durations

Prior to the present experiment, the birds had been trained to discriminate various anchor training durations of filled and empty intervals within-subject (1 vs. 4 s, 2 vs. 8 s, and 4 vs. 16 s) with psychophysical testing conducted after training at each set of durations. Subsequent to this, various experiments were conducted which investigated pigeons memory for empty and filled time intervals signaled by light (Santi, Hornyak, & Miki, 2003). The birds were then retrained to discriminate various training durations of filled and empty intervals within-subject (2 vs. 8 s), as well as being trained with a novel set of anchor durations (0.5 and 2 s). For the present study, the birds were retrained to discriminate between short (2 s) and long (8 s) durations of filled and empty intervals of light with the background of the video monitor dark. The visual stimulus consisted of the presentation of a homogeneous white square, 3.3 x 3.3-cm, in the central area of the monitor (approximately 12-cm from the left and right bezel, as measured to the nearest edge). On filled interval trials, the white square was presented for either 2 or 8 s. On empty interval trials, the white square was presented for 500 ms at the beginning and at the end of a 2 or 8 s unfilled interval. Comparison stimuli were presented in two rectangular response areas, each measuring approximately 3.4-cm x 3.2-cm (width x height), one on the left and one on the right side of the monitor (approximately 15.6-cm apart, as measured by their inside edges). The position of the comparison stimuli was counterbalanced over trials. For five of the birds, red and green comparison stimuli were presented following an empty interval duration, and blue and yellow comparison stimuli were

presented following a filled interval duration. For the remaining two birds, blue and yellow comparison stimuli were presented following empty interval durations, and red and green comparison stimuli were presented following filled interval durations. The comparison stimulus that was designated as correct following the short and the long sample durations was also counterbalanced across birds. One of the eight different combinations of comparison stimuli designated as correct following the short and long signals was randomly assigned to each bird. For example, the correct associations for one of the birds was as follows: the red comparison with the short empty interval, the green comparison with the long empty interval, the blue comparison with the short filled interval and the yellow comparison with the long filled interval. The remaining six birds were trained with one of the seven other comparison combinations; the relationship between the type of interval and the durations of the interval, and corresponding comparison stimulus remained constant for each bird throughout the entire experiment.

For all of the birds, a single response to one of the comparison stimuli terminated them and, if correct, provided a 4 s access to mixed grain randomly presented at either the left or the right hopper opening with the probability of 0.5. Incorrect responses to the comparison stimuli produced a 4 s blackout, followed immediately by the re-presentation of the same interval duration and comparison stimuli. A correct response on a correction trial produced a 4 s access to mixed grain, however, only the choice response on the initial (noncorrection) trial was used to calculate matching accuracy. Within each block of eight trials, all combinations of the four duration stimuli (two interval types x two signal durations) and the two

comparison stimulus configurations occurred once. The order in which trials were presented was randomized individually for each bird. The duration of the intertrial interval was randomly varied within sessions (4, 8, 16, or 32 s). Baseline training continued until subjects were able to achieve a matching accuracy of at least 75% on both the filled and empty anchor durations, for four out of five consecutive sessions.

Psychophysical Testing with 2 s and 8 s Anchor Durations

Psychophysical testing sessions consisted of 160 trials. The anchor durations were presented on 80 of those trials and intermediate durations on the remaining 80 trials. The intermediate durations were 2.6, 3.2, 4.0, 5.0, and 6.4 s. Within test sessions, each intermediate duration was randomly tested 8 times for each type of interval (filled or empty). The birds were still reinforced for responding correctly following the four training anchor durations (two interval types x two signal durations), however, responses following intermediate signals were never reinforced. All subjects underwent fifteen test sessions as described above. In all of the statistical analyses reported in this experiment, the rejection region was $p < .05$.

Results

Baseline Training with 2 s and 8 s Anchor Durations

To evaluate the acquisition of the subjects' ability to discriminate between filled durations of light and empty durations designated by two light markers, the percent correct for short and long durations were averaged and grouped into blocks of two sessions for a total of eleven blocks. By the end of 22 sessions (i.e., eleven blocks) of baseline training with 2 s and 8 s anchor durations, all subjects were performing above the set criterion (i.e., above 75% for both empty and filled trials,

for four out of five consecutive sessions). The mean accuracy on filled interval trials during the last baseline training session was 92.7%, and the mean accuracy on empty interval trials during the last baseline session was 86.0%. There was one subject that finished 19 training sessions, and had a discrimination accuracy of 85.0% correct for filled intervals and 78.8% for empty intervals in the last session completed. For statistical analysis, these averages were used to complete block #10 and #11. The two functions shown in Figure 9 represent the average percent correct for short and long filled responses compared to short and long empty responses as a function of blocked sessions. Over the eleven blocks of sessions, it appeared that filled intervals of light were easier to discriminate relative to empty intervals throughout baseline training, which corresponds to earlier studies where filled intervals were discriminated easier than empty intervals (Kraemer et al., 1997; Mantanus, 1981, Santi et al., 2003). A 2 X 11 repeated measures analysis of variance (ANOVA) was conducted with the type of interval (i.e., filled vs. empty) and blocks of sessions as the within-subjects factors. This was to examine whether there were overall differences in the acquisition of filled and empty interval trials. There was a significant main effect of type of interval where, overall, filled intervals were discriminated more accurately than empty intervals, $F(1, 6) = 22.88, p < 0.05$. There was also a main effect for blocks of sessions, $F(10, 60) = 37.37, p < 0.05$, in addition to a significant type of interval by blocks of sessions interaction, $F(10, 60) = 3.58, p < 0.05$. This means that although matching accuracy on filled and empty interval trials was above 75% at the end of baseline training, matching accuracy on filled intervals was consistently above the matching accuracy of empty intervals throughout training.

An analysis was conducted to investigate whether there were significant matching accuracy differences between the short and long anchor durations for filled and empty intervals marked by light. The last five training sessions prior to psychophysical testing for each subject were averaged and compared in a 2 X 2 repeated measures ANOVA with the type of interval (i.e., filled or empty) and anchor duration (i.e., short or long) as within-subjects variables. A significant main effect of interval was found which provided additional evidence that filled intervals ($M = 91.4\%$, $s.e. = 2.32$) were discriminated more accurately than empty intervals ($M = 83.6\%$, $s.e. = 2.81$), $F(1, 6) = 11.98$, $p < 0.05$. The main effect of anchor duration as well as the interaction was not found to be significant. Therefore, before psychophysical testing began, there appeared to be no difference in the matching accuracy on short versus long interval trials, regardless of whether the intervals were filled or empty.

Psychophysical Testing with 2 s and 8 s Anchor Durations

The percentage of long responses was plotted as a function of signal duration for both the filled and empty interval trials and can be seen in Figure 10. Both psychophysical functions were analyzed in a similar manner. A 2 X 7 repeated measures ANOVA with the type of interval (i.e., filled vs. empty) and the signal duration (i.e., two anchor durations + five intermediate durations) as the within-subjects factors was conducted. This analysis was performed to investigate whether main effects of filled intervals vs. empty intervals, signal duration, and a type of interval by signal duration interaction were present. A main effect of type of interval, $F(1, 6) = 7.30$, $p < 0.05$, signal duration, $F(6, 36) = 157.62$, $p < 0.05$, and the

interaction, $F(6, 36) = 14.31$, $p < 0.05$ were statistically significant. A simple main effects analysis demonstrated significant differences at the 2 s signal duration between the filled (% long = 10.4%, $s.e. = 2.23$) and empty (% long = 17.8%, $s.e. = 2.75$), $F(1, 6) = 11.39$, $p < 0.05$, in addition to significant differences at the 8 s signal duration for the filled (% long = 90.3%, $s.e. = 1.30$) and empty (% long = 80.2%, $s.e. = 3.45$), $F(1, 6) = 7.63$, $p < 0.05$. More importantly, significant differences were also found at intermediate signal durations of 2.6, 3.2 and 4 s, $F_s(1,6)=9.73, 12.63$, and 19.35, all $p_s < 0.05$. This indicates that empty intervals were more likely than filled intervals to be classified as long at these intermediate durations. In addition, there was no statistically significant differences in the proportion of long responses at the intermediate durations of 5.0 and 6.4 s between filled and empty interval trials, the differences were found between the psychophysical functions at signal durations of 2.0, 2.6, 3.2, 4.0 and 8.0 s.

The point of subjective equality (PSE) for each subject was calculated by conducting linear regressions of the proportion of long responses for each of three adjacent signal durations. The regression equation with the greatest slope for each subject was used to estimate the PSE by calculating the signal duration associated with 50% of the long responses (Meck, 1991; Miki, 2001; Miki & Santi, 2001; Ross & Santi, 2000; Stanford & Santi, 1998). For filled intervals of light, the mean PSE was 4.21 s, and for empty intervals marked by light, the mean PSE was 3.35 s (refer to Experiment 1 of Table 1). A one-way repeated measures ANOVA with type of interval (i.e., filled vs. empty) as the within-subjects factor was conducted, and demonstrated a significant difference between the PSE for filled intervals and empty

intervals, $F(1, 6) = 17.26, p < 0.05$. The PSEs were also compared to the corresponding geometric mean (i.e., 4 s). The PSE for empty intervals (3.35 s) was significantly below the geometric mean, $t(6) = -3.268, p < 0.05$. However, the PSE for filled intervals (4.21 s) did not differ significantly from the geometric mean.

The regression equations were also used to calculate difference limens (DL), which represent the average difference between the signal duration associated with 75% long responses and the signal duration associated with 25% long responses. The mean DL for filled intervals and empty intervals was 1.07 and 0.92 respectively (refer to Table 1). A similar one-way ANOVA with type of interval (i.e., filled vs. empty) as the within-subjects factor was conducted, and no significant difference between these DLs were found.

The DLs and PSEs were used to calculate the Weber fraction ($WF = DL/PSE$). A similar one-way ANOVA was conducted with type of interval (i.e., filled vs. empty) as the within-subjects factor. The WF for filled intervals was 0.25, and did not differ significantly from the WF for empty intervals, which was 0.27 (Table 1). Both the DL and WF analyses indicated that the subjects were equally sensitive to the passage of time for both the filled and empty signal durations in this experiment.

Discussion

The purpose of the present experiment was to assess the perception of filled and empty time intervals in pigeons. More specifically, the purpose was to find a reliable timing difference between empty and filled durations of light. Previous research has demonstrated that whether the temporal duration to-be-timed is filled or empty, will affect the temporal perception of these durations. This filled-empty

timing difference has been found in both humans (Abel, 1972a, 1972b; Grondin, 1993; Rammsayer & Lima, 1991) and pigeons (Kraemer et. al., 1997; Mantanus, 1981). However, the results of these various studies have demonstrated conflicting results due to procedural differences. Most recently, Miki (2001) conducted a study to assess the perception of filled and empty intervals in pigeons by training them in a within-subjects design to discriminate durations of filled intervals and empty intervals with three sets of anchor durations. Psychophysical testing was able to demonstrate an empty-filled timing difference with each of the three sets of anchor durations. However, this timing difference opposed findings from previous research in that intermediate empty intervals were perceived to be longer than filled interval trials of equal duration. This occurrence was termed the Empty Interval Illusion and counteracts what is demonstrated in humans who seem to display a Filled Interval Illusion (Goldfarb & Goldstone, 1963; Goldstone & Goldfarb, 1963; Thomas & Brown, 1974).

By training pigeons with anchor durations that have previously shown evidence for the Empty Interval Illusion (i.e., 2 vs. 8 s), and then conducting psychophysical testing, the present study was able to replicate the empty-filled timing difference displayed in Miki (2001). More specifically, there was a tendency for pigeons to display an increased proportion of long responses on empty intervals when the signal durations were shorter (i.e., 2.0, 2.6, 3.2, and 4.0 s). In other words, shorter empty intervals were perceived as longer than filled intervals of equal duration. However, as the signal durations increased, there was a decreased tendency for this pattern to continue. At the intermediate signal durations of 5.0 and 6.4 s, there was no

difference in the proportion of long responses between empty and filled intervals. In other words, pigeons perceived these empty intervals as being similar to the filled intervals of equal duration. In addition, at the long anchor duration (i.e., 8 s), there was a tendency for pigeons to display an increased proportion of long responses on filled intervals relative to empty intervals.

When examining the psychophysical functions for filled and empty intervals in this experiment, a reliable timing difference was demonstrated. Pigeons judged empty intervals marked by visual markers to be longer in duration than filled intervals of light of equal duration. Though Miki (2001) demonstrated this timing difference at all intermediate durations, and not at the anchor durations, the present study replicated the Empty Interval Illusion at shorter intermediate durations as well as at the short anchor duration. The most convincing evidence of demonstrating the timing difference between filled and empty intervals would be the divergence of the two psychophysical functions at the shorter signal durations, including the significant divergence at the signal duration corresponding with the geometric mean (i.e., 4 s). Additional evidence of the timing difference can be seen in the significant differences in the PSE for empty and filled intervals. The PSE for empty intervals was significantly less than the PSE for filled intervals.

The difference in PSEs between empty signal durations and filled signal durations can be best explained by the Mixed Memory Model (Penney et al., 2000) discussed earlier. According to the Mixed Memory Model, a timing difference between two types of stimuli include a clock rate difference in addition to the presence of mixed distributions of values present in reference memory. There is one

memory distribution for short signals, and a second distribution for long signals in reference memory. Therefore, the values that are reinforced from both types of stimuli are stored in the same distribution. The clock rate difference must be present where one type of stimulus is able to drive the clock at a faster rate than the second type of stimulus. Accordingly, the stimuli with the faster clock rate results in an overestimation of the interval to-be-timed, and the stimuli with the slower clock rate results in an underestimation of the interval to-be-timed relative to each other.

Taking this into consideration, the properties of the Mixed Memory Model can be applied to the PSE difference found between the empty and filled intervals in the present study. This can occur if it is assumed that the accumulation of pulses is faster for empty intervals than for filled intervals. In addition, that the memory of empty and filled interval accumulations are being mixed in the two reference memory distributions. If this were the case, the PSE for empty intervals should not only be below the PSE for filled intervals, but it should also be below the geometric mean. In addition, the PSE for filled intervals should not only be above the PSE for empty intervals, but also be close to the geometric mean, if the reference memory distributions were dominated by filled interval durations. This is precisely what occurred in the present study. The PSE for empty intervals was found at 3.35 s (i.e., below the geometric mean of 4 s), and the PSE for filled intervals was found at 4.21 s (i.e., close to the geometric mean). This is similar to the timing difference found in Miki's (2001) study. Pigeons demonstrated a significant empty-filled timing difference at three sets of anchor durations (i.e., 1 vs. 4 s, 2 vs. 8 s, and 4 vs. 16 s). What is most interesting is the fact that at the 2 vs. 8 s, and at the 4 vs. 16 s, the PSE

for empty intervals was significantly below the geometric mean, and the PSE for filled intervals was consistently at the geometric mean, which corresponds with the current study. In addition, the differences in the PSEs for empty and filled intervals for the three sets of anchor durations was multiplicative. This supports a clock rate difference, and the presence of mixed reference memory distributions (Miki, 2001).

Attentional explanations of time estimation can account for the empty-filled timing difference found with pigeons at shorter signal durations. This is possible if differential stimulus properties between filled and empty time intervals are placed within the context of STT, in addition to considering the properties of the Mixed Memory Model. When attention is diverted away from timing a stimulus, the closure of the attentional switch within the internal clock model is delayed, or may promote the switch to open during the course of the duration. When the attentional switch is open, pulses emitted from the pacemaker are prevented from being accumulated in the accumulator, which results in the underestimation of the duration being timed. This attentional interpretation can be further extended to this study in an attempt to explain the Empty Interval Illusion. The presentation of filled intervals of light allow for the visual features of the surrounding area to be visible. This has the possibility of causing attraction of attention towards the features of the operant chamber, in turn, diverting attention away from timing the interval. When attention is diverted from timing the filled interval on some trials, the attentional switch will open, preventing pulses to be accumulated in the accumulator. A resulting underestimation of time will occur on those trials, creating the illusion that these filled intervals are shorter than the empty intervals of equal duration.

This explanation based on diversion of attention during the timing of filled intervals may appear surprising given the evidence that the bisection point for filled intervals was found at the geometric mean. This result appears consistent with Scalar Timing Theory. Rather than focusing the explanation on distraction during the timing of filled intervals, it may appear that the explanatory focus should be on the processing of empty intervals. However, as indicated earlier it is possible for pulse accumulations to be smaller for filled intervals than for empty intervals and yet the bisection point for filled intervals could still be at the geometric mean if reference memory is dominated by the filled intervals. Consequently, the present research will investigate whether the smaller pulse accumulations for filled intervals is due to decreased attention during the timing of filled intervals. This interpretation of the Empty Interval Illusion will be further studied in Experiment 2.

Experiment 2

The second experiment further investigated the differential attentional allocation explanation for the Empty Interval Illusion. The presentation of filled intervals of light illuminates the surrounding operant chamber. This may provide an opportunity to be distracted away from timing, and to be attracted towards the visual features of the operant chamber. An attentional interpretation of time estimation would suggest that upon distraction from timing (i.e., upon the presentation of the filled interval), the attentional switch of the internal clock would flicker open allowing pulses from the pacemaker to be lost. This would result in the underestimation of time for filled intervals on some trials during psychophysical testing. Due to the fact that empty intervals consist of an interval of darkness bound

by two light markers, pigeons are never given the opportunity to be distracted by visual features of the operant chamber. Therefore, there would be no resulting underestimation of time on some trials. The purpose of the second experiment was to create a procedure where an equal opportunity to be distracted during the presentation of empty and filled intervals was provided.

Roberts and Grant (1978) found that houselight presented during the delay within a delayed matching-to-sample task promoted pigeons to exhibit lower matching accuracy, as compared to a delay that was spent in darkness. The degree of this retroactive inhibition was a function of the length of the illuminated delay. If attention was being directed to the visual features of the chamber, a decreased rehearsal of the working memory code for the sample would have occurred, promoting the lowered matching accuracy. If the Empty Interval Illusion is a result of decreased attention being given to timing filled intervals of light due to illumination of the chamber during the presentation of filled intervals, then providing the opportunity for pigeons to be distracted during timing empty intervals via illumination should eliminate the timing difference.

The procedure used was similar to Experiment 1 in that pigeons were trained to discriminate between short (2 s) or long (8 s) filled and empty intervals of light in a within-subjects design. However, the background of the video monitor was changed from a black (i.e., dark) background to a light gray (i.e., illuminated) background. This modification of the background illumination was to provide visual input during the presentation of both filled and empty intervals for the entire session. As stated previously, if the Empty Interval Illusion is due to decreased attention being given to

timing filled intervals, providing the opportunity for distraction to occur on both filled and empty intervals should eliminate the empty-filled timing difference.

Method

Subjects

Six subjects used in Experiment 1 were also used in Experiment 2. One subject was removed from the study due to illness.

Apparatus

The apparatus used in Experiment 1 were also used in Experiment 2.

Procedure

Baseline Training with Illuminated Background

Following the testing conducted in Experiment 1, the birds were introduced to a set of baseline training trials consisting of 160 trials as previously described. However, the difference between these baseline trials, and those the birds were previously trained with was the illumination of the background of the video monitor. In Experiment 1, the presentation of the signal duration and the comparison stimuli were always presented on a dark background. In the present study, the background of the video monitor was changed to light gray (i.e., illuminated), and was present for the entire session. The first phase of baseline training with the illuminated background condition continued for approximately 15 to 25 sessions depending on whether the birds were able to reach a matching accuracy of at least 75% on both filled and empty signal durations for four out of five consecutive sessions.

Baseline Training with Alternating Dark and Illuminated Background

Subsequent to this, the second phase of baseline training began. This consisted of alternating sessions of the illuminated background condition with the dark background condition the birds were trained with in Experiment 1. In order for psychophysical testing to begin, all birds needed to reach a matching accuracy of at least 70% (i.e., this was decreased from 75% due to pigeons finding it difficult to attain the higher percentage with alternating black and gray background sessions) on both filled and empty signal durations, in both the dark and illuminated background conditions. This matching accuracy had to be met for four out of five consecutive sessions and was obtained by all subjects within 24 sessions (i.e., 12 sessions of alternating dark and illuminated background sessions).

Psychophysical testing with 2 s and 8 s Anchor Durations

Psychophysical testing in this experiment was similar to Experiment 1. Each session of testing consisted of 160 trials. The intermediate durations were 2.6, 3.2, 4.0, 5.0, and 6.4 s. In each session, intermediate durations were randomly tested 8 times for each type of interval (filled or empty). The pigeons were reinforced for responding correctly following the presentation of the four anchor durations (two interval types x two signal durations), but responses following the presentation of the intermediate durations were never reinforced. Psychophysical testing in this experiment differed from Experiment 1 in that testing sessions were alternated between the illuminated background condition and the dark background condition. Therefore a total of 30 testing sessions occurred (15 sessions in total of the illuminated background condition, and 15 sessions in total of the dark background

condition). All other aspects of these sessions were identical to those described in Experiment 1.

Results

Baseline Training with Illuminated Background

To evaluate the acquisition of the subjects' ability to discriminate between filled durations of light and empty durations designated by two light markers, the percent correct for short and long durations were examined in a different manner than in Experiment 1. Instead of analyzing the percent correct for short and long durations by averaging and grouping the sessions into blocked sessions of two, a criterion was set. Pigeons could progress to the second phase of baseline training if a percent correct of at least 75% on both filled and empty intervals was met for four out of five consecutive sessions. Subjects took a variable number of sessions to meet criteria and move onto the second phase of training. The mean accuracy for the filled samples of light during the last baseline training session for all of the subjects was 87.4%, and the mean accuracy for the empty samples marked by light during the last baseline training session for all of the subjects was 80.4%. For statistical analysis, the last five baseline training sessions of each subject prior to the second phase of baseline training were averaged and compared in a 2 X 2 repeated measures ANOVA similar to Experiment 1 with the type of interval (i.e., filled or empty) and anchor duration (i.e., short or long) as within-subjects variables. A significant main effect of interval, which provided evidence in the direction of filled intervals ($M = 90.4\%$, $s.e. = 1.68$) being discriminated more accurately than empty intervals ($M = 77.4\%$, $s.e. = 2.63$), $F(1, 5) = 62.19$, $p < 0.05$ was found. The main effect of anchor duration as well as the

interaction were not found to be significant. Therefore, before the subjects were advanced to the second phase of baseline training, there appeared to be matching accuracy differences depending on whether the sample presented was filled or empty. As demonstrated in previous studies, filled intervals were discriminated better than empty intervals (Kraemer et al., 1997; Mantanus, 1981, Santi et al., 2003).

Baseline Training with Alternating Dark and Illuminated Background

To evaluate the acquisition of the subjects' ability to discriminate between filled durations of light and empty durations designated by two light markers, the percent correct for short and long durations were examined for each background condition (i.e., dark or illuminated) similar to the first phase of baseline training. Pigeons could progress to psychophysical testing if a percent correct of at least 70% on both filled and empty intervals was met for four out of five consecutive sessions for both of the background conditions. Subjects took a variable number of sessions to meet criteria. The mean accuracy on the filled samples of light during the last baseline training session for all of the subjects was 92.9% for the dark background and 92.3% for the illuminated background. The mean accuracy of the empty samples marked by light during the last baseline training session for all of the subjects was 86.3% for the dark background and 76.5% for the illuminated background.

For statistical analysis, the last five baseline training sessions of each subject prior to psychophysical testing were averaged and compared in a 2 X 2 X 2 repeated measures ANOVA with the background condition (i.e., dark or illuminated), type of interval (i.e., filled or empty) and anchor duration (i.e., short or long) as within-subjects variables. A significant main effect of interval was found, $F(1, 5) = 24.87$, p

< 0.05 , which indicated that filled intervals and empty intervals were discriminated differently. Also, an interval by signal duration interaction was found to approach significance, $F(1, 5) = 6.32$, $p = 0.054$. There were no other significant main effects, as well as no other significant two-way or three-way interactions found. Therefore, before psychophysical testing began with alternating background illumination, it appeared filled intervals of light were discriminated more accurately than empty intervals marked by light.

Psychophysical Testing with Alternating Dark and Illuminated Background

The percentage of long responses was plotted as a function of signal duration for both the filled and empty interval durations. Refer to the top panel of Figure 11 to examine the percentage of long responses for both the filled and empty intervals of light when the background was dark. In addition, the bottom panel of Figure 11 displays the percentage of long responses for both the filled and empty intervals of light when the background was illuminated. A $2 \times 2 \times 7$ repeated measures ANOVA with the background condition (i.e., dark or illuminated), type of interval (i.e., filled vs. empty), and signal duration (i.e., two anchor durations + five intermediate durations) as the within-subjects factors was conducted. This analysis was performed to investigate whether main effects of background condition, type of interval, or signal duration were present, in addition to any two-way or three-way interactions between the three factors. A main effect of interval, $F(1, 5) = 43.84$, $p < 0.05$, and signal duration, $F(6, 30) = 246.56$, $p < 0.05$ was found, in addition to a background condition by signal duration interaction, $F(6, 30) = 13.67$, $p < 0.05$, and an interval by signal duration interaction, $F(6, 30) = 43.69$, $p < 0.05$. Most importantly, a three-way

condition by interval by signal duration interaction was found to be significant, $F(6, 30) = 4.45, p < 0.05$.

A simple main effects analysis demonstrated significant differences at the 2 s signal duration for the filled (% long = 6.4%, $s.e. = 1.60$) and empty (% long = 16.0%, $s.e. = 2.77$), $F(1, 5) = 8.52, p < 0.05$ when the background was dark. More importantly, significant differences were also found at the intermediate signal durations of 2.6, 3.2, and 4.0 s, $F_s(1, 5) = 37.84, 72.00, 10.97$, all $p_s < 0.05$, when the background was dark. This indicates there were no differences in the proportion of long responses at the intermediate durations of 5.0 and 6.4 s between filled and empty intervals of light, in addition to no difference at the long endpoint (i.e., 8 s) when the background was not illuminated (top panel of Figure 11). When the background was illuminated, the simple main effects analysis demonstrated significant differences at the 2 s signal duration for the filled (%long = 13.1%, $s.e. = 1.30$) and empty (%long = 34.0%, $s.e. = 3.49$), $F(1, 5) = 25.87, p < 0.05$. In addition, significant differences at the 8.0-s signal duration for the filled (%long=85.5%, $s.e. = 1.90$) and the empty (%long=70.1%, $s.e. = 2.14$), $F(1, 5) = 210.68, p < 0.05$ were found. More importantly, significant differences were also found at the intermediate durations of 2.6, 3.2, 4.0, and 6.4 s, $F_s(1, 5) = 33.01, 26.66, 6.72, 29.32$, all $p_s < 0.05$. This indicates that when the background was illuminated, there was no difference in the proportion of long responses at the intermediate duration of 5 s between filled and empty intervals of light, the differences were found at all other signal durations. More specifically, the proportion of long responses was greater for empty intervals at signal durations from 2 s to 4 s. However, signal durations longer than 6.4 s produced a greater proportion

of long responses for filled intervals of light relative to empty intervals marked by light (bottom panel of Figure 11).

The simple main effects analysis also demonstrated significant differences in the psychophysical functions for filled intervals when the background was dark versus when the background was illuminated. These differences were found at the 2.0, 2.6, 3.2, and the 8 s signal durations, $F_s(1, 5) = 21.03, 75.98, 6.49$, and 6.29 , all $p_s < 0.05$. More specifically, signal durations of 2.0, 2.6, and 3.2 s for filled intervals had a greater chance of being classified as long when the background was illuminated than when the background was dark. The opposite effect occurred at the 8 s signal duration though this was a marginal effect, $F(1, 5) = 6.29, p = 0.0540$. When examining the psychophysical functions for the empty intervals when the background was either dark or illuminated, a significant difference between these two functions occurred at the 2 s signal duration, $F(1, 5) = 14.26, p < 0.05$, with this short empty interval being classified as long more when the background was illuminated relative to when the background was dark. In addition, significant differences were found at the 6.4 and 8 s signal duration, $F_s(1, 5) = 11.86$ and 20.65 , both $p_s < 0.05$. These durations were classified as long more when the background was dark relative to when the background was illuminated.

The point of subjective equality (PSE) for each subject for both background conditions was calculated by conducting similar linear regressions of the proportion of long responses as in Experiment 1. When the background was not illuminated, the PSE for filled intervals was 4.18 s, and for empty intervals was 3.22 s. When the background was illuminated, the PSE for filled intervals was 3.99-s, and for empty

intervals was 3.33-s (refer to Experiment 2 of Table 1). A 2 X 2 repeated measures ANOVA with background condition (i.e., dark vs. illuminated) and type of interval (i.e., filled vs. empty) as the within-subjects factors was conducted. This demonstrated a significant main effect of type of interval, $F(1, 5) = 77.67, p < 0.05$. The main effect of condition, as well as the interaction was not found to be significant.

The PSEs were also compared to the corresponding geometric mean (i.e., 4 s). When the background was dark, the PSE for empty intervals (3.22 s) was significantly below the geometric mean, $t(5) = -4.034, p < 0.05$. However, the PSE for filled intervals (4.18 s) did not differ significantly from the geometric mean (4 s). When the background was illuminated, the PSE for empty intervals (3.33 s) was significantly below the geometric mean, $t(5) = -2.841, p < 0.05$. However, the PSE for filled intervals (3.99 s) did not differ significantly from the geometric mean.

The regression equations were also used to calculate difference limens (DLs). When the background was not illuminated, the DL for filled intervals was 0.95, and the DL for empty intervals was 0.87. When the background was illuminated, the DL for filled intervals was 1.15, and the DL for empty intervals was 1.82 (refer to Table 1). A 2 X 2 repeated measures ANOVA with background condition and type of interval as the within-subjects factors was conducted. A significant main effect of background condition was found, $F(1, 5) = 30.54, p < 0.05$, as well as a significant condition by interval interaction, $F(1, 5) = 10.80, p < 0.05$. A simple main effects analysis revealed significant differences between the DL for filled and the DL for empty intervals when the background was illuminated, $F(1, 5) = 17.05, p < 0.05$, but

not when the background was dark. In addition, the DL for filled intervals differed depending on whether the background was dark or illuminated, $F(1, 5) = 14.81, p < 0.05$, and this difference was also found for empty intervals, $F(1, 5) = 20.02, p < 0.05$. The DL analyses indicated that subjects were equally sensitive to the passage of time when the background was dark, regardless of interval type. However, subjects were less sensitive to the passage of time of empty intervals relative to filled intervals when the background was illuminated. In addition, it seems as though the illuminated background condition caused an overall decrease in sensitivity for both filled and empty intervals relative to filled and empty intervals in the dark background condition.

The DLs and PSEs were used to calculate the Weber fractions similar to that in Experiment 1. When the background was dark, the WF for filled intervals was 0.23, and the WF for empty intervals was 0.26. When the background was illuminated, the WF for filled intervals was 0.29, and the WF for empty intervals was 0.57 (Table 1). A similar 2 X 2 repeated measures ANOVA with background condition and type of interval as the within-subjects factors was conducted. A significant main effect of background condition, $F(1, 5) = 27.63, p < 0.05$, type of interval, $F(1, 5) = 12.84, p < 0.05$, and the interaction, $F(1, 5) = 10.63, p < 0.05$ were found. A simple main effects analysis found a significant difference between the WFs for filled and empty intervals when the background was illuminated. In addition, the WFs for empty intervals differed depending on the background condition, $F(1, 5) = 18.37, p < 0.05$. The WFs for filled intervals differed depending on the background condition as well, $F(1, 5) = 21.75, p < 0.05$.

An additional 2 X 2 X 7 repeated measures ANOVA where experiment (i.e., Experiment 1 vs. Experiment 2), type of interval (i.e., filled vs. empty), and signal duration (i.e., two anchor durations + five intermediate durations) were the within-subjects factors was conducted. This was to examine whether there were any significant differences with the Empty Interval Illusion found in Experiment 1, and the proportion of long responses found for both the empty and filled intervals of light in Experiment 2 when the background was dark. Refer to the top panel of Figure 12 to examine the percentage of long responses for filled intervals of light when the background was black in Experiment 1 and 2. In addition, the bottom panel of Figure 12 displays the percentage of long responses for empty intervals of light when the background was black in Experiment 1 and 2. Only main effects of type of interval, $F(1, 5) = 15.59, p < 0.05$, and signal duration, $F(6, 30) = 226.20, p < 0.05$, were found. In addition to a type of interval by signal duration interaction, $F(6, 30) = 14.77, p < 0.05$. There were no significant differences between the proportion of long responses for filled intervals in Experiment 1, and those achieved in Experiment 2. The same results were found for the proportion of long responses for empty intervals. In other words, there were no differences between the Empty Interval Illusion found in Experiment 1, and those proportion of long responses found in Experiment 2 when the background was dark. Therefore, introducing the alternating illuminated background sessions with the original dark background condition had no effect on the achievement of the Empty Interval Illusion found in pigeons when the background was dark.

Discussion

The purpose of the present experiment was to investigate the Empty Interval Illusion in terms of a differential attentional allocation explanation. The presentation of filled intervals of light provided illumination of the surrounding operant chamber. It was predicted that presentation of filled intervals of light provides the opportunity for pigeons to be attracted towards the visual features of the operant chamber. More importantly, the presentation of filled intervals could cause pigeons to be distracted away from timing the interval being presented. An attentional interpretation of timing suggests that at the moment of distraction, the attentional switch of the internal clock model would flicker open, preventing pulses from the pacemaker to be accumulated in the accumulator. This would result in the underestimation of time for filled intervals on some trials during psychophysical testing. Taking this into consideration, this would not be the case during the timing of empty intervals because the duration between the light markers that bound the empty interval is a period of darkness. Therefore, there would not be the same opportunity for pigeons to be distracted during the presentation of these intervals. If the Empty Interval Illusion is a result of decreased attention being given to timing filled intervals of light due to illumination of the chamber during the presentation of filled intervals, providing the opportunity for pigeons to be distracted during timing empty intervals via illumination should have eliminated the timing difference. Previously, such manipulation of house-light being provided during delay testing (Grant & Roberts, 1976; Roberts & Grant, 1978) has demonstrated the detracting from the retention of sample information. In addition, houselight in the form of a perceptual distractor

during psychophysical testing produced a general flattening of the psychophysical curve relative to those trials that did not provide the distractor (Sutton & Roberts, 2002).

The source of illumination used in this study was the alteration of the monitor colour during training. Previously, the background colour of the monitor was black (i.e., dark) during training and psychophysical testing which provided no additional illumination of the operant chamber. This is not taking into consideration the illumination provided during the presentation of the filled and empty sample durations. Upon training, pigeons were introduced to a similar delayed symbolic matching-to-sample procedure as previously used, however, the colour of the background was changed from black (i.e., dark) to a light gray (i.e., illuminated) color. This novel background colour was present at all times throughout training and testing sessions. Upon the introduction of the illuminated background condition, subjects tended to produce higher matching accuracy on the filled sample durations relative to the empty sample durations. More specifically, both the short and long filled intervals were more easily discriminated than the short and long empty intervals respectively (Kraemer et al., 1997; Mantanus, 1981). This difference in matching accuracy between filled and empty anchor durations occurred during both the acquisition phase of the illuminated background condition, in addition to the baseline training phase with alternating dark and illuminated background sessions. In other words, filled intervals of light were more easily discriminated relative to empty intervals marked by light regardless of background condition.

The present study was able to replicate the empty-filled timing difference displayed by Miki (2001) when the background condition was dark, as previously demonstrated in Experiment 1 when the pigeons were only given the dark background condition. More specifically, there was a tendency for pigeons to display an increased proportion of long responses on empty intervals when the signal duration was shorter (i.e., 2.0, 2.6, 3.2, and 4 s). In other words, shorter empty intervals were perceived as longer than filled intervals of equal duration. Similar to Experiment 1, as the signal durations increased, there was less of a tendency for this to occur. At the intermediate durations of 5.0 and 6.4 s, there was no difference in the proportion of long responses between empty and filled signal durations. Pigeons seemed to perceive these specific empty intermediate durations as being similar to the filled intervals of equal duration. Though Miki (2001) demonstrated this timing difference at all intermediate durations, and not at the anchor durations, the current study was able to replicate this phenomenon at shorter intermediate durations, in addition to displaying a timing difference at the short endpoint.

When the background was illuminated, there was an increased tendency for shorter empty durations (i.e., 2.0, 2.6, 3.2, and 4 s) to be classified as longer than filled intervals of equal duration. Similar to the dark background condition, as the signal durations increased, there was less of a tendency for this pattern to continue. At the intermediate duration of 5 s, there was no difference in the proportion of long responses between empty and filled signal durations. Pigeons seemed to classify this intermediate durations as being similar to the filled interval of equal duration. Most interestingly was what occurred at signal durations longer than 5 s. Pigeons seemed

to classify filled durations of light as being longer than empty durations marked by light when the signal duration to-be-timed was longer than 5 s.

When considering empty intervals when the background was illuminated, there was a tendency for empty intervals to be perceived as longer than filled intervals of equal duration. This empty-filled timing difference is supported by the difference in the PSEs between empty and filled intervals where the PSE for empty intervals was significantly lower than the PSE for filled intervals. Therefore, the introduction of the illuminated background condition did not eliminate the empty-filled timing difference that was found when the background was dark.

Most importantly, the absence of superimposition of the psychophysical functions for empty and filled intervals at the endpoints when the background was illuminated occurred. The matching accuracy for empty intervals on the anchor durations was poor relative to the matching accuracy for empty intervals when the background was dark (i.e., a general flattening of the psychophysical curve was observed). This overall decrease in timing ability bears a resemblance to Sutton and Roberts (2002) who attempted to divert pigeons' attention away from timing using a perceptual distracter during psychophysical testing, and found a general loss of stimulus control in the distracter condition relative to the condition with no perceptual distracter. It is possible that empty intervals were less discriminable when the background was illuminated relative to when the background was dark.

With this said, the general decrease in matching accuracy found at the endpoints for empty intervals may have been due to the introduction of the illuminated background, but not in the attentional influence that was originally

anticipated. The decline in matching accuracy at the endpoints for empty intervals may have been an artifact of reduced contrast between the markers that bound the empty intervals (i.e., white 500 ms markers) and the illuminated background the markers were presented on (i.e., light gray in colour). Therefore, on a small proportion of trials, pigeons may have been less able to detect the presentation of the markers, increasing the chance of guessing whether the signal duration being presented was short or long. In turn, pigeons would not have been utilizing a timing strategy to base their decision on, but a random guess instead causing the flattening of the psychophysical curve. These findings can be supported by the results found from the DL and WF analyses due to the fact that both values were larger for empty intervals in the illuminated background condition, relative to the dark background condition. This indicates that subjects were less sensitive (i.e., increased loss of stimulus control) to the passage of time of empty intervals relative to filled intervals when the background was illuminated.

When a comparison is made between the psychophysical functions for filled intervals in each of the two background conditions, no difference in the PSEs was found, however, there was a significant difference in the DLs. Therefore, the introduction of the illuminated background altered sensitivity to time but it did not systematically cause filled intervals to be perceived as longer or shorter.

Taking into consideration the attentional interpretation of time estimation, it seems as though the empty-filled timing difference when the background was illuminated cannot be thoroughly explained within the context of Mixed Memories, if an attentional component is added. The Mixed Memory Model assumes that the

empty-filled timing difference will occur if the accumulation of pulses is faster for empty intervals than it is for filled intervals. In addition, the model assumes that memory for empty and filled intervals accumulations are being mixed in two reference memory distributions. If this were the case, it would be expected that the PSE for empty intervals would lie below the geometric mean (i.e., 4 s), and the PSE for filled intervals would lie above the geometric mean by an equivalent amount. When examining the PSE differences between the empty and filled intervals, in both the dark and illuminated background conditions, it becomes evident that this is not what occurred. Regardless of whether the background was dark or illuminated, the PSE for empty intervals was located below the geometric mean by a significant amount. However, the PSE for filled intervals, regardless of background condition, was not significantly different from the geometric mean. This could only occur if the reference memory distributions were dominated by the short and long filled intervals, which would have been established during training. This would explain the reason for the PSEs for empty intervals to be below the geometric mean for two reasons. First, the clock rate for empty intervals is faster, and the accumulation of subjective time is larger than filled intervals. Therefore, an empty interval marked by light, will be perceived as being longer than a filled interval of light of the equivalent duration. Second, if the reference memory distributions are dominated, if not completely created by the short and long filled intervals, upon psychophysical testing, an empty interval will be compared to these values present in reference memory and be perceived as longer than filled intervals of equivalent duration. In addition, domination of filled intervals in the reference memory distributions will result in the

bisection of these intervals to be at the geometric mean, which is what occurred in the current study.

It does not seem that creating a condition whereupon empty intervals were given an equal opportunity to be distracted away from the temporal aspect of the procedure was able to account for the timing difference found between filled and empty intervals of light displayed in Experiment 1. Illuminating the background to promote the distraction of timing empty intervals did demonstrate evidence in the direction of an attentional reason for the timing difference (i.e., an increase in the PSE for empty intervals when the background was illuminated relative to when then background was dark), but was not found to be significant.

Experiment 3

The third experiment investigated the possibility that the introduction of the illuminated background in Experiment 2 was reason for the general decrease in matching accuracy found at the endpoints for empty intervals. In an attempt to explain the Empty Interval Illusion, Experiment 2 introduced illumination during alternating sessions so the timing of empty intervals would have equal opportunity to be distracted by the visual features of the operant chamber, eliminating the empty-filled timing difference found in Experiment 1.

Illumination has been provided once before; therefore, illuminating the chamber for the entire session would not be as distracting after several training sessions. However, introducing illumination into the chamber has the possibility of impeding the timing of empty intervals. The illumination provided to decrease the attention being paid to timing both filled and empty intervals was a change in the

background illumination of the video monitor. Empty intervals consist of two light markers bounding the interval to-be-timed. The markers may have been difficult to detect against the illuminated background causing a general disruption of matching accuracy for empty intervals.

The purpose of the third experiment was to create a procedure whereupon the markers that bound the empty intervals were more easily detected. The procedure utilized was similar to Experiment 2 except the colour of the empty interval markers was changed from a white to brown, and the duration of the markers was lengthened from 500 ms to 1000 ms. This modification of the empty interval markers was intended to improve detection of the markers when contrasted against the illuminated background. Grant and Talarico (2002) conducted a study where two groups of pigeons were trained with either 2 or 8 s samples of either empty or filled intervals. In both groups, 1 s visual markers bound the filled and empty intervals similar to the visual markers utilized in the present study to indicate the presentation of empty intervals. Manipulation of the marker duration provided evidence that only those pigeons trained with filled intervals, but not those trained with empty intervals, incorporated the duration of the visual markers into the sample durations. Therefore, increasing the duration of the visual markers that bound the empty intervals from 500 ms to 1000 ms in Experiment 3 should not promote the incorporation of the marker duration into the sample durations when timing empty intervals.

Pigeons were trained with the brown 1000 ms empty markers in both the dark and illuminated background conditions and psychophysical testing followed training similar to Experiment 2. It was anticipated that the dark background condition would

still demonstrate the Empty Interval Illusion, however, the illuminated background condition would not.

Method

Subjects

Six subjects used in Experiment 1 and 2 were also used in Experiment 3.

Apparatus

The apparatus used in Experiment 1 and 2 was also used in Experiment 3.

Procedure

Baseline Training with 2 s and 8 s Anchor Durations

Following the testing conducted in Experiment 2, the birds were introduced to a set of baseline training trials consisting of 160 trials as previously described in Experiment 1 and 2. However, the difference between these baseline trials, and those the birds were previously trained with was the colour and duration of the markers bounding the empty intervals. In the present study, the colour of the empty markers was changed from white to brown, and the duration of the markers was changed from 500 ms to 1000 ms. The properties of the visual stimuli representing the filled signal durations were not altered in any way. The first phase of this baseline training with the brown 1000 ms empty markers resembled that from Experiment 2 in that sessions alternated with the dark and illuminated conditions until the birds were able to reach a matching accuracy of at least 75% on both the filled and empty anchor durations, with both the dark and illuminated background for four out of five consecutive sessions. To begin, each of the pigeons was placed on alternating training sessions of dark and illuminated background conditions for 26 sessions (i.e., 13 sessions of each

background type). At this time, pigeons were then put on blocked sessions of whichever condition resulted in lower accuracy (i.e., if a pigeon produced higher accuracy in the illuminated background condition, blocked sessions with the dark background condition were given until matching accuracy met criterion). Two subjects were removed from the study due to an inability to reach criterion with respect to matching accuracy in this first phase of baseline training. The second phase of baseline training began with the alternation of the dark and illuminated background conditions similar to Experiment 2. Once criterion was met, psychophysical testing followed.

Psychophysical Testing with 2 s and 8 s Anchor Durations

Psychophysical testing in this experiment was similar to Experiment 2. One session consisted of 160 trials. The intermediate durations were 2.6, 3.2, 4.0, 5.0, and 6.4 s. In each session, intermediate durations were randomly tested eight times for each type of interval (i.e., filled and empty). The pigeons were reinforced for responding correctly following the presentation of one of the four anchor durations, but responses following the presentation of one of the intermediate durations was not reinforced. Psychophysical testing in this experiment was similar to Experiment 2 in that testing sessions were alternated between the dark and illuminated background conditions. Therefore, a total of 30 testing sessions were implemented (15 sessions of the illuminated background and 15 sessions of the dark background). All other aspects of these sessions were identical to those described in Experiment 1.

Results

Baseline Training with 2 s and 8 s Anchor Durations

To evaluate the acquisition of the subjects' ability to discriminate between filled durations of light and empty durations designated by 1 s brown visual markers, the percent correct for short and long durations were examined in a similar manner to that in Experiment 2. When pigeons were able to achieve matching accuracy of at least 75% on both empty and filled trials for four out of five consecutive sessions, pigeons could progress to the second phase of baseline training where alternating sessions of dark and illuminated background continued. Subjects took a variable number of sessions to meet the set criterion in order to move to psychophysical testing. When the background was dark, the mean accuracy of filled intervals of light for the last five baseline training sessions for all of the subjects was 95.2%, and the mean accuracy of the empty intervals marked by light for the last five baseline training sessions for all of the subjects was 82.9%. When the background was illuminated, the mean accuracy of filled intervals of light for the last five baseline training sessions for all of the subjects was 91.2%, and the mean accuracy of the empty intervals marked by light for the last five baseline training sessions for all of the subjects was 83.5%.

For statistical analysis, the last five baseline training sessions of each subject prior to psychophysical testing were averaged and compared in a 2 X 2 X 2 repeated measures ANOVA with the background condition (i.e., dark or illuminated), type of interval (i.e., filled or empty), and anchor duration (i.e., short or long) as within-subjects variables. A significant main effect of condition was found, $F(1, 3) =$

2187.00, $p < 0.05$, which indicated that matching accuracy was greater in the dark background condition than in the illuminated background condition. In addition, a significant main effect of interval was found, $F(1, 3) = 20.46$, $p < 0.05$. This indicated that filled intervals were discriminated better than empty intervals, regardless of background condition. No other significant main effects, or significant two-way or three-way interactions were found.

Psychophysical Testing with 2 s and 8 s Anchor Durations

The percentage of long responses was plotted as a function of signal duration for both the filled and empty interval durations. Refer to the top panel of Figure 13 to examine the percentage of long responses for both the filled and empty intervals of light when the background was dark. In addition, the bottom panel of Figure 13 displays the percentage of long responses for both the filled and empty intervals of light when the background was illuminated. A $2 \times 2 \times 7$ repeated measures ANOVA with the background condition (i.e., dark or illuminated), type of interval (i.e., filled or empty), and signal duration (i.e., two anchor durations + five intermediate durations) as the within-subjects factors was conducted. A main effect of signal, $F(6, 18) = 208.14$, $p < 0.05$ was found, though main effects were not found for the type of interval or the background condition. However, a type of interval by signal interaction, $F(6, 18) = 7.39$, $p < 0.05$ was also found. When the proportion of long responses for filled and empty intervals was collapsed over background condition, empty intervals consistently had higher proportions of long responses than filled intervals at the signal durations of 2.0, and 2.6, $F(1, 3) = 51.37, 12.21$, both $ps < 0.05$,

in addition to being marginally higher at 3.2 s, $F(1, 3) = 7.77, p = 0.069$. No other interactions were found to be significant.

The point of subjective equality (PSE) for each subject for both background conditions was calculated by conducting similar linear regressions of the proportion of long responses as in Experiment 1 and 2. When the background was dark, the PSE for filled intervals was 4.39 s, and for empty intervals was 3.72 s. When the background was illuminated, the PSE for filled intervals was 4.46 s, and for empty intervals was 4.12 s (refer to Experiment 3 of Table 1). A 2 X 2 repeated measures ANOVA with background condition (i.e., dark vs. illuminated) and type of interval (i.e., filled vs. empty) as the within-subjects factors was conducted. There were no significant main effects or interaction found in this analysis.

The PSEs were also compared to the corresponding geometric mean (i.e., 4 s). When the background was dark, the PSE for empty intervals (3.72 s) was not significantly different from the geometric mean. In addition, the PSE for filled intervals (4.39 s) did not differ significantly from the geometric mean (4 s). When the background was illuminated, the PSE for empty intervals (4.12 s) was found to not be significantly different from the geometric mean. In addition, the PSE for filled intervals (4.46 s) did not differ significantly from the geometric mean.

The regression equations were also used to calculate difference limens (DLs). When the background was dark, the DL for filled intervals was 1.00, and the DL for empty intervals was 1.21. When the background was illuminated, the DL for filled intervals was 1.18, and the DL for empty intervals was 1.20 (Table 1). A 2 X 2 repeated measures ANOVA with background condition and type of interval as the

within-subjects factors was conducted. There were no significant main effects of background condition or type of interval. In addition, no significant interaction was found.

The DLs and PSEs were used to calculate the Weber fractions similar to that in Experiment 1 and 2. When the background was dark, the WF for filled intervals was 0.23 and the WF for empty intervals was 0.32. When the background was illuminated, the WF for filled intervals was 0.26, and the WF for empty intervals was 0.30 (Table 1). A similar 2 X 2 repeated measures ANOVA with background condition and type of interval as the within-subjects factors was conducted. There were no significant main effects of background condition or type of interval. In addition, no significant interaction was found. Both the DL and WF analyses indicated that subjects were equally sensitive to the passage of time, regardless of interval type, and background condition.

Two separate 2 X 2 X 7 repeated measures ANOVA's where experiment (i.e., Experiment 2 vs. Experiment 3), type of interval (i.e., filled vs. empty), and signal duration (i.e., two anchor durations + five intermediate durations) were the within-subjects factors, for each of the two background conditions was conducted on the four subjects used in Experiment 3. In order for this analysis to be conducted, only the data from the four subjects were used from both Experiment 2 and 3. This was to examine whether there were any significant differences between the psychophysical functions for filled and empty intervals found in Experiment 2, and those found in Experiment 3, when the background was either dark or illuminated. Refer to the top panel of Figure 14 to examine the percentage of long responses for filled intervals of

light when the background was dark in Experiment 2 and 3. In addition, the bottom panel of Figure 14 displays the percentage of long responses for empty intervals of light when the background was dark in Experiment 2 and 3. Refer to the top panel of Figure 15 to examine the percentage of long responses for filled intervals of light when the background was illuminated in Experiment 2 and 3. In addition, the bottom panel of Figure 15 displays the percentage of long responses for empty intervals of light when the background was illuminated in Experiment 2 and 3.

In the dark background condition, only main effects of type of interval, $F(1, 3) = 13.34, p < 0.05$, and signal duration, $F(6, 18) = 233.62, p < 0.05$, were found. In addition, a type of interval by signal duration interaction was found, $F(6, 18) = 8.69, p < 0.05$. There were no significant differences between the proportion of long responses for empty intervals in Experiment 2, and those achieved in Experiment 3. The same results were found for the proportion of long responses for filled intervals. In other words, there were no differences between the Empty Interval Illusion found in Experiment 2, and those proportion of long responses found in Experiment 3, when the background was dark.

In the illuminated background condition, a main effect of type of interval, $F(1, 3) = 25.01, p < 0.05$, signal duration, $F(6, 18) = 169.91, p < 0.05$, and experiment, $F(1, 3) = 21.52, p < 0.05$, was found. In addition, an experiment by signal duration interaction, $F(6, 18) = 4.27, p < 0.05$, and a type of interval by signal duration interaction, $F(6, 18) = 8.47, p < 0.05$ were found. Most importantly, a three-way experiment by interval by signal duration interaction, $F(6, 18) = 4.94, p < 0.05$, was found.

A simple main effects analysis revealed no significant differences in the proportion of long responses for filled intervals, when the background was illuminated, in Experiment 2 and 3. However, the proportion of long responses for empty intervals was higher in Experiment 2, relative to Experiment 3 at the 3.2 s intermediate duration, $F(1, 3) = 36.27$, $p < 0.05$, in addition to marginal differences found at the 2.0, 2.6, and 4 s signal durations, $F_s(1, 3) = 9.28$, 10.05, and 6.97, $p_s = 0.056$, 0.051, and 0.078. This demonstrates that the introduction of the 1 s brown empty markers decreased the proportion of long responses for empty intervals at the signal durations of 2.0, 2.6, 3.2, and 4 s.

Discussion

The purpose of the present experiment was to investigate the possibility that the introduction of the illuminated background in Experiment 2 was the reason for the general decrease in matching accuracy found at the endpoints for empty intervals. Upon the introduction of the brown coloured 1 s empty markers in both the dark and illuminated background conditions, subjects tended to produce higher matching accuracy on the filled sample durations relative to the empty sample durations. More specifically, both the short and long filled intervals were more easily discriminated than the short and long empty intervals respectively regardless of whether the background was dark or illuminated (Kraemer et al., 1997; Mantanus, 1981; Santi et al., 2003). In addition, matching accuracy for filled intervals of light and empty intervals marked by light were consistently better in the dark background condition relative to the illuminated background condition prior to psychophysical testing.

The present study was unable to find the empty-filled timing difference displayed by Miki (2001) when the background condition was dark, as previously demonstrated in Experiment 1 and Experiment 2, though a trend in the direction of the timing difference was evident. Though there was a tendency for pigeons to display an increased proportion of long responses on empty intervals when the signal duration was shorter (i.e., 2.0, 2.6, and 3.2 s), there was no significant difference found at the signal durations that corresponds to the geometric mean (i.e., 4 s) between filled and empty intervals. The absence of the Empty Interval Illusion in this particular study can be accounted for by the differential performance of the individual subjects. When examining the individual percentage long responses for empty and filled intervals of light when the background was dark for each of the four subjects, it was noticed that the PSE was at 4.1 s for filled intervals and 4.6-s for empty intervals for one particular subject. All other subjects in the experiment did not display this opposite filled-empty timing difference, nor did this particular subject display this timing difference in Experiment 1 and 2. Using these PSE values in the calculation of the overall PSEs for empty and filled intervals when the background was dark caused a significant rightward shift in the psychophysical function for empty intervals. In turn, the PSE for empty intervals increased in the direction of the geometric mean, eliminating the Empty Interval Illusion found in Experiment 1 and 2.

Similar to Experiment 1 and Experiment 2, as the signal durations increased, there was less of a tendency for this empty-filled timing difference to occur. At the intermediate durations of 4.0, 5.0, and 6.4 s, there was no difference in the proportion of long responses between empty and filled signal durations. Pigeons seemed to

perceive these empty intermediate durations as being similar to the filled intervals of equal duration. Most importantly, though the PSEs for filled and empty intervals did not differ from each other due to differential performance by an individual subject, the proportion of long responses for both filled and empty intervals of light did not differ from those obtained in Experiment 1 and 2. Therefore, the empty-filled timing difference found at shorter signal durations was replicated in the current study when the empty markers that bound the interval were increased in duration, in addition to changed from white to brown.

When the background was illuminated, there was an increased tendency for the empty short anchor duration (i.e., 2 s) to be classified as longer than the filled interval of equal duration. In contrast to the dark background condition, there were no additional differences between the judgment of empty and filled intervals of light at any other signal durations. In other words, the presentation of empty intervals via brown 1 s markers could be interpreted as facilitating in the timing of filled and empty intervals to be similar in all signal durations except at the shortest signal duration. This differs from the results obtained in Experiment 2 in the illuminated background condition, where all signal durations between empty and filled intervals differed except at the 5 s signal duration.

Taking into consideration the attentional explanation of time estimation, the Mixed Memory Model assumes that the empty-filled timing difference will occur if the accumulation of subjective time is greater for empty intervals than it is for filled intervals. In addition, a second assumption states that the memory for empty and filled interval accumulations are being mixed in two reference memory distributions.

As explained in Experiment 2, if the assumptions of the Mixed Memory model were correct, it would be expected that the PSE for empty intervals would consistently lie below the geometric mean when the background was black, regardless of the properties of the markers that bound the empty intervals. Moreover, if illuminating the background of the video monitor did promote distraction to timing empty intervals, the PSE for these empty intervals would have displayed a rightward shift, relative to the PSE for empty intervals in the black background condition. The results were in this direction but were not significant. The PSE for empty intervals did increase when the background was illuminated, but was not found to be significant. In addition, the PSE for filled intervals would lie above the geometric mean by the same amount that empty intervals lay below the geometric mean, if the reference memory distributions were equally mixed between empty and filled intervals. When examining the psychophysical functions for filled intervals, regardless of background condition, the PSEs were not significantly different from the geometric mean. According to the Mixed Memory Model, this could only occur if the reference memory distributions were dominated by the short and long filled intervals, which would have been established during training.

When the markers that bound the empty intervals were changed to 1 s brown markers, two important features of the psychophysical function for empty intervals occurred that differed from Experiment 2 when the background was illuminated. First, the psychophysical curve regained a steeper slope, and resembled the psychophysical curve for filled intervals. This is supported with the result that the DL values displayed no difference between the filled and empty intervals when the

background was illuminated, compared to Experiment 2, which did display a significant decrease in sensitivity to timing empty intervals when the background was illuminated. More importantly, this demonstrates a higher matching accuracy for empty intervals when the markers that bound the interval were changed to increase contrast between the markers and the background. Second, the PSE for empty intervals did not differ from the geometric mean when the background was illuminated in the current experiment. This differs from Experiment 2 that found the PSE for empty intervals to be significantly below the geometric mean regardless of the background condition. This is essential to the current study because the PSE for empty intervals was significantly below the geometric mean regardless of the background condition in the two previous experiments. Therefore, elimination of the empty-filled timing difference occurred once the increased performance on the anchor durations for empty intervals was established. It can be concluded that once the performance of empty intervals was increased at the anchor durations, illuminating the background was able to produce distraction during the presentation of empty intervals. According to the attentional explanation of time estimation, this distraction from timing the empty intervals being presented caused an increase in the flicker of the attentional switch present within the internal clock, promoting a loss of accumulated pulses. With this said, illuminating the background in Experiment 3 produced a level of distraction similar to that produced during the presentation of filled intervals. This is shown by the PSEs for both of these intervals (i.e., filled and empty intervals) to be at the geometric mean when the background was illuminated.

General Discussion

The purpose of the present study was to replicate the Empty Interval Illusion in pigeons, and attempt to explain this phenomenon utilizing an attentional interpretation of time estimation in the context of Scalar Timing Theory and mixed memories. In the past, Scalar Timing Theory has been able to account for and predict a wide collection of timing properties involving a variety of experimental procedures. More recently, the Mixed Memory Model (Penney et al., 2000) modified the earlier Scalar Timing Theory to include reasons for the differential psychological representation of time between equal durations of two types of sample stimuli that are presented within the same session.

The present study took advantage of the temporal bisection procedure and demonstrated a reliable Empty Interval Illusion (i.e., Experiment 1), which corresponds to the results obtained by Miki (2001). An attentional explanation of time estimation was used to explain this empty-filled timing difference. This is possible if it was assumed that the presentation of filled intervals of light allowed for visual features of the surrounding area to be visible, in turn, causing a diversion of attention away from timing the filled interval. By creating a condition whereby empty intervals were being timed with equivalent distraction, a general loss of timing ability was observed for empty intervals in the within-subjects design (i.e., Experiment 2). It was speculated that this loss of timing ability was due to the decreased contrast between the presentation of the markers and the illuminated background the markers were being presented on. When the colour of the empty markers was changed from white to brown, and the duration of the markers was increased from 500 ms to 1000 ms, the

Empty Interval Illusion was eliminated in the illuminated condition (i.e., Experiment 3). These results can be best explained by assuming that changing the properties of the empty markers improved performance on these empty trials. In addition, an absence of the empty-filled timing difference in the illuminated background is explained as being an increase of flicker of the attentional switch on a large proportion of empty interval trials during psychophysical testing

The Empty Interval Illusion

The purpose of Experiment 1 was to determine the reliability of the Empty Interval Illusion that has been previously established in pigeons (Miki, 2001). Previous research has demonstrated that specific stimulus properties affect the temporal perception of the durations to-be-timed. More specifically, whether the temporal duration to-be-timed is filled or empty produces significant timing differences when these durations are presented within the same session. This empty-filled timing difference has been found in both humans (Abel, 1972a, 1972b; Grondin, 1993; Rammsayer & Lima, 1991) and pigeons (Kraemer et. al., 1997; Mantanus, 1981). However, the results of these various studies have demonstrated conflicting results due to procedural differences. Most recently, Miki (2001) conducted a study to assess the perception of filled and empty intervals in pigeons by training them in a within-subjects design to discriminate durations of filled intervals and empty intervals with three sets of anchor durations. Psychophysical testing was able to demonstrate a filled-empty timing difference with each of the three sets of anchor durations. However, this timing difference opposed findings from previous research in that intermediate empty intervals were perceived to be longer than filled

interval trials of equal duration. This occurrence was termed the Empty Interval Illusion and counteracts what is demonstrated in humans who seem to display a Filled Interval Illusion (Goldfarb & Goldstone, 1963; Goldstone & Goldfarb, 1963; Thomas & Brown, 1974).

By training pigeons with anchor durations that have previously shown evidence for the Empty Interval Illusion (i.e., 2 vs. 8 s), and then conducting psychophysical testing, the current study was able to demonstrate the empty-filled timing difference to be a reliable one (Miki, 2001). In comparison to the human literature, these results could be predicted because conflicting results have indicated that under specific experimental conditions, time discrimination is better with empty intervals compared to filled intervals (Grondin, 1993; Grondin, Meilleur-Wells, Ouellette, & Macar, 1998). In Experiment 1, a timing difference was established where pigeons perceived empty intervals marked by lights to be subjectively longer than equivalent durations of filled intervals. The empty-filled timing difference occurred even though filled intervals were discriminated easier than empty intervals during training, which corresponds to past research involving filled and empty intervals (Kraemer et al., 1997; Mantanus, 1981; Santi et al., 2003). Although Miki (2001) displayed the Empty Interval Illusion at all intermediate durations, the present study was able to replicate the phenomenon at shorter intermediate durations. Most importantly, the timing difference between filled and empty intervals was the divergence of the two psychophysical functions at the geometric mean. In addition, evidence for the empty-filled timing difference can be seen in the significant

differences in the PSE for empty and filled intervals, where the PSE for empty intervals was significantly less than the PSE for filled intervals.

The empty-filled timing difference could be interpreted as a bias to respond to the comparison correct for the long empty anchor duration on some proportion of trials where no sample representation is present in the comparator. If this were the case, the proportion of long responses for empty intervals would have been greater than the proportion of long responses for filled intervals regardless of signal duration. However, the proportion of long responses for filled intervals was greater than the proportion of long responses for empty intervals at the longer signal durations. This response difference at the longer anchor duration was found throughout the entire study when the background was dark, although it was not found to be significant in Experiments 2 and 3.

An Attentional Explanation of Time Estimation

Grant and Roberts (1976) examined pigeons' memory for time utilizing a delayed matching-to-sample procedure but either darkness or illumination filled the delay interval. Results demonstrated that accuracy was substantially lower when illumination filled the delay interval, relative to when the delay interval was dark. In addition, this light-induced retroactive inhibition increased as the intensity of illumination increased. A further analysis of these results carried out by Roberts and Grant (1978) found that brief exposure to light produced significant retroactive inhibition, and this effect increased as the length of the exposure to the light increased. An attentional interpretation of timing would suggest that upon the introduction of the light during the delay interval, pigeons would have the tendency to

be distracted away from remembering the sample stimulus due to the opportunity to view the surrounding area of the operant chamber. This would result in the lower matching accuracy for the sample stimulus, and the level of retroactive inhibition would increase as the length of exposure to the light increased.

It was predicted that the Empty Interval Illusion could be best explained in terms of differential attentional allocation being given to filled and empty intervals of light (Experiment 2). With respect to results shown in previous research (Grant & Roberts, 1976; Roberts & Grant, 1978), it was predicted that presentation of filled intervals of light provided the opportunity for pigeons to be attracted towards the visual features of the operant chamber, in turn, perceiving these intervals as being shorter relative to empty intervals of equivalent duration. By providing the opportunity for equivalent distraction to occur during the presentation of empty intervals, an elimination of the Empty Interval Illusion was anticipated. The present study was able to demonstrate the reliable empty-filled timing difference displayed by Miki (2001) when the background condition was dark, as previously demonstrated in Experiment 1 when the pigeons were only given the dark background condition. The psychophysical functions for filled intervals in Experiment 2 were found to resemble those in Experiment 1 when the background was dark (i.e., superimposition of the psychophysical functions for filled intervals occurred). Similar results were obtained when examining the psychophysical functions for empty intervals when the background was dark.

When the background was illuminated, the psychophysical function for filled intervals did not differ from the psychophysical function for filled intervals when the

background was dark. Therefore, the introduction of the illuminated background did not alter the way in which filled intervals were perceived. The absence of any timing difference found for filled intervals in the two conditions is supported by the absence of difference in the PSEs for these two psychophysical functions. When considering empty intervals when the background was illuminated, there was a tendency for empty intervals to be perceived as longer than filled intervals of equal duration. This empty-filled timing difference is supported by the difference in the PSEs between empty and filled intervals where the PSE for empty intervals was significantly lower than the PSE for filled intervals. Although the PSE for empty intervals increased slightly in the illuminated background (i.e., the empty-filled timing difference was attenuated slightly), the introduction of the illuminated background condition did not eliminate the empty-filled timing difference found when the background is dark.

What is important to note is the absence of superimposition of the psychophysical functions for empty and filled intervals at the endpoints when the background was illuminated. The matching accuracy for empty intervals on the anchor durations was poor relative to the matching accuracy for empty intervals when the background was dark (i.e., a general flattening of the psychophysical curve was observed). This overall decrease in timing ability bears a resemblance to that of Sutton and Roberts (2002) who attempted to divert pigeons' attention away from timing using a perceptual distracter during psychophysical testing, and found a general loss of stimulus control in the distracter condition relative to the condition with no perceptual distracter. It is possible that empty intervals were less discriminable when the background was illuminated relative to when the background was dark. With this

said, the general decrease in matching accuracy found at the endpoints for empty intervals may have been due to the introduction of the illuminated background, but not in the attentional influence that was proposed. The decline in matching accuracy at the endpoints for empty intervals may have been an artifact of reduced contrast between the markers that bound the empty intervals (i.e., white 500 ms markers) and the illuminated background the markers were presented on (i.e., light gray in colour). If this were the case, on a proportion of trials, pigeons may have been less able to detect the presentation of the markers, increasing the chance of guessing whether the signal duration being presented was short or long. In turn, pigeons would not have been utilizing a timing strategy to base their decision on, but a random guess instead causing the flattening of the psychophysical curve.

Increasing the Contrast of the Markers that Bound the Empty Interval

Taking the attentional explanation of time estimation further, it does not seem that creating a condition whereupon empty intervals were given an equal opportunity to be distracted away from the temporal aspect of the procedure was able to account for the timing difference found between filled and empty intervals of light displayed in Experiment 1 and 2 when the background was dark. Although the PSE difference was attenuated slightly for empty intervals, matching accuracy for empty intervals on anchor durations was poor relative to the dark background. Introducing the illuminated background was assumed to have minimized contrast between the empty markers that bound the interval to be timed, and the illuminated background. In other words, the visual markers could have been undetected, creating a general loss of stimulus control, decreasing accuracy on those trials. Experiment 3 attempted to

account for this general loss of stimulus control, because the markers that bound the empty interval were changed in colour (i.e., from white to brown), and lengthened in duration (i.e., from 500 ms to 1000 ms in duration) to increase contrast between the markers being presented and the background to which they were being presented on.

As discussed previously, Grant and Talarico (2002) conducted a study where two groups of pigeons were trained with either 2 or 8 s samples of either empty or filled intervals. In both groups, 1 s visual markers bound the filled and empty intervals similar to the visual markers utilized in the current study to indicate the presentation of empty intervals. Manipulation of the marker duration displayed evidence that only those pigeons trained with filled intervals, but not those trained with empty intervals, incorporated the duration of the visual markers into the sample durations. Therefore, increasing the duration of the visual markers that bound the empty intervals from 500 ms to 1000 ms in Experiment 3 was not expected to promote the incorporation of the marker duration into the sample durations when timing empty intervals. If incorporating the duration of the markers with the duration of the empty intervals did occur, the anchor durations for empty intervals would have been 4 s for the short anchor duration, and 10 s for the long anchor duration (i.e., instead of the 2 s and 8 s anchor durations assumed to be presented during baseline training and psychophysical testing). The incorporation of the empty interval markers with the empty interval duration to-be-timed could account for the increased tendency of classifying empty intervals as being longer than filled intervals of equal duration. However, three results refute this explanation of the empty-filled timing difference. Firstly, if pigeons were starting to time during the onset of the first marker, and

stopping their timing at the offset of the second marker, a consistent overestimation of time would have occurred throughout psychophysical testing in Experiment 3. In other words, empty intervals would have been classified as longer than filled intervals at all durations being presented. Nonetheless, there was no significant difference between the proportion of long responses between filled and empty intervals of light at longer durations regardless of background condition. Secondly, if the anchor durations being used for empty intervals were 4 s and 10 s, the ratio between the two is 2:5, or 0.40. According to Scalar Timing Theory, the closer the ratio is to the value one, the worse the pigeons should have performed during baseline training. However, compared to Experiment 1 and 2 where the ratio between the anchor durations of 2 s and 8 s is 1:4 or 0.25, performance during baseline training in Experiment 3 was better, and reaching the criterion set for matching accuracy was acquired more rapidly. Lastly, it is important to consider the results obtained in Miki's (2001) study when the perception of time for filled and empty intervals was examined in a within-subjects design. Three sets of psychophysical testing demonstrated a reliable difference in the PSEs for the two types of intervals (i.e., the PSE for empty intervals was below the PSE for filled intervals). As explained earlier, the multiplicative differences of the PSEs indicated that the differential accumulation of pulses was the result of the presence of mixed reference memory distributions in addition to either different speed of the pacemaker or a flickering switch. If pigeons had included the duration of the markers that bound the empty interval as basis for their discrimination, a slight additive difference in the PSEs would have been apparent within the three sets of anchor durations. However, this was not the case, therefore, it can be assumed

that pigeons were not using empty interval durations that included the duration of the visual markers that bound them as a basis for their discrimination. This assumption can be carried over into the present study.

When the background was dark, a trend in the direction of the empty-filled timing difference demonstrated in Experiment 1 and 2, was found in Experiment 3 (i.e., empty intervals were perceived to be longer than filled intervals of equal duration). The absence of a significant timing difference is explained as being due to the differential performance of one individual subject who displayed evidence of an empty-filled timing difference but in the opposite direction as the other subjects (i.e., Filled Interval Illusion). The psychophysical functions for filled intervals in Experiment 3 were found to resemble those in Experiment 1 and 2 when the background was dark (i.e., superimposition of the psychophysical functions for filled intervals occurred). Therefore, the introduction of the brown 1000 ms empty markers did not affect the perception of filled intervals in this study. Similar results were obtained when examining the psychophysical functions for empty intervals when the background was dark, except that small discrepancies were found at the 3.2 and 4 s signal durations due to the differential performance of one of the subjects mentioned previously. Although this was the case, the PSE for empty intervals was below the PSE for filled intervals, although was not found to be significant.

Besides the difference in percent long responses at the short anchor duration, the illuminated background condition did not produce an empty-filled timing difference. The PSEs for both the filled and empty intervals did not differ significantly from the geometric mean. Therefore, relative to when the background

was dark, the PSE for empty intervals marked by visual stimuli experienced a rightward shift towards the geometric mean when the background was illuminated. When comparing the psychophysical function for empty intervals in the illuminated condition to the psychophysical function for empty intervals in the dark condition in Experiment 3, superimposition of the functions occurred. This means that not only did accuracy improve at the endpoints for the empty intervals relative to Experiment 2, when the markers that bound these intervals were altered, but also the illuminated background produced a rightward shift of the function for empty intervals, eliminating the empty-filled timing difference found in Experiment 2. Similar results were found for filled intervals when a comparison is made between the psychophysical functions when the background is dark and illuminated. More specifically, no differences were found between the psychophysical functions obtained for filled intervals in Experiment 2 and 3, regardless of background condition.

Scalar Timing Theory and the Mixed Memory Model

The information processing approach of the Scalar Timing Theory has been established as one of the most prominent models of timing in both humans and non-human animals. Gibbon et al., (1984) created a model that was able to predict and account for a variety of timing properties such as the superimposition of psychophysical functions using different anchor durations, in addition to the point of subjective equality being found at the geometric mean. Scalar Timing Theory makes the assumption that subjects are able to abstract the relevant information with respect to the sample stimulus being presented. Therefore, regardless of the modality (i.e.,

visual or auditory), type of interval (i.e., filled or empty), or some other manipulation (i.e., physical) placed on the stimulus, subjects are assumed to use any type of stimulus as a cue in the timing procedure as long as duration is the most relevant feature (Buhsu & Meck, 2000). Most recently, studies have been conducted and have found timing differences where one type of stimulus is judged to be longer than a second type of stimulus of equivalent duration. However, the Scalar Timing Theory had not been able to account for these timing differences until Penney et al. (2000) included the concept of mixed reference memory distributions when two types of sample stimuli are tested within the same session.

Although Scalar Timing Theory is one of the most prominent timing theories, minor adjustments to the concept of mixed memories must be made in order to account for the results found in the current study. When a standard temporal bisection procedure was used in a within-subjects design that involved the perception of time for filled and empty intervals of time, keeping the background of the video monitor dark produced an empty-filled timing difference where empty intervals were perceived to be longer than the equivalent duration of filled intervals. However, the PSE for the empty intervals was below the geometric mean, and the PSE for filled intervals was at the geometric mean. These same results were produced in the dark and illuminated background conditions in Experiment 2, as well as showing a trend for this in the dark condition in Experiment 3. Scalar Timing Theory predicts that when a single stimulus is being timed, the PSEs should fall on the geometric mean if ratio comparisons are calculated, and the psychological representation of time in accumulated in a linear fashion. However, according to the Mixed Memory Model,

when two stimuli are being timed within the same session and a timing difference is found, the PSEs should straddle the geometric mean. This would occur if there was an equal distribution of filled and empty intervals present in the reference memory distributions for short and long durations.

According to the Mixed Memory Model, this could only occur for two reasons. As explained earlier, the empty-filled timing difference could only occur if accumulation of subjective time was faster for empty intervals relative to filled intervals. Secondly, it is assumed the reference memory distributions were being dominated by the filled intervals. Upon psychophysical testing, an empty interval would be compared to the filled-dominated reference memory distributions, the appropriate ratios would be calculated, and a decision would be based on these ratio calculations. Also, domination of filled intervals in the reference memory distributions would result in bisection of filled intervals at the geometric mean, which is what occurred in all three experiments regardless of background condition. It does not seem that the attentional component included in the Mixed Memory Model was able to account for the empty-filled timing difference found in both the current study and in Miki (2001). Illuminating the background to promote the distraction of timing empty intervals did demonstrate evidence in the direction of an attentional reason for this timing difference (i.e., an increase in the PSE for empty intervals when the background was illuminated relative to when the background was black in Experiment 3), but was only found when the markers that bound the empty intervals were made more distinct against the illuminated background the markers were being presented on.

When the background was illuminated in Experiment 3, the psychophysical function for empty intervals regained a steeper slope relative to the curve represented in Experiment 2 when the background was illuminated. This demonstrates a higher matching accuracy for empty intervals when the markers that bound the interval were changed to increase contrast between the markers and the background. In addition, the PSE for empty intervals did not differ from the geometric mean when the background was illuminated. This is important because the PSE for empty intervals was significantly below the geometric mean regardless of the background condition in the two previous experiments. Therefore, it can be said that the elimination of the empty-filled timing difference occurred once the increased performance on the anchor durations for empty intervals was established. Taking the attentional explanation of time estimation into consideration, it was seen that once the performance of empty intervals was increased at the anchor durations, illuminating the background was able to produce distraction during the presentation of empty intervals. This distraction from timing the intervals being presented caused an increase in the flicker of the attentional switch present within the internal clock, preventing the accumulation of pulses. With this said, illuminating the background in Experiment 3 produced some evidence in the direction of explaining the empty-filled timing difference as being a result of decreased attention being paid to timing filled intervals of light, though some discrepancies found within the data must be accounted for. For example, although there was an elimination of the difference in the accumulated time between empty and filled intervals in Experiment 3, and was shown by the PSEs for both of these intervals (i.e., filled and empty intervals) to be at the geometric mean when the

background was illuminated, the empty-filled timing difference was not eliminated in Experiment 2 when the background was illuminated. Therefore, further studies need to be conducted in order to fully account for the Empty Interval Illusion within the context of Scalar Timing Theory and mixed memories.

Future Research

The present study was able to replicate the Empty Interval Illusion in pigeons when filled and empty intervals of light were trained and tested within the same session. The establishment of the Empty Interval Illusion with pigeons supports the Mixed Memory Model if a few assumptions are made. Firstly, the empty-filled timing difference is established when both empty and filled intervals of light are trained and tested within the same session. Secondly, the anchor durations to which the pigeons are trained with must be identical for both the empty and filled intervals in order for memory mixing to occur. Thirdly, the empty and filled intervals in which pigeons are being trained and tested on are visual stimuli in order for the attentional component of mixed memories to play an important role in the promotion of the Empty Interval Illusion. Fourth, the accumulation of subjective time must be faster for empty intervals than it is for filled intervals. Fifth, the memory for filled and empty interval accumulations are mixed into two reference memory distributions; one represents the memory for short intervals and the other represents the memory for long intervals. Sixth, a domination of filled intervals in the reference memory distributions is present when memory mixing occurs. Lastly, if the markers that bind empty intervals are made highly discriminable against the background to which the markers are being

presented, as well as being highly discriminable against filled intervals, an empty-filled timing difference will not be found.

Several studies can be conducted in order to address the importance of these assumptions when examining reasons for the empty-filled timing difference that occurs with pigeons when trained with short (i.e., 2 s) and long (i.e., 8 s) durations of light. One possible study can address whether the anchor durations are responsible for the mixed reference memory distributions. If this were the case, a procedure that inhibited the mixing of memory distributions in reference memory would promote the formation of four separate reference memory distributions (i.e., short empty, long empty, short filled, long filled), eliminating the empty-filled timing difference found in the current study. A way in which this can be done is to train pigeons with one set of anchor durations for empty intervals (e.g., 2 s vs. 8 s), and train with a second set of durations for filled intervals (e.g., 4 s vs. 16 s). If the anchor durations of the two types of intervals need to be identical in order for memory mixing to occur, training pigeons with two sets of anchor durations within the same session should prevent memory mixing from occurring, in turn, not demonstrating the Empty Interval Illusion when psychophysical testing is conducted.

Another study could examine the possibility that instructional ambiguity could be reason for the empty-filled timing differences found at longer signal durations (i.e., dark background condition in Experiment 1). Throughout the current study, the ambient conditions in the operant chamber were the same during the presentation of empty intervals and the intertrial interval (ITI) (i.e., either dark or illuminated throughout the sessions). If it is assumed that pigeons have the tendency to reset their

memory of the event duration from the trial that precedes it, it is possible that pigeons may reset their internal clock during the duration of an empty interval. This may be due to the similar ambient conditions present during the ITI and empty intervals (Kaiser, Zentall, & Neiman, 2002). This resetting of the internal clock on some proportion of empty interval trials would result in the underestimation of time relative to filled intervals of the same duration. A way in which instructional ambiguity can be examined is to train pigeons with a procedure that accounts for this confusion. By creating an experimental design that distinguishes the ITI from the presentation of empty intervals (i.e., ambient conditions for empty intervals are dark, while ITI is illuminated) may be able to account for the discrepancy between filled and empty intervals at longer signal durations.

An additional study that would be advantageous would be to train pigeons in a similar procedure used in the present study, except the filled intervals would be auditory durations instead of visual durations used here, and empty intervals would be kept visual. If evidence for the Empty Interval Illusion is not found utilizing auditory filled and visual empty signal durations, it can be concluded that the modality of filled intervals is important in demonstrating the Empty Interval Illusion. More importantly, filled intervals of light do promote a level of distraction during their presentation, in turn, demonstrating an underestimation of these filled intervals during psychophysical testing. Presentation of auditory signal durations would not provide the opportunity for distraction to occur, if the background of the video monitor remained black.

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Table 1

Mean PSEs (in seconds), DLs, and WFs for the Filled and Empty Intervals at Each Signal Duration in Experiment 1, 2, and 3.

			PSE		DL		WF	
			M	SEM	M	SEM	M	SEM
Experiment 1								
	Empty		3.35	0.02	0.92	0.13	0.27	0.03
	Filled		4.21	0.13	1.07	0.09	0.25	0.02
Experiment 2								
Dark	Empty		3.22	0.19	0.87	0.16	0.26	0.03
	Filled		4.18	0.11	0.95	0.06	0.23	0.01
Illuminated	Empty		3.33	0.24	1.82	0.13	0.57	0.06
	Filled		3.99	0.08	1.15	0.09	0.29	0.02
Experiment 3								
Dark	Empty		3.72	0.35	1.21	0.24	0.32	0.04
	Filled		4.39	0.15	1.00	0.05	0.23	0.01
Illuminated	Empty		4.12	0.28	1.20	0.14	0.30	0.05
	Filled		4.46	0.24	1.18	0.13	0.26	0.02

Figure Captions

Figure 1. A typical psychophysical function from a temporal bisection procedure.

Figure 2. A typical response curve for a FI(20) schedule.

Figure 3. A typical response curve for an empty trial on a FI (20) schedule.

Figure 4. Predictions of how the PSE would indicate the function that represents the accumulation of the psychological representation of time.

Note. From "Bisection of temporal intervals," by R. M. Church and M. Z. Deluty, 1977, *Journal of Experimental Psychology: Animal Behavior Processes*, 3, p. 224.

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Figure 5. The information-processing model of the Scalar Timing Theory.

Figure 6. An onset-latency model with independent memories for auditory and visual signals where the timing onset is delayed for the visual signal (top panel). The predicted proportion "long" responses for both auditory and visual signals (bottom panel).

Note. From "Memory Mixing in Duration Bisection," by T. B. Penney, L. G. Allan, W. H. Meck, and J. Gibbon, 1998, in D. A. Rosenbaum and C. E. Collyer (Eds.), *Timing of behavior: Neural, Psychological, and Computational Perspectives* (p. 179)

Cambridge, MA: MIT Press. Copyright 1998 by MIT Press.

Figure 7. A clock rate model with mixed memories for auditory and visual signals where the clock rate is slower for visual signals (top panel). The predicted proportion of "long" responses for both auditory and visual signals (bottom panel).

Note. From "Memory Mixing in Duration Bisection," by T. B. Penney, L. G. Allan, W. H. Meck, and J. Gibbon, 1998, in D. A. Rosenbaum and C. E. Collyer (Eds.),

Timing of behavior: Neural, Psychological, and Computational Perspectives (p. 179)

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Figure 8. The psychological functions for timing filled and empty intervals in a within-subjects design displaying the Empty Interval Illusion.

Note. From "Timing Differences: The Modality Effect and Filled Interval Illusion with Rats and Pigeons," by A. Miki, 2001, *Unpublished master's thesis*, Copyright 2001 by Wilfrid Laurier University.

Figure 9. The mean percent correct as a function of the type of interval (filled vs. empty) and blocks of sessions during the baseline training phase of Experiment 1. Error bars represent standard error of the mean.

Figure 10. The mean percent of long responses as a function of the type of interval (filled vs. empty) and signal duration during psychophysical testing in Experiment 1.

Figure 11. The mean percent of long responses as a function of the type of interval (filled vs. empty) and signal duration during psychophysical testing when the background was dark (top panel) and illuminated (bottom panel) in Experiment 2.

Figure 12. The mean percent of long responses as a function of the experiment (Experiment 1 vs. Experiment 2) and signal duration during psychophysical testing when the type of interval was filled (top panel) and empty (bottom panel) and background condition was dark.

Figure 13. The mean percent of long responses as a function of the type of interval (filled vs. empty) and signal duration during psychophysical testing when the background was dark (top panel) and illuminated (bottom panel) in Experiment 2 utilizing 1 s brown markers in Experiment 3.

Figure 14. The mean percent of long responses as a function of the experiment (Experiment 2 vs. Experiment 3) and signal duration during psychophysical testing when the type of interval was filled (top panel) and empty (bottom panel) and background condition was dark.

Figure 15. The mean percent of long responses as a function of the experiment (Experiment 2 vs. Experiment 3) and signal duration during psychophysical testing when the type of interval was filled (top panel) and empty (bottom panel) and background condition was illuminated.

Figure 1

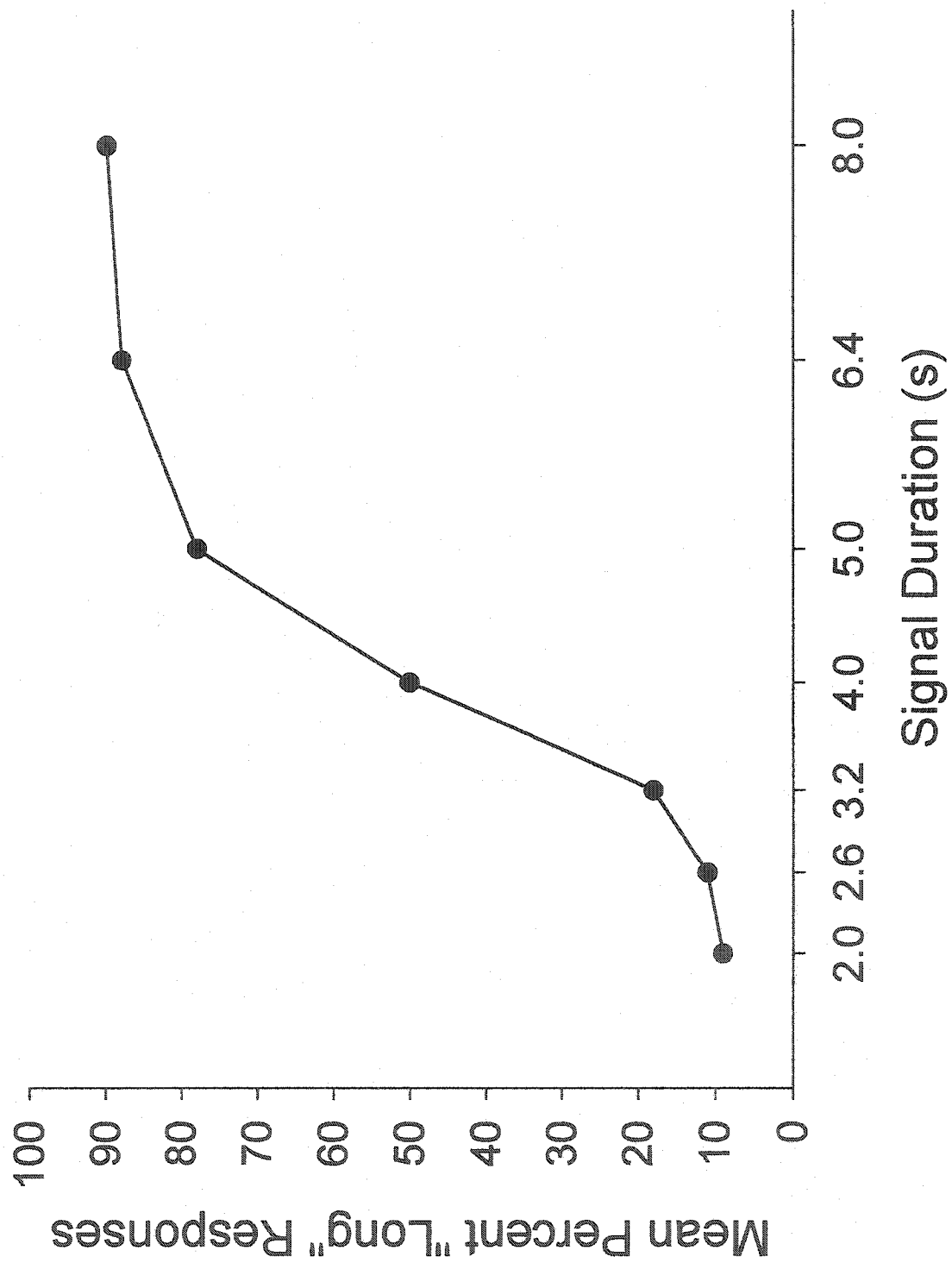


Figure 2

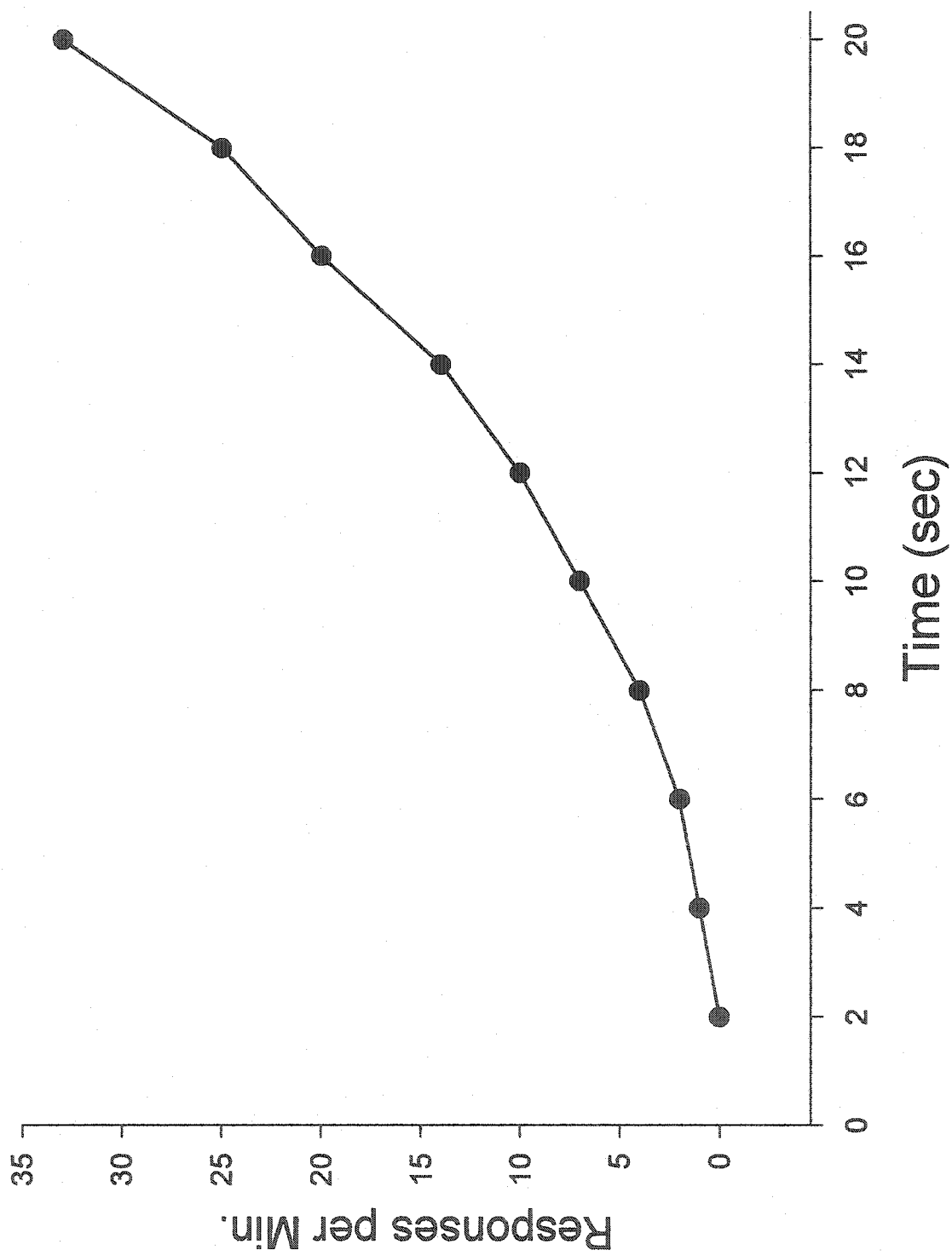


Figure 3

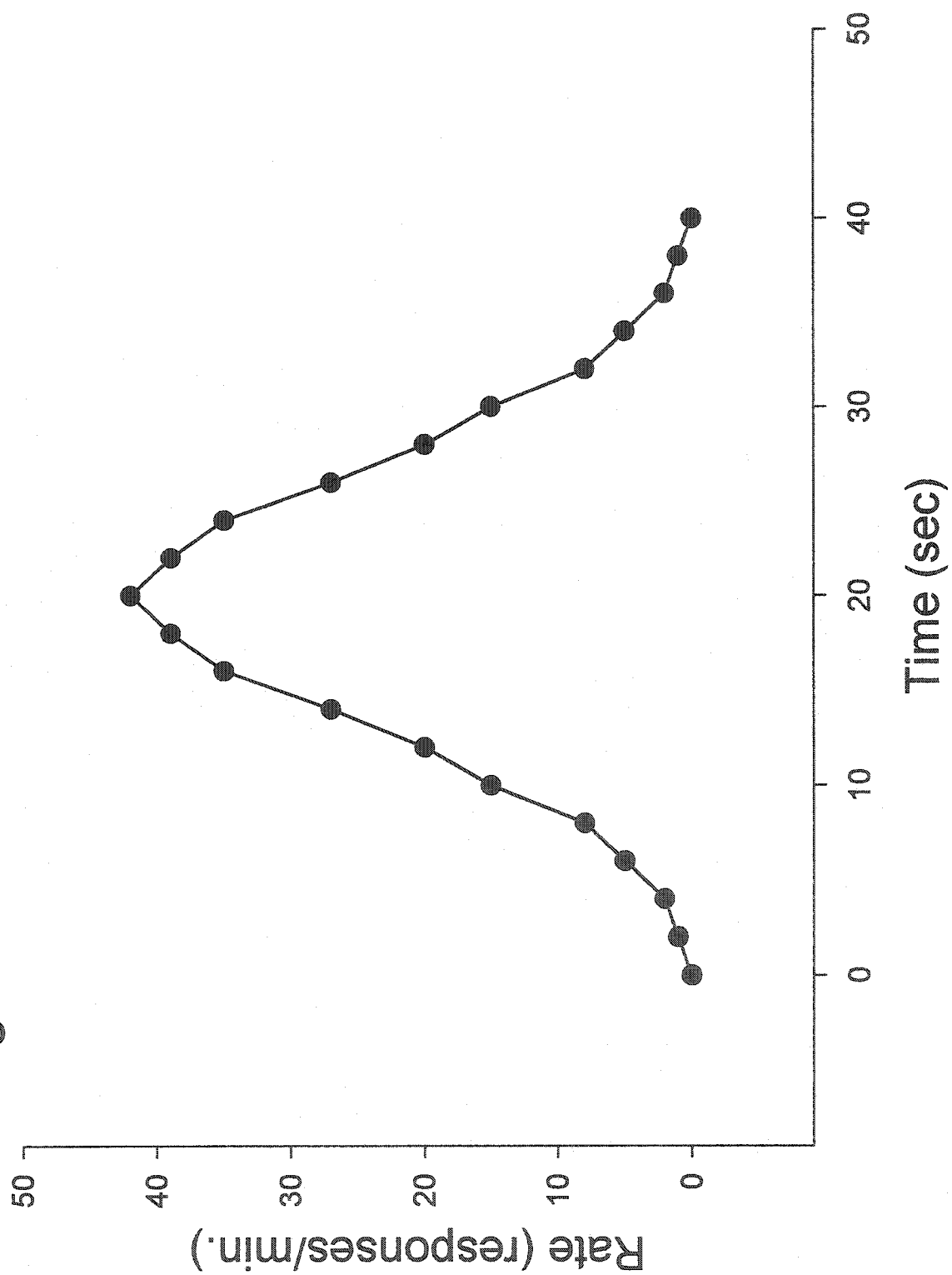


Figure 4

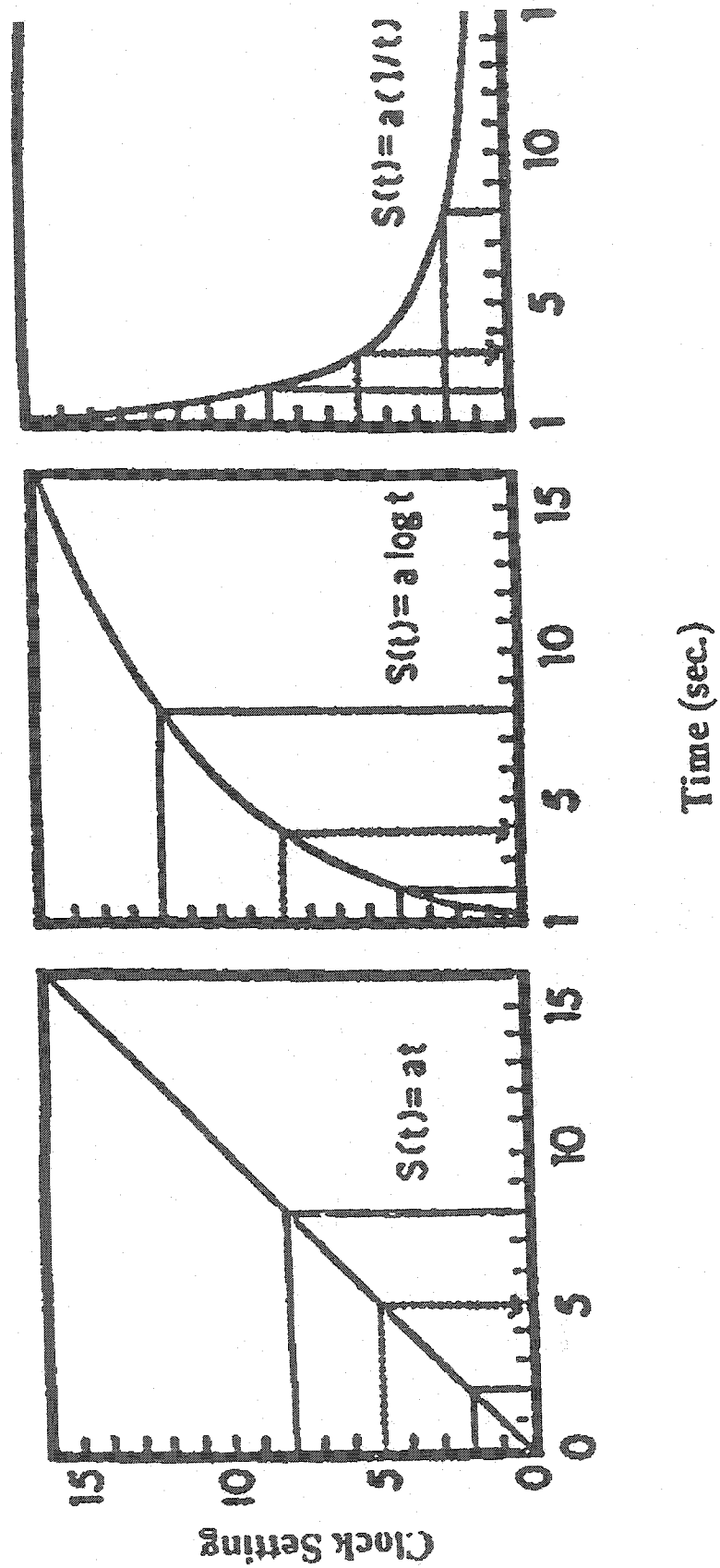


Figure 5

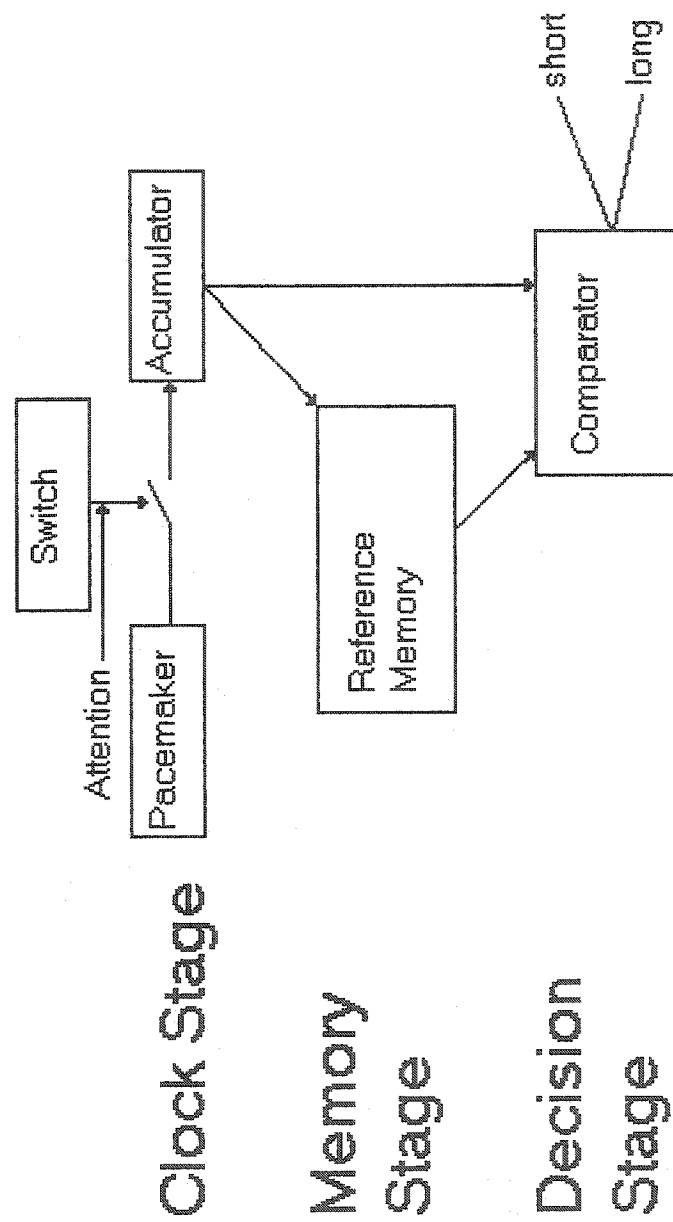


Figure 6

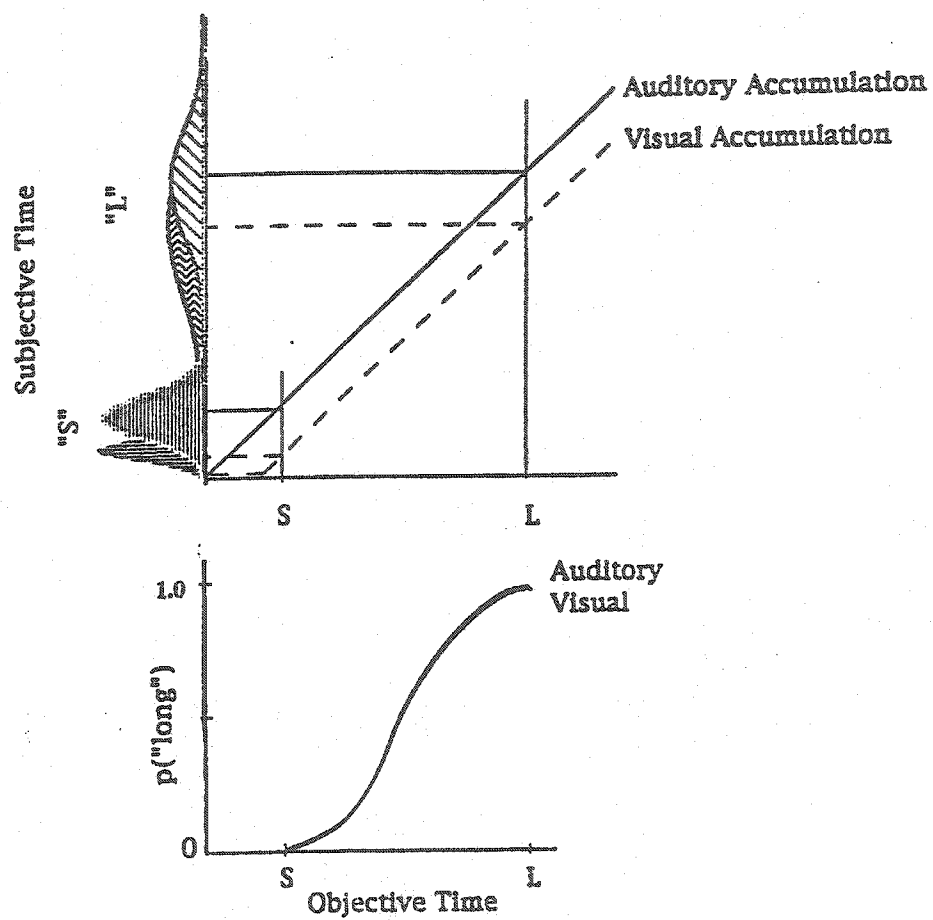


Figure 7

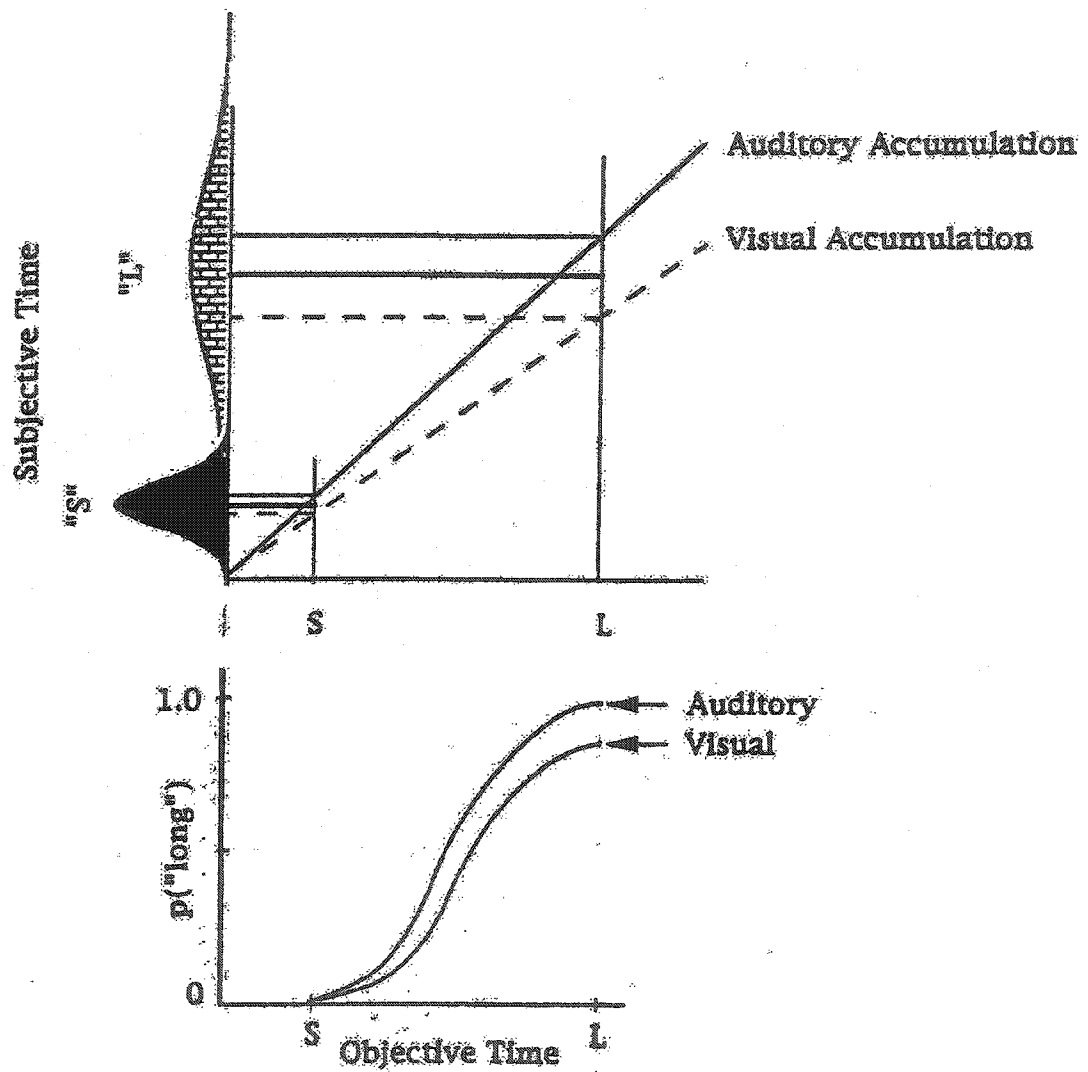


Figure 8

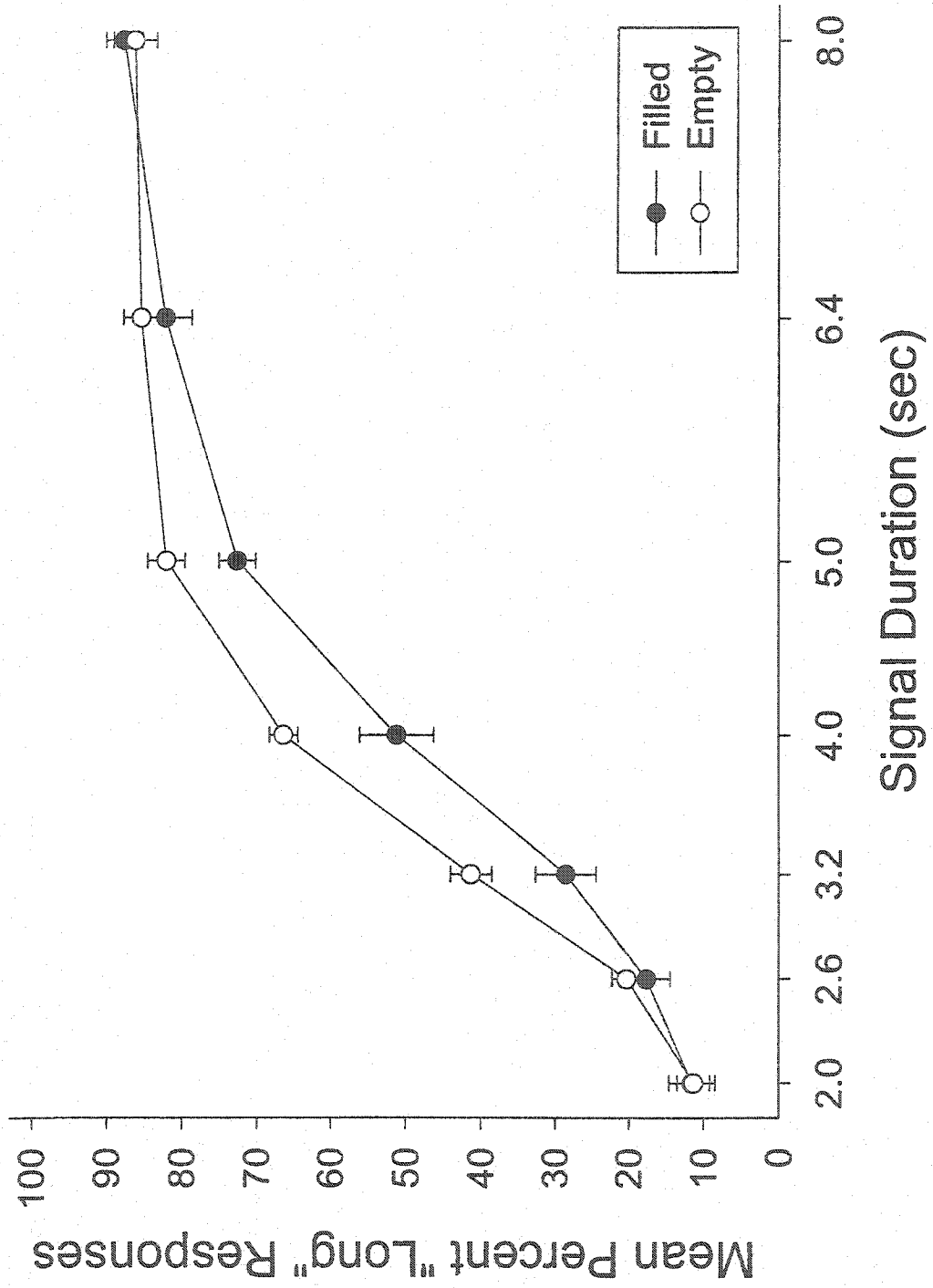


Figure 9

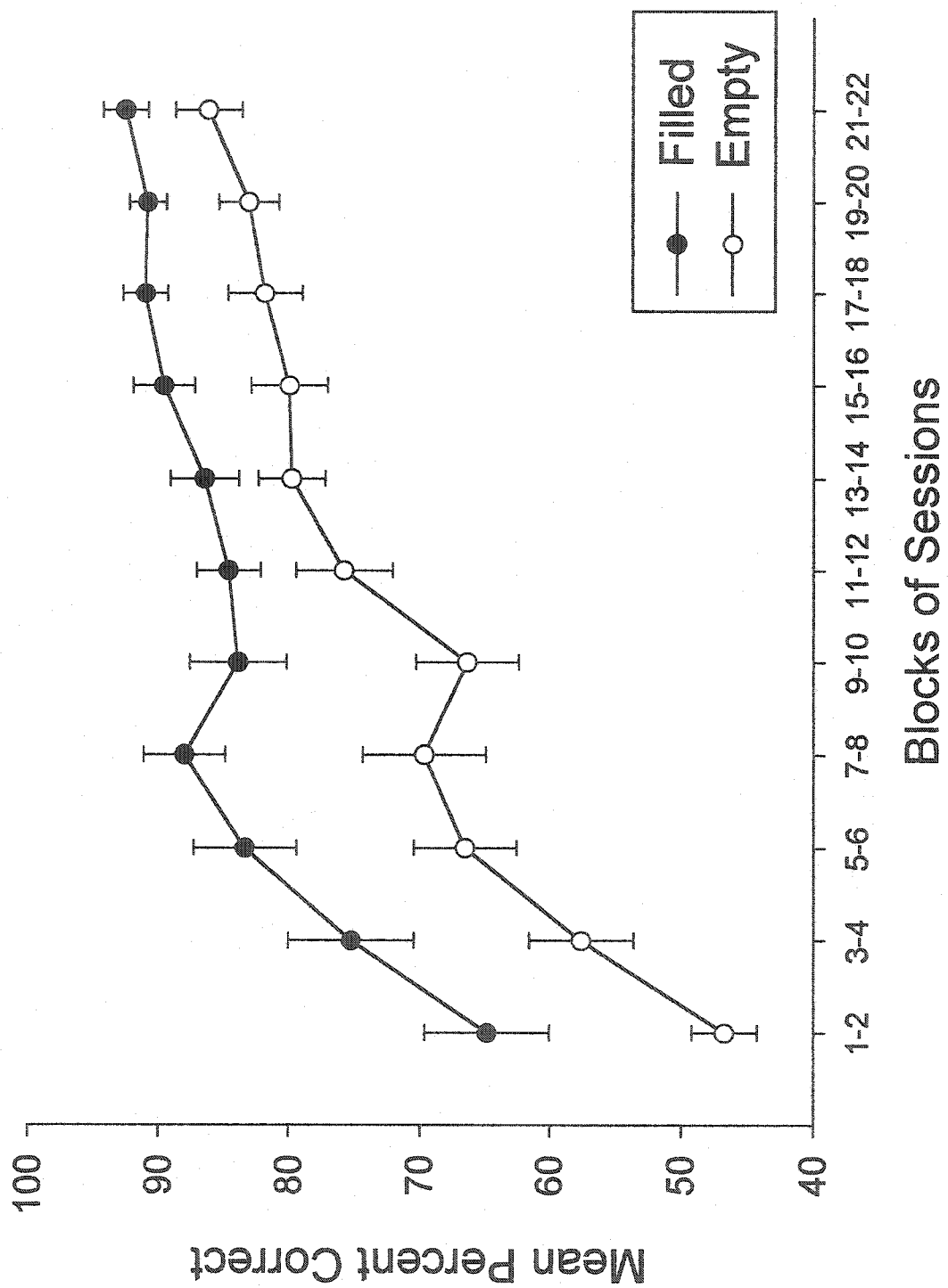


Figure 10

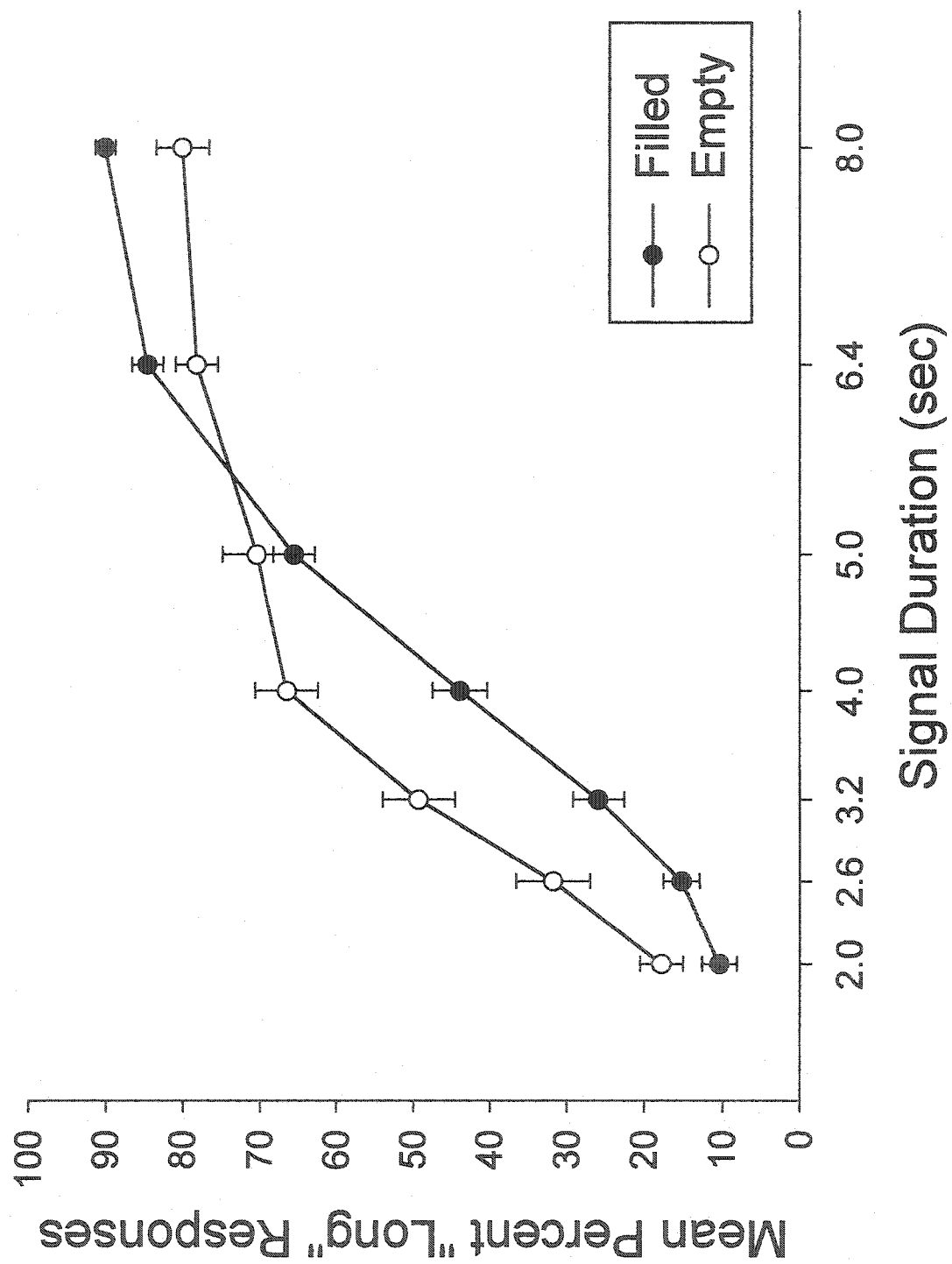


Figure 11

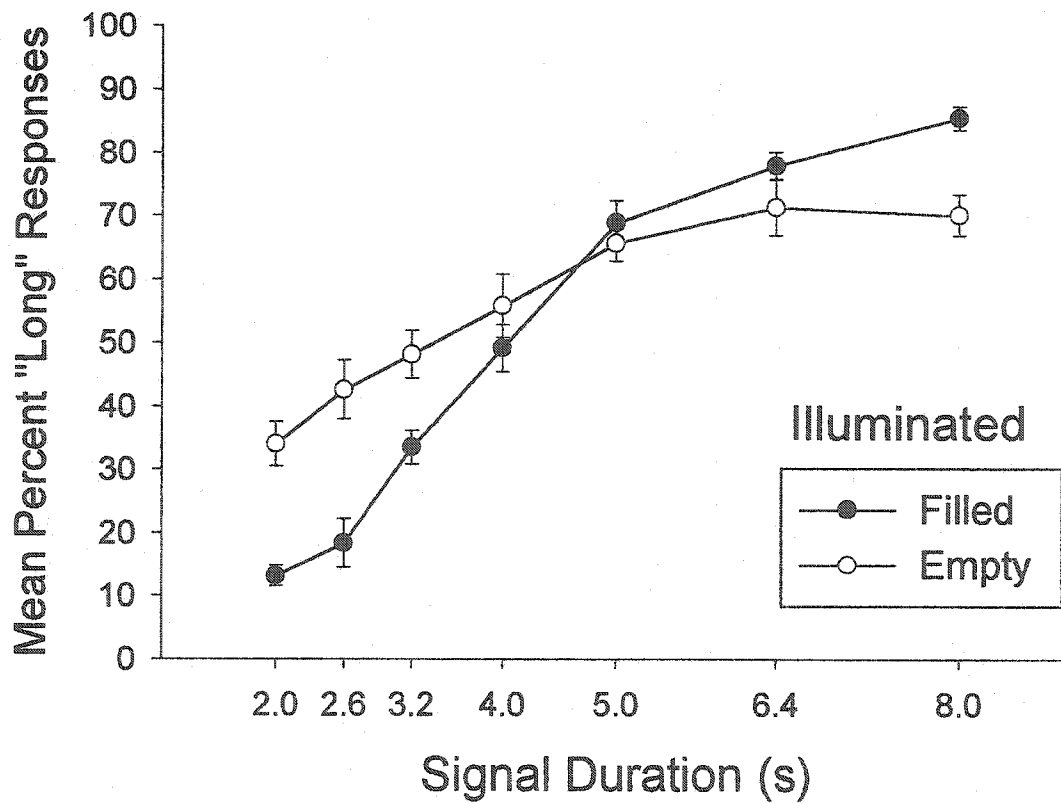
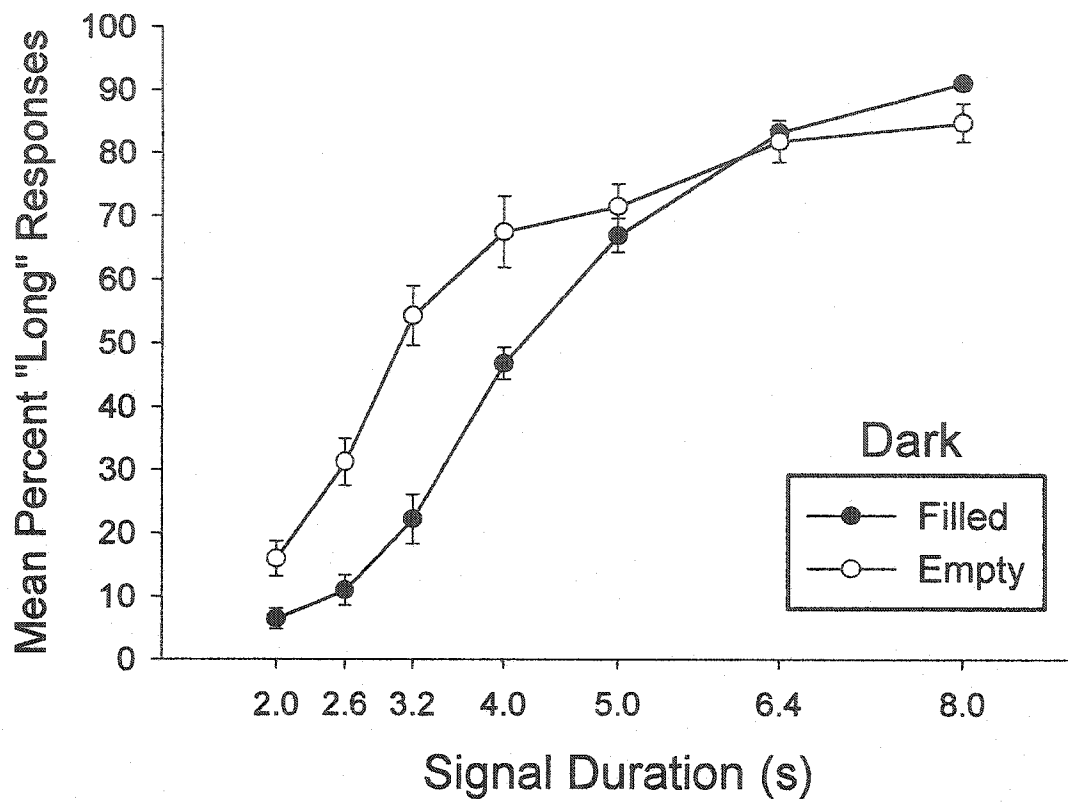


Figure 12

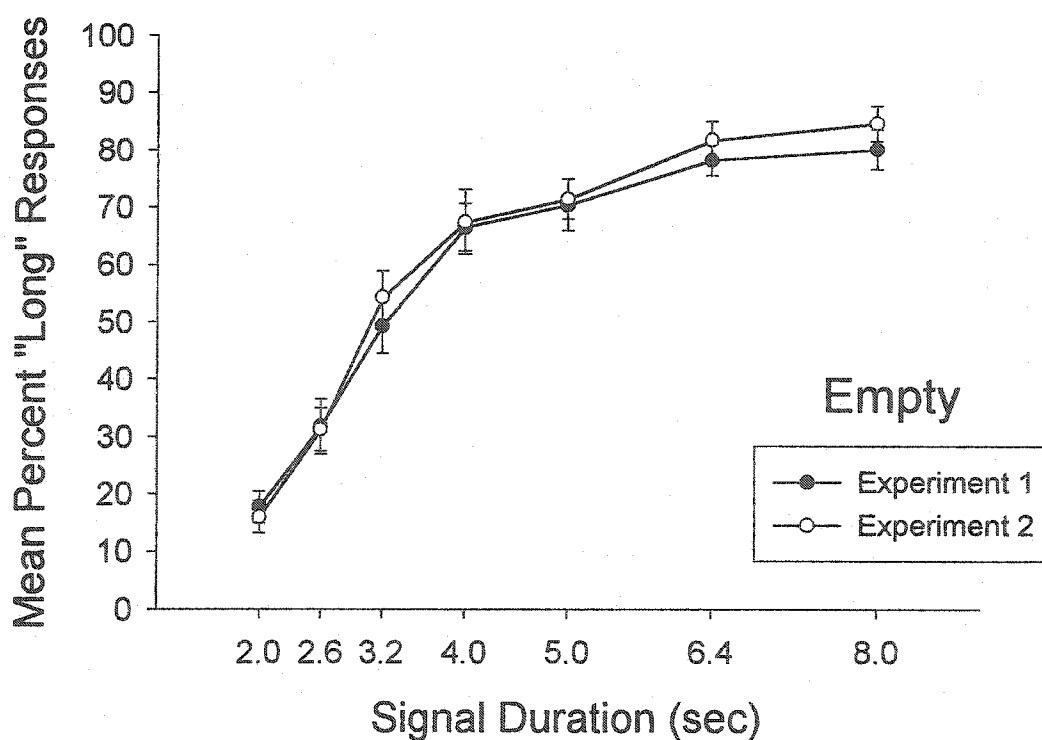
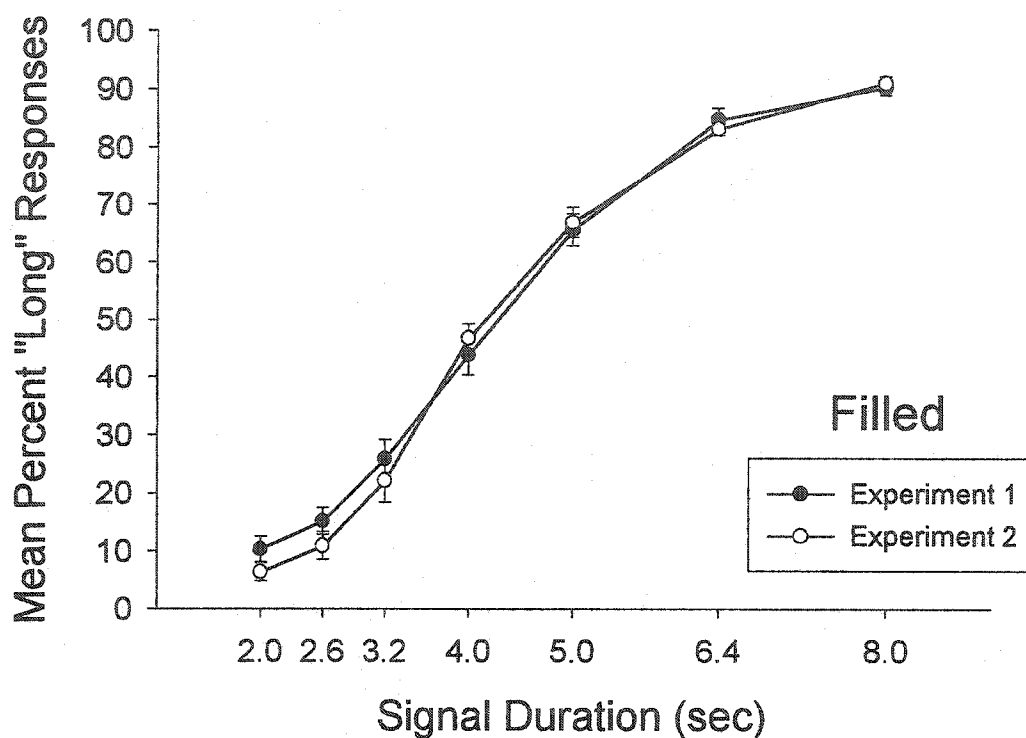


Figure 13

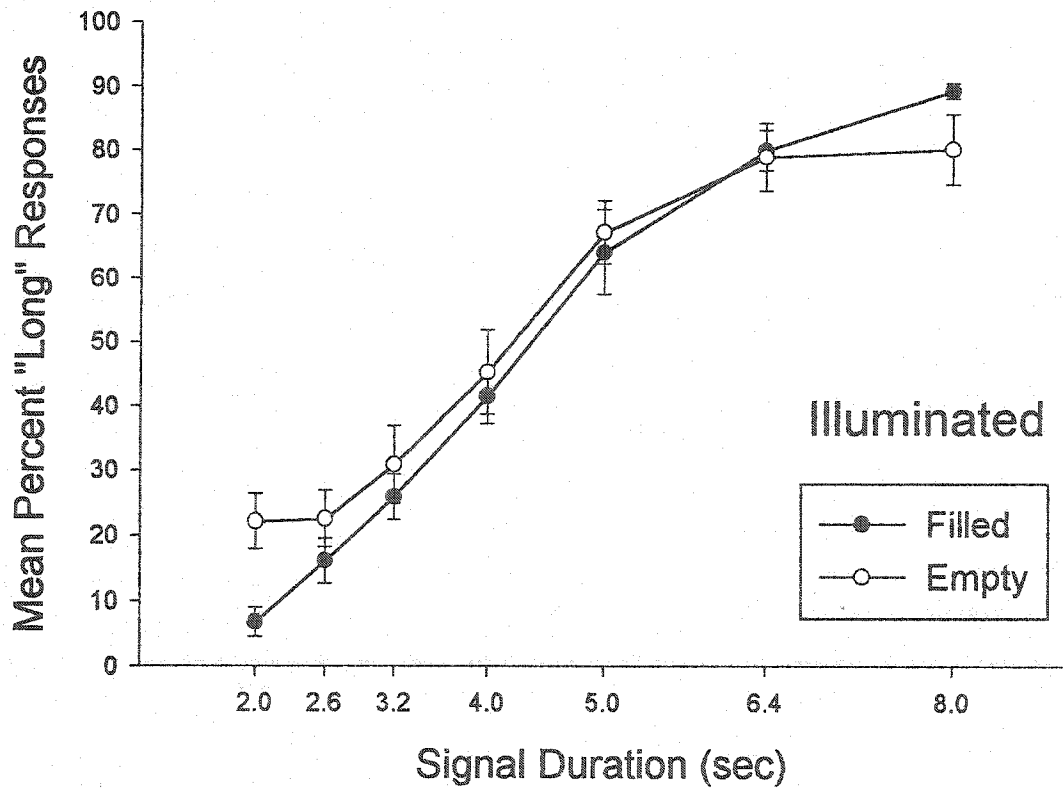
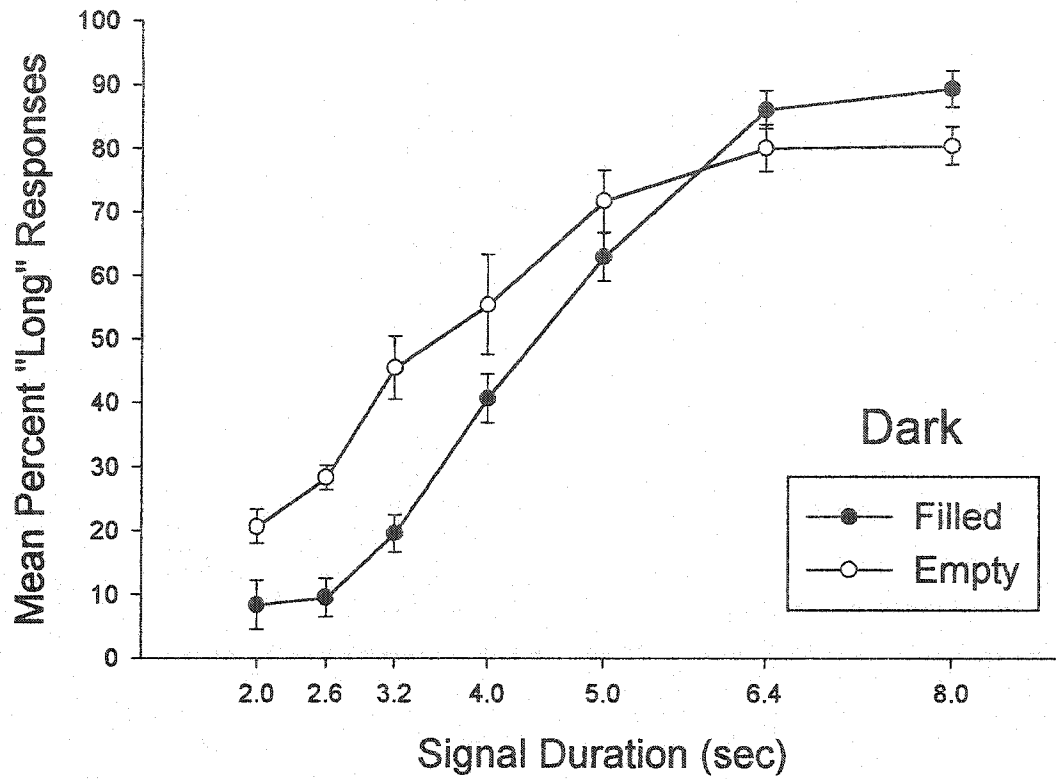


Figure 14

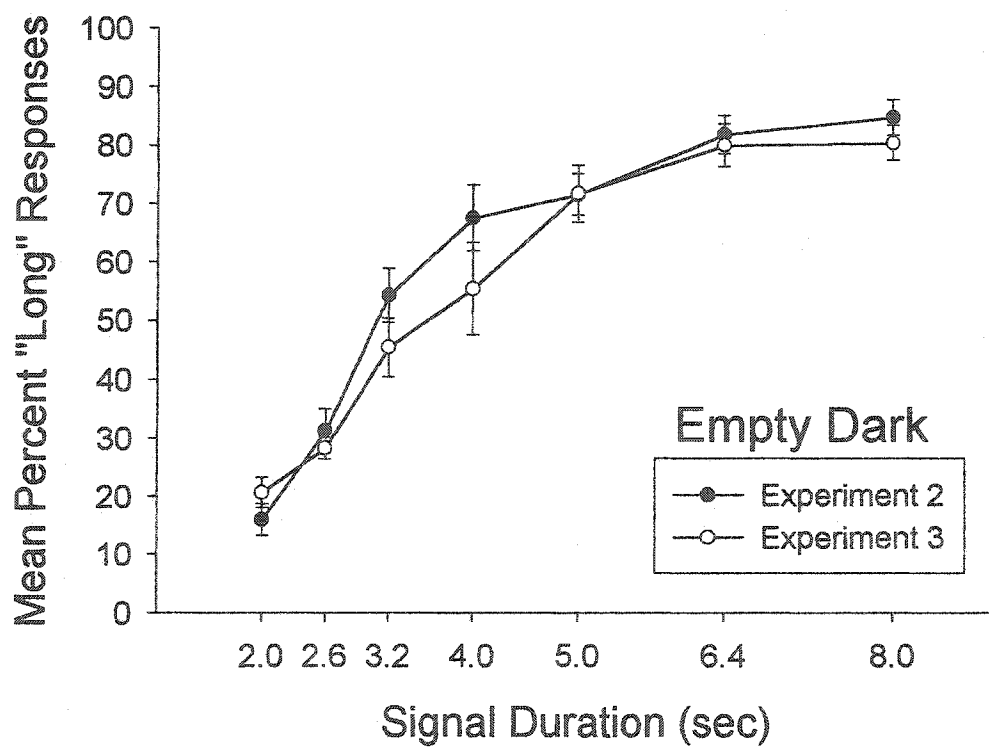
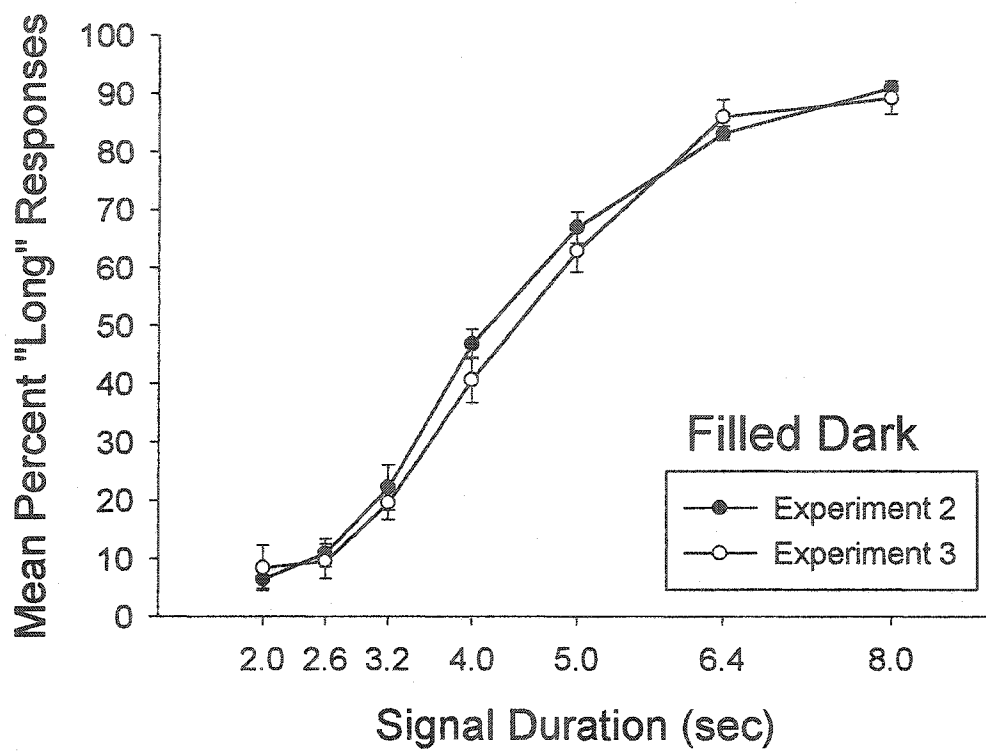


Figure 15

