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Errors in pigeons' memory for number: Effects of ITI and DI illumination

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Errors in pigeons' memory for number: Effects of ITI and DI illumination

by

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THESIS

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Abstract

In Experiment 1 all pigeons were trained to discriminate 2 flashes of hopper light in 4 sec from 8 flashes in 4 sec, at a 0 sec delay. One group of pigeons experienced dark ITI's (Group Dark) while the other experienced an illuminated ITI (Group Light). All birds were then tested with dark delays of 0, 5, 10, 15, and 20 sec. Analysis showed a significant bias to respond to the comparison correct for small at extended delays, with no difference between groups. In Experiment 2 training was identical to that in Experiment 1 except that a 5 sec baseline delay was used. The pigeons were then tested at delays of 0, 5, 10, 15, and 20 sec. Again, analysis showed a tendency to choose the comparison correct for small at delays longer than baseline, while at delays shorter than baseline they showed a bias to respond large. No group differences were observed. In Experiment 3, an illuminated DI was introduced for both groups. Analysis showed a reversal of the biases observed in Experiment 2. At delays longer than baseline a choose-large bias occurred, while at delays shorter than baseline a choose-small bias was observed. Again, there were no group differences. It was hypothesized that illuminating the DI added pulse counts to the pigeons' memory for the samples, suggesting that an event switch was not being used, but that the total amount of light in each trial was being summed. The results are clearly inconsistent with the confusion hypothesis and support a subjective shortening account of memory biases for temporal discriminations. However, whether this theory can be extended to include a subjective shrinking of number remains in question.

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Recent animal cognition studies have shown that human cognitive abilities must be viewed from an evolutionary perspective, in that many of our cognitive behaviors that were once believed to be exclusively human abilities, have been shown to exist in other animals. This includes the ability to accurately time events, and judge relative numerousness. Clearly, animals have to be sensitive to both time and number to be able to survive within their habitats. The best hunter has to be able to judge the relative number of prey captured, as well as the amount of time spent hunting to know where the optimal hunting sites are and what species represent the easiest capture. Likewise, the forager must monitor the time spent foraging as well as the number of reinforcements, or the amount of food eaten to find the most abundant source of nourishment.

Temporal Processing

Despite the obvious place that timing and counting abilities hold in the wild, studying the mechanisms of these behaviors in a laboratory setting requires some highly specialized procedures. The focus of the current paper is on the nature of the memory code used in temporal and numerical processing, necessitating a brief overview of memory and coding processes. Because the dual-mode model states that time and number are processed by the same mechanism, memory biases should also arise by a similar process. Therefore, the following section, while describing a timing procedure, can also be applied to a numerical procedure.

Memory codes

An important issue in the examination of working memory processes is the form of the code used to bridge the delay between the end of a to be remembered event and the time of test. Studying memory and coding processes in animals usually involves the use of a delayed-symbolic-matching-to-sample (DSMTS) procedure. A DSMTS task requires the animal to retain information from a sample stimulus in working memory until the appropriate response is required. To do this, the animal is first presented with a sample stimulus and is then given a choice between two or more comparison stimuli. In a typical time discrimination study a pigeon may be required to peck a red comparison stimulus following a short (2 sec) sample stimulus and to peck a green comparison stimulus following a long (8 sec) sample stimulus, in order to receive reinforcement.

The DSMTS procedure is believed to utilize capacities of both working and reference memory. Grant (1993) defines working memory as a mechanism by which dynamic information, that is only temporarily relevant, is stored, while reference memory is viewed as a storage space for more permanent information that may be relevant for a long period of time. For example, training an animal in a working memory task is believed to establish representations of the specific contingencies in reference memory. The associated codes in reference memory can then be activated from working memory by presentation of the appropriate stimuli. Thus, at any particular time working memory contains a subset of the total number of codes stored in reference memory.

In a broad sense the information held in working memory during a DSMTS task may be maintained retrospectively or prospectively. In a retrospective coding strategy the memory of the sample stimulus is held over the delay in working memory until the

comparison stimuli are presented, at which point the sample is compared to reference memory and the appropriate response is made. For example, if a pigeon is presented with a short sample stimulus, "short" will be held in working memory over the delay. When the comparison stimuli of red and green are presented at test, memory of the short sample will retrieve the reinforced rule, "if short peck red", from reference memory. In a prospective coding strategy, the response decision is made before the onset of the delay interval, and it is this response that is held in working memory. Using the example above, when the short sample is presented, "peck red" is activated from reference memory, and is then held in working memory over the delay until the comparison stimuli are presented. Retrospective coding, then, can be viewed as looking backward at the time of test to remember what sample was presented, while prospective coding is looking forward anticipating the correct response.

Memory biases in temporal discriminations

The dominant interpretation in the timing literature is that animals use an analogical, retrospective code to remember event duration. This means that the animal maintains the specific duration of the event in memory, as opposed to a categorical code such as "short" or "long". This comes from studies in which a delay is inserted between the end of the sample stimulus and the onset of the comparison stimuli, thereby testing the animal's memory for the sample. Thus, a pigeon may be required to peck a green comparison stimulus after a 2 sec sample stimulus and peck a red comparison stimulus after an 8 sec sample stimulus. Once this task has been acquired by the animal at a 0 sec delay between the end of the sample stimulus and the presentation of the comparison stimuli, the delay can be manipulated. The common finding from this procedure is that at

delays longer than baseline training, the animal will continue to respond to the short

samples with high accuracy, while accuracy of responding to the long samples drops to

well below 50% correct (Fetterman, 1995; Gaitan & Wixted, 2000; Grant, 1993; Grant &

Kelly, 1996, 1998; Grant & Spetch, 1991, 1993; Kraemer, Mazmanian, & W. A. Roberts,

1985; Santi, Bridson, & Ducharme, 1993; Santi, Ducharme, & Bridson, 1992; Spetch &

Rusak, 1989; Spetch & Wilkie, 1983). This result is commonly known as the "choose-

short effect".

Theories of the choose-short effect

Spetch and Wilkie (1983) proposed, in the subjective shortening hypothesis, that

this bias to respond short at extended delays occurs because temporal information is held

as an analogical, retrospective code in working memory. The subjective shortening

hypothesis is compatible with the internal clock model developed by Gibbon and Church

(1984). In this model a continuous stream of pulses is emitted from a pacemaker. At the

onset of a stimulus to be timed, a switch closes allowing pulses to collect in an

accumulator. When the stimulus terminates, the switch is opened at which point the

pulses stop accumulating and the total pulses are sent to working memory. With the

presentation of the comparison stimuli, this value is compared with values in reference

memory that were established during training, leading to a response decision. For

example, during training, a 2 sec stimulus might produce a pulse count of 200 and an 8

sec stimulus a pulse count of 800, both of which would be stored in reference memory

along with the correct response decision. On subsequent trials a stimulus that produces a

pulse count closer to 200 than to 800 will elicit a short response, while any stimulus

closer to 800 will produce a long response. However, when a delay is introduced

between the end of the sample stimulus and the presentation of the comparison stimuli, the subjective shortening hypothesis suggests that the pulse counts in working memory deteriorate. Therefore, after a 10 sec delay a pulse count that was originally 800 may deteriorate to around 200 in which case a short response is observed.

A direct prediction from the subjective shortening hypothesis is that if an animal is trained with a constant delay that is then shortened, a choose-long bias should be observed. If, for example, the comparison stimuli are presented at a 5 sec delay during training, the pulse counts being transferred to reference memory will be smaller than if training were done at a 0 sec delay. If testing is then conducted at delays shorter than the 5 sec baseline, the pulse counts in working memory will on average, be larger than those in reference memory. This should result in a bias to respond long on delays shorter than the baseline training delay. The choose-long effect was first reported by Spetch (1987).

Additional support for the subjective shortening hypothesis comes from a study performed by Grant and Kelly (1998). Training involving temporal discriminations typically involves a single fixed delay. Grant and Kelly performed a study in which they trained birds to make temporal discriminations with variable delays. The birds were required to discriminate 2 sec samples from 8 sec samples, first with variable delays ranging from 1 to 3 sec and then with delays ranging from 1 to 30 sec. If the samples do subjectively shorten over time then with a larger set of delays the use of an analogical code should be impossible, as the pulse counts for both samples will overlap at some point. For example, the pulse count for the 2 sec sample at a 1 sec delay may equal the pulse count for the 8 sec sample at a 10 sec delay. Therefore, with the larger range of delays the pigeons would be required to switch to some form of categorical code to be

able to perform the task successfully, meaning that at extended delay testing the choose-short effect should be eliminated. However, when delays ranging from 1 to 3 sec are used, a choose-short effect should still occur with extended delay testing, as the use of an analogical code is still possible. Results showed that delay testing following training with 1 to 3 sec delays produced a choose-short effect, while testing following training with 1 to 30 sec delays did not.

To show that this elimination of the choose-short effect was actually due to a switch from analogical coding to some form of categorical coding Grant and Kelly performed a second experiment in which the pigeons were required to distinguish a 1 sec sample from a 30 sec sample. Because the difference between the samples is so large, the possibility of overlap in pulse counts even at relatively long delays is negated. Therefore, analogical coding should be possible meaning that delay testing should reveal a choose-short bias. Even when the birds were trained to discriminate 1 sec samples from 30 sec samples with variable delays ranging from 1 to 30 sec, a choose-short effect occurred at delays longer than the mean training delay of 15 sec. Thus, it appears as though the use of samples differing by a large amount of time allows for discrimination using analogical codes even with the large amount of pulse count deterioration that would occur at longer delays.

A second procedure used to examine temporal processing is the peak procedure. In time studies, a visual or auditory stimulus signals the beginning of a trial. The first response made after a fixed interval (FI) of time since the beginning of the trial results in reinforcement. Schedules such as this generally produce a low rate of responding during the first half of the trial with a rapid acceleration in responding during the second half, up

until the time of reinforcement. On intermittent test trials, the signal is presented for

much longer than the FI, and no reinforcement is offered (i.e. an "empty trial"). When

response rate is plotted against the time of signal presentation and averaged over a

number of empty trials, a function is produced that approximates a Gaussian curve with a

peak occurring very close to the FI (S. Roberts, 1981; W. A Roberts, Cheng, & Cohen,

1989; W. A. Roberts & Boisvert, 1998). Using this procedure it is possible to ascertain a

measure of an animal's estimate of the length of the FI.

Because the results from both the DSMTS and the peak procedures have been

well accounted for by the internal clock model, one would expect that certain phenomena

found using one procedure should have a parallel in the other. Cabeza de Vaca, Brown,

and Hemmes (1994) used the peak procedure to examine both clock switch effects and

memory effects by introducing a gap into an FI schedule. For example, a pigeon might

be trained to respond to the presence of a light on a regular FI schedule. At test,

traditional empty trials would be presented to the pigeon, as well as empty trials with a

gap occurring at some point before the FI. The gap in procedures such as this consists of

a period of darkness interrupting the FI stimulus. Previous studies examining the

introduction of a gap into an FI have produced varying results. W. A Roberts et al (1989)

found that in pigeons the clock stopped accumulating pulses and was reset during a gap.

On the other hand, S. Roberts (1981) found that in rats the peak responding time was

shifted by the duration of the gap, suggesting that the clock stopped accumulating pulses

during the gap and that the pre-gap time was added to the post-gap time. In fact S.

Roberts found that the amount of time added to the peak responding time was not exactly

equal to the duration of the gap, but was actually a few seconds longer. He interpreted

this finding as being indicative of a latency for the switch to re-close after the gap. A different interpretation is also possible, however. When the gap is introduced during probe trials, thereby stopping the accumulation of pulses, the pre-gap duration must be maintained in memory if it is to be added to the post-gap duration. If this duration is maintained in the same manner as during a delay in a DSMTS procedure, then the pulse count from the pre-gap duration should deteriorate. Thus, if the pre-gap duration is subjectively shortened, the subjects estimate of the amount of time passed on the current trial will be shorter, thereby requiring a longer time to reach peak responding than the addition of the gap time alone would predict. This would result in a peak time that is shifted right even when the addition of the gap time is controlled for. This effect then, would be similar to the choose-short effect frequently observed in temporal tasks using the DSMTS procedure.

Cabeza de Vaca et al (1994) performed a study examining whether the gap effect was due to a switch latency or to subjective shortening. To do this they first trained pigeons to respond to an FI 30 sec schedule as signaled by the presentation of a white keylight. During testing, empty trials were inserted in which the trial was extended and reinforcement was not available. The signal on empty trials was interrupted by a gap during which the keylight was turned off. The location and the duration of the gap were varied from trial to trial. Examination of the peak curves showed that when the gap was introduced later in the interval, there was an increased rightward shift in the function. This effect would not be expected if the rightward shift of the function were occurring because of a switch latency. However, it is possible that different accumulations deteriorate at different rates. Thus, a larger accumulation produced by the longer pre-gap

duration may result in a faster rate of pulse count deterioration and an increased rightward shift in the peak function.

Most important are the results of varying gap duration. If the rightward shift in the peak function is due to switch latency then the duration of the gap should have no impact on the amount of shift. If, on the other hand, the shift is due to subjective shortening of the pre-gap duration, then a longer gap should result in an increased rightward shift in the function outside of the addition of the gap duration itself. This is exactly what was found, strongly suggesting that when a gap is introduced into an FI there is a subjective shortening of the pre-gap duration. Buhusi and Meck (2000) found a similar result.

An alternative explanation of the choose-short effect is based on the similarity between the choose-short effect and the bias to respond "no sample" on presence versus absence discriminations (Gaitan & Wixted, 2000). A typical study involving this type of discrimination requires a pigeon to respond on the basis of whether or not a sample occurred. On sample present trials the intertrial interval (ITI) is followed by the presentation of the sample, which is followed by the delay interval (DI) and then the onset of the comparison stimuli. On sample absent trials the ITI is followed immediately by the DI and then by the comparison stimuli. A response to one comparison is correct for the presence of the sample and the other for the absence of the sample. What has been repeatedly found in studies of this type is that, as the delay interval is increased, response accuracy for the absence of the sample remains high, while response accuracy for the presence of the sample drops to below 50% correct (Colwill, 1984; Grant, 1991; Sherburne & Zentall, 1993; Wixted, 1993). The fact that this is a very similar result to

the choose-short effect found with temporal discriminations was first pointed out by

Kraemer et al. (1985).

From these observations arose the default coding hypothesis, which suggests that

the birds only select the comparison associated with the short sample when they have no

recollection of the long sample (Grant & Spetch, 1994). Thus, this model assumes that

only the long sample is coded, and only in the absence of a memory for that code does

the animal respond short. When an extended delay is introduced, the memory for the

long sample is forgotten, resulting in a default to respond short.

Grant and Spetch (1994) conducted a test of the default coding hypothesis by

training pigeons to perform a 2 sec vs. 10 sec discrimination and a 4.5 sec vs. 22.5 sec

discrimination simultaneously. One task was associated with color comparisons and the

other with line comparisons. Both sets of discriminations showed clear choose-short

biases at extended delay testing. Grant and Spetch then performed transfer tests in which

the two short samples were followed by the comparison correct for the 2 sec sample and

the comparison correct for the 4.5 sec sample. If the choose-short biases observed

resulted from a default to respond short in the absence of a memory for the long sample,

neither the 2 sec sample nor the 4.5 sec sample should have a code associated with it in

reference memory. Therefore, discriminating between these two samples should be

impossible. Results showed that the pigeons were able to make this discrimination,

suggesting that the choose-short biases observed did not occur as a result of default

coding.

Sherburne, Zentall, and Kaiser (1998) performed a test of two other alternate

explanations of the choose-short effect. The relative duration hypothesis and the

confusion hypothesis were proposed as explanations for data found by Spetch and Rusak

(1992), which showed that the choose-short effect was eliminated when either the ITI or

the DI was illuminated by the houselight. Spetch and Rusak proposed the relative

duration hypothesis, which suggested that the effect was eliminated because the pigeons

were judging the duration of the sample on each trial, relative to the temporal background

composed of the ITI preceding it and the DI following it. When the DI or the ITI is

lengthened a bias to respond short is observed, and when the DI or the ITI is shortened

there is a bias to respond long. When the lighting conditions of the ITI and the DI do not

match, the sample can no longer be compared to a uniform background, causing the

elimination of any memory biases.

Sherburne et al. (1998) had a different interpretation of the results and proposed

the confusion hypothesis, which states that the choose-short effect arises because of

confusion between the ITI used in training and the DI presented at test. Pigeons trained

with dark ITI's may confuse the novel DI presented at test with the ITI. Therefore, when

the comparison stimuli are presented after the DI the pigeon responds as though no

sample had occurred. Because no sample is closer to short than it is to long, a choose-

short bias is observed (Grant, 1991; Sherburne & Zentall, 1993; Wixted, 1993). To test

this hypothesis Sherburne et al. trained two groups of pigeons on a 0 sec delay, temporal

discrimination involving 2 and 10 sec sample stimuli. One group of pigeons was trained

with a lit ITI and the other with a dark ITI. Both groups were then tested with both lit

and dark ITI's and lit and dark DI's. The relative duration hypothesis predicts that the

choose-short effect will only occur when the stimulus condition in the ITI and the DI are

the same on the current test trial. Only when the ITI and DI are the same on the current

trial, is the temporal background uniform, allowing a comparison between the sample stimulus and the summed duration of the ITI and the DI. The confusion hypothesis, on the other hand, predicts that the choose-short effect will occur when the illumination condition in the ITI used during training is the same as the DI used during test. When the DI is the same as the ITI used during training, confusion should result causing the pigeon to respond as though no sample occurred, thereby producing a choose-short bias. Their results showed that the choose-short effect only occurred when the ITI condition used in training was the same as the DI condition used at test, and was eliminated under all other conditions. This result supports the confusion hypothesis and is inconsistent with the relative duration hypothesis.

Dorrance, Kaiser, and Zentall (2000) performed an experiment in which 2 groups of pigeons were trained to discriminate 2 sec samples from 10 sec samples with variable delays of 0, 1, 2, and 4 sec. They hypothesized that variable delay training should reduce the novelty of the delay interval at test, thereby minimizing the possibility for confusion. However, because extending the DI at test would still be a novel event that may lead to confusion, they further disambiguated the ITI from the DI for half of the pigeons by presenting a light in the ITI. Group Light-Dark was presented with a lit houselight during the ITI followed by the sample and a dark DI, while Group Dark-Dark spent both the ITI and the DI in darkness. If extending the delay at test still results in ambiguity between the ITI and the DI, the confusion hypothesis predicts that Group Dark-Dark should continue to show a choose-short bias, while Group Light-Dark should produce parallel retention functions. They found that under these training conditions a choose-short effect was not produced for either of the groups when delays were extended up to 16 sec at test.

They interpreted these results in favour of the confusion hypothesis suggesting that the choose-short effect did not occur because the DI was no longer novel at test due to the variable delay training, meaning that confusion between the ITI and the DI did not result. However, it is also possible that training with the variable delays made analogical coding of the samples impossible due to a large amount of pulse count deterioration. In the study by Grant and Kelly (1998), variable delays ranging from 1 to 3 sec were used, leading to a choose-short effect. When they used a larger range of delays the effect was eliminated. While Grant and Kelly used delays ranging from 1 to 30 sec to show parallel retention functions, it may be that the use of delays ranging from 0 to 4 sec is all that is necessary to allow for enough pulse count deterioration to render analogical coding impossible. Although the difference in the range of delays used between the two studies is only 2 sec, the choose-short effect is often found to be very robust at a delay of 5 sec. This suggests that at some delay between 0 sec and 5 sec the pulse count for the long sample becomes closer to the reference memory count for the short sample. Thus, if trained with variable delays ranging from 0 to 5 sec, one would expect the use of analogical coding to be impossible. It is not unreasonable then, to suspect that this may also be the case using variable delays ranging from 0 to 4 sec. This would result in the elimination of the choose-short effect, much like the results of Grant and Kelly when longer delays were used. Therefore, the conclusions to be drawn from this study may require further testing.

Because the current study proposes to examine the predictions of the confusion hypothesis and the predictions of the subjective shortening hypothesis in terms of a numerical discrimination, the next section describes evidence of numerical competencies

in animals, as well as research supporting the hypothesis that time and number are processed by a common mechanism. Furthermore, numerical discrimination studies are cited showing memory biases which parallel those of the timing literature.

Numerical Processing

The majority of evidence pertaining to numerical processing in non-human animals has involved experiments in which the animal is required to perform a fixed number of behaviors in order to get reinforcement. For example, rats readily learn to press a lever a fixed number of times to have food delivered at some other location (Mechner, 1958; Mechner & Guevrekian, 1962). More recently, however, a number of studies have shown that relative numerousness of external stimuli is also able to control behavior. For example, rats have been shown to learn to press one lever after a certain number of noise flashes and another lever after a different number of noise flashes (Davis & Albert, 1986; Fernandes & Church, 1982).

The accumulation of evidence suggesting that non-human animals have some form of timing and counting ability led Meck and Church (1983) to ask whether animals could simultaneously time and count a sequence of events. During training rats were required to press one lever after the presentation of 2, .5 sec noise bursts occurring at a rate of 1 per sec, and to press a different lever after the presentation of 8, .5 sec noise bursts also occurring at a rate of 1 per sec. The rats were then tested on two different types of trials, those in which number was the relevant discriminating stimulus and those in which time was the relevant discriminating stimulus. To test for number, time was held constant at 4 sec while the number was varied between 2 and 8 bursts. To test for time, number was held constant at 4 bursts while the time was varied between 2 and 8

sec. Analyses examining the probability of choosing the lever correct for the 8 flash or 8

sec sequence revealed equally strong control by both time and number. When the

stimulus presented was less than 4 flashes or 4 sec., responding to the lever correct for 8

flashes or 8 sec. was below chance. When the stimulus presented was greater than 4

flashes or 4 sec., responding to the lever correct for the 8 flash or 8 sec. sequence was

above chance. Finally, when the stimulus was equal to 4 sec on time relevant trials or

equal to 4 flashes on number relevant trials, responding was at chance levels.

To account for the ability to process time and number simultaneously, Meck and

Church (1983) proposed the dual-mode model of time and number processing. This is an

extension of the internal clock model, allowing for the processing of number by a similar

mechanism as that for time. Information for number and time is recorded in two separate

accumulators, by the operation of two switches. For time discrimination there is a

separate switch that functions in "run" mode, allowing the pulses to collect in the time

accumulator for the entire duration of the stimulus. The temporally sensitive switch can

also operate in "stop" mode, summing the total durations of events in a sequence. This

can be seen when a gap is introduced in a peak procedure and the animal adds the pre-gap

duration to the post-gap duration to reach the total duration of the FI. When assessing

numerical information the number switch functions in an "event" mode, allowing pulses

to collect in the number accumulator for a constant duration in response to the

presentation of each stimulus in a set. This duration is believed to be 200ms in rats

(Meck, Church, & Gibbon, 1985). Hence, if 8 flashes were presented in 8 sec, the time

switch would operate in "run" mode, thereby allowing pulses to accumulate for the entire

8 sec. At the same time the number switch would operate in an "event" mode, allowing

pulses to accumulate only for a fixed duration at the presentation of each flash in the sequence.

W. A. Roberts and Mitchell (1994) performed a series of experiments showing that pigeons are able to respond accurately on ambiguous trials that require different responses for time and number. W. A. Roberts and Mitchell reported that the pigeons could accurately report the total duration or the total number of flashes even though the cue telling the bird to respond on the basis of time or number was presented after the flash sequence was completed. This finding suggests that a cue following the sequence is able to access either time or number information in working memory. In light of these findings, W. A. Roberts and Mitchell suggested some alterations to the dual-mode model first proposed by Meck and Church (1983). They suggested an extension of the pulse count representations from the accumulator stage to the working memory stage. Thus, time and number counts are sent from the separate accumulators to separate locations in working memory, where either one, or both can be retrieved for comparisons with reference memory. This revised model, as proposed by W. A. Roberts and Mitchell is the most current model available and can be seen in Figure 1.

Additional evidence of numerical competence in animals can be found in a modification of the peak procedure. While the peak procedure has received a great deal of attention in timing studies, W. A. Roberts and Boisvert (1998) were the first to extend this technique to a study of numerical processing. Instead of using the presentation of a filled light interval as the fixed interval stimulus, a key that flashed from red to green at varying rates was used. In the fast rate the key flashed twice per second, in the medium rate once per second, and in the slow rate once every 2 seconds. One group of pigeons

was reinforced for the first response occurring after 20 seconds, regardless of the flash

rate. Thus, this group performed a regular FI 20 sec schedule. A second group of

pigeons was reinforced for the first response that occurred after the first 20 flashes. This

group then, was required to perform a fixed number (FN) 20 flashes schedule. During

testing, intermittent probe trials were inserted that extended the interval to 100 sec and

did not allow for reinforcement. When response rate was plotted against signal

presentation time averaged over numerous sessions, the normal Gaussian shaped

response curve was produced. For the FI 20 sec group the peak occurred near 20 sec

regardless of the rate of flash presentation. The FN 20 flash group, on the other hand,

showed a peak time of 20 sec only for the medium flash rate. The slow flash rate

condition produced a peak time near 40 sec, while the fast flash rate condition maintained

a peak time near 10 sec. A peak time of 20 sec for the medium condition, 40 sec for the

slow, and 10 sec for the fast, all occur at 20 flashes of the key light. This is the expected

result if the pigeons were responding on the basis of the number of flashes presented.

Therefore, it appears as though pigeons can perform accurately in a peak procedure,

when either time or number of flashes is the appropriate cue.

Despite the above studies, which provide a substantial amount of evidence

suggesting that pigeons and rats can count using the mechanisms implicated in the dual-

mode model, the existence of number discrimination abilities in animals is still debated

(Davis & Perusse, 1988). Breukelaar and Dalrymple-Alford (1998) suggested two

reasons why the validity of studies, such as those performed by Meck and Church (1983)

and W. A. Roberts and Mitchell (1994), may be questioned. First of all, because a fixed

number of identical events is used with an identical interevent duration, a temporal ratio

arises between the total stimulus duration and the cycle duration. These ratios covary with the number of events, thereby creating a potential confound. For example, when there are two cycles presented in the four sec stimulus, the cycle to total duration ratio is 2:4, when there are 3 cycles this ratio is 1.33:4, and when there are 4 the ratio becomes 1:4. Second, there is the possibility that the sample sequences presented during testing are stored as patterns and are simply matched to the training patterns stored in reference memory. Thus, response will depend upon which training pattern most closely resembles the test pattern.

To eliminate both of these possible confounds Breukelaar and Dalrymple-Alford (1998) varied event and interevent duration during testing. Rats were first trained to discriminate 8 bursts in 8 sec from 2 bursts in 2 sec. The rats were then tested in the same manner as they were tested by Meck and Church (1983) with sequences in which time was held constant at 4 sec while the number of events varied between 2 bursts and 8 bursts, and with sequences in which number was held constant at 4 bursts while time varied between 2 sec and 8 sec. Unlike the results of the study performed by Meck and Church, the rats showed a strong ability to discriminate on the basis of time but virtually no control by number. The rats were then trained specifically on the number relevant test sequences and after about 15 sessions showed control by number that was still significantly less than that found by Meck and Church. Once the rats showed control by time as well as number, test sequences were introduced in which the duration of the events and the interevent duration varied randomly. The rats maintained strong control by time as well as by number, thereby showing that rats do not need to discriminate sequences such as these on the basis of temporal ratio or sequence pattern.

Memory biases in numerical discriminations

Memory biases similar to the choose-short effect in time discrimination studies have also been found to occur when the number of sample responses (Fetterman & MacEwan, 1989) or the number of light flashes (Fetterman, 2000; W. A. Roberts, Macuda, & Brodbeck, 1995) has been the distinguishing variable. W. A. Roberts et al. (1995) attempted to extend the choose-short effect from time studies, to a choose-small effect in a number study. The dual-mode model predicts that if pulse counts for time are depleted after a delay interval, than pulse counts for number estimation should also be reduced over a delay period. Therefore, the prediction was that as the delay interval increased the probability that a pigeon would select the comparison stimulus associated with a small number of flashes, would also increase.

W. A. Roberts et al. trained a group of pigeons to discriminate between sample stimuli consisting of two flashes of light in 4 sec (2f/4s) and eight flashes of light in 4 sec (8f/4s). Thus, time and number were unconfounded by holding time constant while varying the rate. Once the pigeons were able to perform this task with a high degree of accuracy at a 0 sec delay, the birds were tested at delays of 2, 5, and 10 sec. The retention curves showed a clear choose-small effect. Pigeons showed very high levels of accuracy with both the 2f/4s and 8f/4s sequences at 0 sec delays. However, at longer delays, while the 2f/4s sequence showed almost no loss in accuracy, the 8f/4s sequence dropped dramatically to below 30% accuracy. Thus, these results confirmed the hypothesis that a choose-small effect would arise, thereby adding support to the dual-mode model and suggesting that the process of the subjective shortening of time can be extended to include the subjective shrinking of number.

Another parallel to be drawn between the time and the number literature comes from a study performed by Santi and Hope (in press). In this study pigeons were trained on a similar discrimination as that used by W. A. Roberts et al. (1995). However, in this study the pigeons were trained with a 5 sec baseline delay between the end of the sample stimulus and the onset of the comparison stimuli. The pigeons were then tested at delays longer and shorter than baseline. The dual-model model in conjunction with the subjective shortening hypothesis predicts that delays longer than baseline should produce a choose-small bias, while delays shorter than baseline should produce a choose-large bias. This is what the results showed, again supporting the dual-mode model and the subjective shortening hypothesis.

Present Study

The current study was intended as a test of the predictions of the confusion hypothesis using a numerical discrimination. Because the research described above suggests that the memory biases occurring in number discriminations are a product of the same processes as the memory biases shown in the timing literature, the confusion hypothesis should apply to the choose-small effect as it does to the choose-short effect. In Experiment 1 pigeons were trained to discriminate 2 flashes in 4 sec from 8 flashes in 4 sec at a 0 sec delay. One group of pigeons experienced dark ITI's during training and the other group lit ITI's. Delay testing was then conducted with dark DI's of 0, 5, 10, 15, and 20 sec. The confusion hypothesis predicts that a choose-small bias should be shown for the group trained with dark ITI's but not for the group trained with lit ITI's. Because only dark DI's were used, only the group trained with dark ITI's should experience

confusion resulting in a choose-small effect. The subjective shortening hypothesis, on the other hand, predicts that both groups should show a choose-small bias.

In Experiment 2, the birds performed the same discrimination as in Experiment 1 except that a 5 sec baseline delay was used during training. The ITI illumination conditions were maintained and testing was again conducted with dark delays of 0, 5, 10, 15, and 20 sec. The confusion hypothesis again predicts that a choose-small bias should only occur at extended delays for the group trained with dark ITI's. At delays shorter than baseline the confusion hypothesis does not predict any bias. If some form of confusion were to result from the shortening of the DI, there would be no reason for accuracy on one sample to be affected more than another. The subjective shortening hypothesis predicts a choose-small bias at extended delays for both groups, and a choose-large bias at delays shorter than baseline for both groups.

In Experiment 3 a light was introduced in the DI while maintaining the lighting conditions of the ITI. A study by Kelly and Spetch (2000) found that the choose-short effect was eliminated when a light was introduced during the DI. However, when they examined the individual data they found that some of the birds were showing a choose-short bias while others were showing a choose-long bias, which when averaged together cancelled each other out to produce parallel retention functions. They hypothesized that the birds showing a choose-long bias did so because they timed through the DI until the presentation of the comparison stimuli. Therefore, at extended delays they responded long. The advantage of using numerical discriminations under these conditions is that if an event counter is in fact used, timing through a lit DI on a number discrimination is

unlikely. Thus, a more accurate assessment of the true memory biases that occur when a light is introduced in the DI, should emerge.

Experiment 1

Experiment 1 was conducted as a test of the hypothesis that the choose-small effect arises as a result of confusion between the ITI and the DI. Since a great deal of literature supports the hypothesis that time and number are processed by the same mechanism, and the same memory biases that have been demonstrated in the timing literature also occur in numerical discriminations, we tested the confusion hypothesis using a numerical discrimination. The pigeons were first trained to discriminate 2 200ms flashes of hopperlight occurring in 4 sec from 8 200ms flashes occurring in 4 sec. One group of pigeons (Group Dark) experienced dark ITI's while the other group (Group Light) was presented with the houselight on during the ITI. Once the pigeons were able to perform accurately on this task, testing was started with dark delays of 0, 5, 10, 15, and 20 sec.

The confusion hypothesis predicts that Group Dark will show a bias to respond small at increasing delays, while group light will show parallel retention functions at extended delays. This is because the pigeons in Group Dark should confuse the dark DI with the dark ITI, causing them to respond as though no sample had occurred when the comparison stimuli are presented. Because no sample is closer to small than it is to large, a bias to respond small should be found. Group Light, on the other hand, should not confuse the DI with the ITI, meaning that parallel retention functions should be obtained.

The subjective shortening hypothesis predicts that the memory for the sample stimuli should deteriorate over extended delays whether the ITI's used in training were dark or lit. Therefore, both conditions should show a choose-small effect.

Method

Subjects

The subjects were 12 adult Silver King pigeons that had previous experience performing numerical discriminations. They were maintained at approximately 80% of their free-feeding weight with constant access to water and grit. Post session feedings of Purina Pigeon Chow were provided to maintain their target weights. The pigeons were individually housed in a room maintained at approximately 22°C. The colony room was illuminated on a 12:12 cycle by fluorescent light turned on at 6:00 am each day. Testing was conducted 5 days a week between 9:00 am and 3:00 pm.

Apparatus

Four Coulbourn modular operant test cages (Model #E10-10), each housed within isolation cubicles (Model #10-20), were used. Each cubicle utilized baffled air intake exhaust systems and ventilation fans. Each test cage contained three horizontally aligned, translucent plastic keys positioned approximately at a pigeon's standing sight line. Behind each key was a projector which displayed red, green, or white onto a frosted rear projection screen (Coulbourn Model #E21-18). Vertical and horizontal lines were presented as white bars with a black background. Directly below the center key there was a 5.7 X 5 cm opening which, during reinforcement, provided access to a hopper containing mixed grain. Within the opening was a lamp (Coulbourn Model #E14-10 with bulb #S11819X) that was illuminated only during reinforcement and for presentation of

the samples. Located 6.5 cm above the center key was a houselight that directed light upward to reflect light from the top of the cage (Coulbourn Model #14-10). The organization of all experimental events and recording of response choices was performed by a microcomputer system located in the same room.

Procedure

After 12 sessions of baseline training with all pigeons experiencing dark ITI's, they were randomly assigned to either Group Dark or Group Light. Group Light received 9 sessions with the houselight on during the ITI and Group Dark received 9 sessions with the ITI dark. Thus, for Group Dark the chamber remained dark for the entire trial except during the presentation of the samples and the comparison stimuli. See Figure 2 for the ITI and DI conditions for both groups. Due to previous training, half of the pigeons discriminated the samples with color comparison stimuli and the other half with line comparison stimuli. An equal number of birds discriminating on the basis of color and line were in groups dark and light.

Each trial began immediately with either the small or the large sample stimulus, since a trial-initiating stimulus was not used. The sample stimuli consisted of a flashing of the hopper light, each flash lasting for 200 ms, with flashes equally spaced throughout a particular sequence, and each sequence starting and ending with the presentation of a flash. A pictorial representation of the sequence can be seen in Figure 3. The sample stimulus was immediately followed by the appropriate comparison stimuli. All pigeons performing the task with color comparisons were reinforced for a red key peck following the 2 flash per 4 sec sample (small), and a green key peck following the 8 flash per 4 sec sample (large). The pigeons presented with the line comparisons were reinforced for a

vertical key peck following the small sample and a horizontal key peck following the large sample. The left-right positions of all the green and red keys and the horizontal and vertical keys were balanced. A correct response was reinforced by 4s access to mixed grain from the food hopper. An incorrect response resulted in a 3s blackout followed by the presentation of the same sample stimulus and the particular comparison stimuli. This correction procedure continued until a correct response was made, which would result in reinforcement, although only the initial response was used to calculate the matching accuracy. All training sessions consisted of 160 trials, each trial being separated by either a lit or a dark, 15 sec intertrial interval. On the ninth and final day of training Group Dark showed 90.2% correct on the small samples and 94.2% correct on the large samples. Group Light showed 90.6% correct on the small samples and 93.3% correct on the large samples.

Once training was completed delay testing was conducted for 15 sessions with 160 trials per session. Within the test sessions, dark delays of 0, 5, 10, 15, and 20 sec were inserted between the end of the sample stimuli and the presentation of the comparison stimuli. There were 8 trials of the small and large samples at each of the 5, 10, 15, and 20 sec delays. 48 small and 48 large trials were presented at the 0 sec delay so as to maintain the contingencies established in reference memory during training. While correct responses were reinforced at all delays, the correction procedure was only in effect for those trials with the 0 sec delay.

All effects with $p. < .05$ were considered significant.

Results

A 2 X 2 X 2 mixed analysis of variance (ANOVA) was performed comparing the last day of baseline training with the dark ITI's to the first day of training with the lit ITI's (see Figure 4). This analysis showed a significant overall effect of session (before vs. after), $F(1, 10) = 29.84$, as well as a session X group (light vs. dark ITI) interaction, $F(1, 10) = 9.91$. Examination of the simple main effects indicated that Group Dark did not show any difference on the before and after dimension while Group Light showed a significant decrease in accuracy with the addition of the light in the ITI, $F(1, 10) = 37.07$. A near significant interaction between sample and session, $F(1, 10) = 4.60$, $p = .058$, revealed a highly significant effect of session on the small sample, $F(1, 10) = 23.33$, and only a marginally significant effect on the large sample, $F(1, 10) = 5.34$. This was indicative of an initial bias to respond large.

A 2 X 2 X 9 ANOVA performed on the acquisition data (see Figure 5) showed no overall group or sample effects, but did present a significant effect of session, $F(8, 80) = 8.97$, as well as a significant session X group interaction, $F(8, 80) = 2.39$. Examination of the simple main effects clarified this interaction, showing only a significant effect of session for Group Light, $F(8, 80) = 9.49$, and not for Group Dark. This is to be expected since only Group Light experienced a change in ITI conditions from baseline training.

A 2 X 2 X 5 ANOVA was performed analyzing sample type X group X delay. This showed no significant main effect of group or group X sample type interaction. There was, however, a group X delay interaction, $F(4, 40) = 3.72$. This was due to the fact that delay had a larger effect on Group Light than on Group Dark at the 5 sec delay, $F(1, 10) = 7.64$, as seen in Figure 6.

There was not a significant three-way interaction. As expected there were significant effects of sample type, $F_{(1, 10)} = 18.57$, and delay, $F_{(4, 40)} = 381.00$. There was also a significant sample type X delay interaction, $F_{(4, 40)} = 13.45$. This interaction can be seen in Figure 7, which shows the delay test data with mean percent correct when the small sample was presented and mean percent correct when the large sample was presented. Examination of the simple main effects showed that at the baseline training delay of 0 sec there was a significant bias to respond large, $F_{(1, 10)} = 11.80$. At delays of 5, 10, 15, and 20 sec there was a significant bias to respond to the comparison correct for small, $F_{(1, 10)} = 26.21$, 13.40, 14.94, and 16.47, respectively.

Discussion

The results of delay testing showed that regardless of whether the ITI was illuminated or dark, extended delay testing with a dark DI, caused the birds to choose the comparison correct for the small sample over the one correct for the large sample. Thus, both groups showed strong choose-small biases. This result contrasts with those found by Sherburne et al. (1998), in which they found that having differential illumination conditions between the ITI used during training and the DI used at test, eliminated the choose-short bias in a temporal discrimination study. Although it is possible that the different results obtained from this study and the one performed by Sherburne et al. is due to the fact that we used a numerical discrimination, a study done by Kelly and Spetch (2000) suggests that this is not the case.

Kelly and Spetch trained pigeons to match short (2 sec) and long (8 sec) food samples to red and green comparison stimuli at a 5 sec baseline delay. In one group the ITI and the DI were both illuminated, in another group the ITI and the DI were both dark,

a third group experienced a lit ITI and a dark DI, and finally a fourth group was presented with a dark ITI and a lit DI. The first three groups all showed a choose-short bias at extended delay testing, in contrast to the predictions of the confusion hypothesis. The fourth group showed parallel retention functions when averaged over all subjects. However, when the individual pigeon data was examined some of the birds were showing a bias to respond short while others were showing a bias to respond long. The two types of biases cancelled each other out when averaged together, thereby creating parallel retention functions.

Thus, it does not appear as though results inconsistent with the confusion hypothesis are unique to numerical discriminations. The results obtained by Kelly and Spetch closely resemble the results shown in Experiment 1, strengthening the contention that the predictions of the confusion hypothesis are inaccurate.

<u>Experiment 2</u>

Experiment 2 was conducted to examine the effect of disambiguating the ITI from the DI using a 5 sec baseline delay, and testing at delays longer and shorter than baseline. Again half of the birds experienced lit ITI's and the other half dark ITI's, with all delays remaining dark. The introduction of the 5 sec baseline training delay should further reduce the possibility of any confusion resulting at test, since the DI is no longer novel.

Dorrance et al. (2000) found that when pigeons were trained with a variable delay, thereby reducing the novelty of the DI, the choose-short effect was eliminated whether the ITI was lit or not. They suggested that this occurred because the pigeons were no longer confusing the ITI with the DI, due to previous experience with the DI. Therefore, the confusion hypothesis predicts that at delays longer than baseline a choose-

small bias should not occur for Group Light-Dark or for Group Dark-Dark. Regardless

of whether the ITI is lit or dark, the pigeons should no longer become confused when the

sample is followed by a DI because of their previous experience with 5 sec baseline delay

training. The subjective shortening hypothesis, on the other hand, predicts a replication

of the results of Experiment 1 at delays longer than baseline.

At delays shorter than baseline, the confusion hypothesis predicts parallel

retention functions for both the light and the dark groups. Although previous literature

has shown choose-long biases and choose-large biases at delays shorter than baseline

when the illumination conditions of the ITI and the DI match, the confusion hypothesis

has no explanation for this finding. The subjective shortening hypothesis predicts that

testing at delays shorter than baseline should produce a bias to respond to the comparison

correct for the large sample for both the dark and the light groups.

Method

Subjects and Apparatus

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

Procedure

Due to a break between Experiments 1 and 2, the pigeons were given 5 sessions

of the training described in Experiment 1, to ensure stable performance at the 0-sec delay

before proceeding with testing.

The training conditions in Experiment 2 were identical to those in Experiment 1,

except that a 5 sec dark DI was inserted between the end of the sample stimuli and the

onset of the comparison stimuli. ITI and DI conditions for both groups can be seen in

Figure 8. On the thirty-ninth and final day of training Group Dark-Dark (dark ITI and

dark DI) showed 83.96% correct on the small samples and 82.29% correct on the large

samples. Group Light-Dark (light ITI and dark DI) showed 78.96% correct on the small

samples and 73.75% correct on the large samples.

Testing was also very similar to that done in Experiment 1, the only difference

being that 5 sec was now treated as the baseline delay and 0 sec as a test delay. For this

experiment there were 8 trials of the small sample and 8 trials of the large sample at each

of 0, 10, 15, and 20 sec delays. At the baseline delay of 5 sec there were 48 trials each of

the small sample and the large sample. While correct responses were reinforced at all

delays, the correction procedure was only in effect for those trials with the 5 sec delay.

Results

A 2 X 2 X 2 mixed ANOVA was done comparing the last day of baseline 0 sec

training with the first day of baseline 5 sec training on the small and large samples for

Group Dark-Dark and Group Light-Dark (see Figure 9). While there was a significant

effect of sample type, $F(1, 10) = 30.66$, and session, $F(1, 10) = 114.96$, there was no

effect of group. There was also a significant sample type X session interaction, $F(1, 10)$

$= 37.29$. Examination of the simple main effects clarified this interaction, showing a

significant effect of sample type only after the 5 sec baseline was introduced, $F(1, 10) =$

35.95, and not before, $F(1, 10) < 1$. This indicated a choose-small bias following the

introduction of the 5 sec baseline.

A 2 X 2 X 39 ANOVA performed on the acquisition data (see Figure 10) at the 5

sec baseline showed an overall effect of session, $F(38, 380) = 10.83$, and sample, $F(1, 10)$

$= 9.05$, but not group. Sample and session also interacted significantly, $F(38, 380) =$

3.19. Examination of the simple main effects showed a significant effect of sample at

session 1, $F(1, 10) = 35.90$, session 2, $F(1, 10) = 13.44$, session 5, $F(1, 10) = 5.29$, and

session 6, $F(1, 10) = 5.50$. This was due to an initial bias to respond to the comparison

correct for small following the introduction of the 5 sec baseline delay, which

disappeared over sessions.

A 2 X 2 X 5 ANOVA was performed analyzing sample type X group X delay,

which showed no significant overall difference between Group Light-Dark and Group

Dark-Dark, and no interactions with the group factor. There was a significant sample

type X delay interaction, $F(4, 40) = 13.01$. This interaction can be seen in Figure 11,

which shows the delay test data with mean percent correct when the small sample was

presented and mean percent correct when the large sample was presented. Again, no bias

was found at the 5 sec baseline. As expected there was a significant bias to respond to

the comparison correct for large at delays shorter than baseline, $F(1, 10) = 54.13$, and

significant biases to respond to the comparison correct for small at 15 sec, $F(1, 10) =$

5.84, and 20 sec, $F(1, 10) = 5.45$. There was not, however, a significant bias to respond

small at the 10 sec delay, although the trend was in the correct direction.

<div align="center">Discussion</div>

Although there were no significant differences in the acquisition data of Group

Light-Dark and Group Dark-Dark, the graphs show a trend of stronger performance for

Group Dark-Dark. The confusion hypothesis predicts that the opposite should occur. If

being presented with both a dark ITI and a dark DI causes confusion, and lighting the ITI

eliminates this confusion, then one would expect better performance with the lit ITI than

with the dark ITI.

The results of delay testing are also inconsistent with the confusion hypothesis. The confusion hypothesis states that adding a light in the ITI should reduce the possibility for confusion when the DI is extended at test, resulting in parallel retention functions for Group Light-Dark. Group Dark-Dark, on the other hand, should experience confusion, causing a bias to respond small at extended delays. The analysis revealed no difference in the biases of Group Dark-Dark and Group Light-Dark. Testing at delays longer than baseline produced a significant bias to respond to the comparison correct for small, while testing at delays shorter than baseline showed the opposite, a choose-large bias. This is a replication of the results of Santi and Hope (in press) in which both choose-large and choose-small effects were found, with all birds experiencing dark ITI's and dark DI's. The subjective shortening hypothesis predicts exactly these results. If the choose-small effect is occurring as a result of a decay in pulse counts, the addition of a light in the ITI should have no effect on the bias, as was found here. Testing at delays shorter than baseline showed strong biases to respond large for both the dark and the light groups. This is also the result predicted by the subjective shortening hypothesis. The confusion hypothesis gives no explanation for the occurrence of a choose-large bias in either group.

Experiment 3

Experiment 3 was done to examine the effect of introducing a light in the DI on a numerical discrimination, with a 5 sec baseline delay. The timing study performed by Kelly and Spetch (2000) showed parallel retention functions when the ITI was dark and the DI lit. However, examination of the individual subjects data showed some of the birds having a bias to respond short at extended delays, while others showed a bias to respond long at extended delays. Only when the individual data was averaged together

did parallel retention functions emerge. Kelly and Spetch explained this by stating that the pigeons showing a choose-long bias were timing through the delay.

Dorrance, et al (2000) also obtained a choose-long bias at extended delay testing, which they explained in a similar manner to Kelly and Spetch. The choose-long bias emerged in birds trained with a lit ITI and a dark DI. They suggested that the birds simply timed from the offset of the ITI to the presentation of the comparison stimuli. Therefore, when the delay was extended a bias to choose-long arose.

If the use of an event counter is in fact employed, using a numerical discrimination is likely to control for problems of this nature. First, both of the samples are equal in duration, which means that the discrimination cannot be done by simply timing from the offset of the ITI to the presentation of the comparison stimuli. Also, if the pigeons are counting the number of flashes by use of the event switch, they are unlikely to time a lit DI and somehow add this duration to their flash count in memory. If the light in the DI is recorded as another event, it presumably should only be counted as a single flash regardless of whether the DI is extended or shortened. Thus, using a lit DI in a numerical discrimination should produce a more accurate assessment of the memory biases in relation to the sample stimuli, if a switch is operating in event mode. However, it is also possible that these discriminations are made simply by operating a switch in stop mode and summing the duration of each flash in the trial. If this is the case, the addition of any light in the trial will add pulse counts proportional to the duration of the light. Therefore, extended delays with a lit DI should actually produce a bias to respond large, due to the addition of pulse counts during the delay.

Method

Subjects and Apparatus

The subjects and apparatus used in Experiments 1 and 2 were also used in Experiment 3.

Procedure

Following the testing from Experiment 2 the birds were retrained at the 5 sec baseline with a dark DI. Once accuracy was equivalent to the criterion used in Experiment 2, a light was introduced in the DI. An analysis was again conducted on the acquisition of the task, which revealed no significant group differences.

All 12 birds were trained under the same conditions as those used in Experiment 2, except that a light was present in the DI. See Figure 12 for ITI and DI conditions for both groups. Training continued for 42 sessions. On the final day of training Group Dark-Light showed 76.48% accuracy following the small samples and 73.57% accuracy following the large samples. Group Light-Light responded with 69.82% accuracy following the small samples and 73.35% accuracy following the large samples. Testing was identical to that done in Experiment 2, except that a light was present in the DI.

Results

A 2 X 2 X 2 ANOVA was performed examining the last day of 5 sec baseline training with a dark DI to the first day of 5 sec baseline training with a lit DI for Group's Light-Light and Dark-Light with the small and large samples (see Figure 13). As expected, there was a significant effect of session $F_{(1, 10)} = 83.36$, indicating that the introduction of the light in the DI had an effect for both groups. There was also a significant effect of sample, $F_{(1, 10)} = 26.64$ as well as a sample X session interaction, F

(1, 10) = 14.92, which was caused by an effect of sample occurring only after the introduction of the lit DI, $F(1, 10) = 23.39$, indicating a choose-large bias. However, the presence of a 3 way interaction between sample, session, and group, $F(1, 10) = 6.74$, indicated that there was a group difference in this bias to respond large. Only Group Dark-Light showed a significant effect of sample after the light was introduced in the DI, $F(1, 10) = 31.66$, although the effect of sample following the introduction of the light for Group Light-Light approached significance, $F(1, 10) = 4.16, p = .068$.

A 2 X 2 X 41 ANOVA performed on the acquisition data (see Figure 14) with the introduction of the lit DI showed an effect of session, $F(41, 410) = 5.04$, but not of group or sample type. There was also a sample type X session interaction, $F(41, 410) = 3.70$. Examination of the simple main effects showed a significant effect of sample at sessions 1, 2, and 3, $F(1, 10) = 29.35, 31.63$, and 17.67, respectively. This was due to an initial bias to respond to the comparison correct for the large sample following the introduction of the light in the DI.

A 2 X 2 X 5 ANOVA was performed on the delay testing data. The analysis showed no overall difference between the Group Light-Light data and the Group Dark-Light data, and no interactions with the group factor. There was a significant sample type X delay interaction, $F(4, 40) = 10.09$. This interaction can be seen in Figure 15, which shows the delay test data with mean percent correct following the small sample and mean percent correct following the large sample. At the 5 sec baseline delay there was not a significant response bias. At the 0 sec delay there was a significant bias to respond to the comparison correct for the small sample, $F(1, 10) = 31.85$. At delays longer than baseline this bias was reversed. Testing with delays of 10 and 15 sec did not show a

significant response bias, but at the 20 sec delay there was a significant bias to choose-large, $F(1, 10) = 5.93$.

Discussion

The analysis examining the differences in accuracy following the introduction of the light in the DI showed a large amount of disruption for both groups. Although only Group Dark-Light showed a significant choose-large bias following the introduction of the light, the trend was in the same direction for Group Light-Light. This suggests strongly that the introduction of the light in the DI was somehow adding to the perceived number of events.

The delay testing seems to have confirmed this possibility. At delays shorter than baseline, there was a choose-small effect for both groups. At delays longer than baseline, the bias is reversed, turning into a choose-large bias. These biases are the opposite of those found in Experiments 1 and 2, indicating that the presence of the light in the DI caused a very different process by which these biases were occurring. The most probable explanation is that the presence of the light in the DI is adding pulse counts to the accumulator values. This would cause a bias to respond large when the light was first introduced, as was found. This bias would then disappear over training as the pulse counts in reference memory also increased. During subsequent delay testing, a shorter delay than that used in training would result in a smaller pulse count, causing a choose-small bias, while a longer delay than that used in training would produce a larger pulse count and, therefore, a choose-large bias would emerge.

GENERAL DISCUSSION

The results of Experiment 1 showed that at extended delay testing pigeons show a bias to respond to the comparison correct for small whether the ITI is lit or dark. This result is inconsistent with the confusion hypothesis, which states that presenting a light in the ITI during training and subsequently testing with a dark DI, should eliminate confusion and thus, the bias to respond small. The subjective shortening hypothesis, on the other hand, predicts that a choose-small bias should occur at extended delays, whether a light is present in the ITI or not. Therefore, the results of testing at extended delays are consistent with the subjective shortening hypothesis.

These results contradict those found by Sherburne et al. (1998) in which pigeons did not show a bias to choose-short on a temporal discrimination study, when the ITI used during training had a different lighting condition than the DI used at test. However, it does not appear as though the results presented here are unique to numerical discriminations, as Kelly and Spetch (2000) found that the choose-short effect was not eliminated when the ITI and the DI were disambiguated. Thus, it appears as though the results found by Sherburne et al. (1998) are the anomaly and not those presented here.

Experiment 2 further investigated the predictions of the confusion hypothesis by training both Group Dark-Dark and Group Light-Dark with an extended baseline delay of 5 sec, and then testing at delays longer and shorter than baseline. Dorrance et al. (2000) suggest that exposure to the DI during training should reduce it's novelty, thereby, reducing the possibility for confusion with the ITI. If this is the case then neither Group Light-Dark nor Group Dark-Dark should show a choose-small bias at extended delay testing. In a replication of the results of Experiment 1 the overall analysis showed a

significant choose-small bias at extended delays with no difference being found between

Group Dark-Dark and Group Light-Dark. Thus, when the possibility for confusion was

reduced further by extending the baseline delay to 5 sec, the choose-small was still

present.

This suggests that the parallel retention functions found by Dorrance et al. (2000)

most likely occurred by the process of a switch from analogical coding to some form of

categorical coding as described by Grant and Kelly (1998). Dorrance et al. trained

pigeons to discriminate a 2 sec sample from a 10 sec sample with variable delays ranging

from 0 to 4 sec. At test a choose-short effect was not found. Grant and Kelly, on the

other hand trained with delays ranging from 1 to 3 sec, which did produce a choose-short

effect at extended delays. Only when Grant and Kelly trained with a larger set of

variable delays was the choose-short effect eliminated. The range of delays used by

Dorrance et al. may have been too large to allow analogical coding to be effective in

making the discriminations.

In Experiment 2 of the present study, both groups showed a bias to respond to the

comparison correct for the large sample at delays shorter than baseline. This replicates

the results of Santi and Hope (in press) and extends them by showing that the choose-

large effect occurs regardless of whether or not the ITI and the DI are disambiguated.

The confusion hypothesis alone has difficulty explaining the occurrence of this effect for

either Group Dark-Dark or Group Light-Dark. However, Zentall (1999) proposed an

explanation suggesting that the biases occurring at delays shorter than baseline were

resulting from a process completely different from that producing the biases found at

delays longer than baseline. Zentall suggested that the choose-long bias (in this case the

choose-large bias) might be occurring as a result of interference from previous trials,

which increases at shortened delays. Thus, when the delay is shortened some residual

memory from previous trials is added to the current sample resulting in a bias to choose-

long or large. In fact, Spetch and Sinha (1989) found evidence supporting this notion.

Spetch and Sinha first trained pigeons on a temporal discrimination procedure and then

tested them with double duration-event trials. They found that on these test trials the

pigeons showed a strong bias to respond long, suggesting that they were summing the

durations, even when the gap between the durations was 10 sec.

The problem with this hypothesis, however, when used to support the viability of

the confusion hypothesis is that it still requires some form of analogical retention code. If

categorical codes were being used, as proposed by the confusion hypothesis, then testing

at delays shorter than baseline should result in symmetrical interference for both the short

and long (small and large) samples. Thus, this explanation is also difficult to fit into a

confusion hypothesis framework.

The results found here and the lack of an explanation for choose-long and choose-

large biases by the confusion hypothesis agrees with the explanations supported by Santi

and Hope (in press). Santi and Hope suggested that the choose-small and choose-large

biases they found using numerical discriminations supported a subjective shortening

account. They further stated that the use of an analogical code, and the subsequent decay

of pulse counts could also be extended to include the subjective shrinking of number.

While the results of the present study clearly support the contention that temporal events

are stored analogically and subjectively shorten over delays, the results of Experiment 3

call into question whether or not delay testing causes the subjective shrinking of number.

The results of Experiment 3 were surprising by the viewpoint of both the subjective shortening hypothesis and the confusion hypothesis. The confusion hypothesis predicts that training with a 5 sec baseline delay, whether lit or dark, should reduce the novelty of the delay at test thereby resulting in parallel retention functions at extended delays. The subjective shortening hypothesis predicts that the pulse counts of the sample should decay whether the DI is lit or dark, resulting in a bias to respond small. At delays shorter than baseline, the pulse counts in working memory should be larger than those in reference memory, causing a bias to respond large. Therefore, finding a choose-small bias at delays shorter than baseline and a choose-large bias at delays longer than baseline was not expected from either hypothesis. However, the results appear to be more applicable to the idea that the memory biases typically result from the use of an analogical code, rather than confusion between the novel DI and the ITI.

By the confusion hypothesis, if the DI is confused with the ITI the choose-short or choose-small effect should occur. If this confusion is eliminated, parallel retention functions should be the result. Also, because the sequences cannot be discriminated on the bases of time, it is impossible for the birds to simply time from the offset of the ITI to the onset of the comparison stimuli, as found in the temporal discrimination studies by Kelly and Spetch (2000) and Dorrance et al. (2000), which would result in a choose-large bias at extended delays. Therefore, a choose-small bias or parallel retention functions appear to be the only possibilities under this hypothesis. If one assumes the use of an analogical code, on the other hand, the results of Experiment 3 seem more plausible. If the samples are maintained analogically then the insertion of a light in the DI could potentially add pulse counts to the representation. This would result in an immediate bias

to respond large when the light was first introduced into the DI, as was found in preliminary training for Experiment 3. As the representations in reference memory changed to account for the added pulses, this bias disappeared over training. On subsequent testing, shortening the delay resulted in fewer pulse counts and a bias to respond to the comparison correct for small. When the illuminated delay was extended, a greater number of pulse counts were added causing a bias to choose-large.

A similar situation seemed to occur in Experiment 1, although to a lesser extent, when the ITI was first illuminated. The illuminated ITI added pulse counts, resulting in an initial bias to respond large, which slowly disappeared over training. This illumination, however, remained a constant source of pulse counts throughout training and testing. Therefore, during delay testing the process of subjective shortening resulted in a bias to respond large at delays shorter than baseline and a bias to respond small at delays longer than baseline. In Experiment 3 the process of subjective shortening was overshadowed by the addition and subtraction of pulse counts that occurred with the lengthening and shortening of the illuminated DI.

Under the current dual-mode model, there are separate switches, one operating in event mode when making a numerical discrimination, and the other operating in run mode when making a temporal discrimination. These switches gate pulses to separate accumulators, which then send pulse count totals to separate stores in working memory. It is unclear then, how pulse counts from a temporal stimulus could be added to those of a numerical stimulus. One possibility is that there is some interaction between the pulse counts for time and number within the working memory store. Also possible is that the switch for the number accumulator continues to close at some fixed rate during the

presentation of the temporal stimulus. The most probable, however, is that the stimuli

used for the current study did not activate a switch in an event mode at all, but simply

acted under a stop mode and summed the duration of each flash in the sequence. The

addition of any extra light then would add to the pulse counts in the accumulator.

This method of sequence discrimination can also be applied to the results of Santi

and Hope (in press). In a time condition pigeons were required to distinguish 4 flashes of

light occurring in 2 sec from 4 flashes of light occurring in 8 sec, and in a number

condition, 2 flashes in 4 sec from 8 flashes in 4 sec. Delay testing showed a bias to

respond long for the time condition and a bias to respond small for the number condition.

However, Santi and Hope argued that the pigeons were actually counting the number of

flashes occurring in the last couple of seconds on the time condition, meaning that the

choose-long effect was, in fact, a choose-small bias. The same results would be expected

if the pigeons were simply summing the total flash duration. The duration of the 4

flashes in the 2 sec sample would deteriorate much less than the 4 flashes in the 8 sec

sample, meaning that the pulse counts for the 2 sec sample would be larger than those for

the 8 sec sample at a 0 sec delay. Thus, at extended delays the deterioration of pulse

counts would cause the subjective summed durations to become closer to the 8 sec

sample than to the 2 sec sample. It is reasonable to suggest that animals can sum

durations of events since this is the basis of the findings of the gap procedure, in which

both rats and pigeons have been found to add the pre-gap duration to the post-gap

duration. (Cabeza de Vaca et al., 1994; W. A. Roberts et al. 1989; W. A. Roberts &

Church, 1978).

This is a fact that was overlooked by W. A. Roberts and Mitchell (1994) when they attempted to replicate the rat study by Meck and Church (1983), using pigeons. An important element in the study by Meck and Church was that the rats could not make the test discriminations for the number condition by summing the total duration of the flashes in the sequence. This was controlled for by using a cycle of events that consisted of an equal amount of signal-on duration and signal-off duration per cycle. When the number of events was varied, the cycle duration was also varied, thereby holding the total signal-on duration and the total signal-off duration constant. This meant that the rats had to use an event switch in order to make this discrimination. In the study by W. A. Roberts and Mitchell, on the other hand, the total signal-on duration was not controlled for. Each flash for all training and testing conditions had a constant duration of 200ms. This meant that when the number of flashes was varied and time was held constant, the total signal-on duration also varied, thereby allowing the pigeons to make the discrimination by summing the durations of each flash in the sequence. Therefore, the pigeons in this study were not required to use an event counter to make the discrimination.

Fernandes and Church (1982) also tested for the existence of an event counter in rats. They first trained rats to discriminate 2 sound bursts from 4 sound bursts, with all bursts lasting .2 sec. They then tested rats with sequences of 4 sounds that each lasted .1 sec and 2 sounds that lasted .4 sec. The 2 sound sequence now had a longer total sound-on duration than the 4 sound sequence. This testing did not affect the rats responding. This suggests that rats, under conditions such as those used in this experiment, will actually make the discrimination based on the number of sound bursts as opposed to the total duration of the sound bursts in a sequence.

The results of the current study may suggest, however, that the activation of this event switch is more selective than previously thought. Also, there may be differences between species in the use of an event switch, some being more apt to time events than to count them under certain conditions. Although the studies by Fernandes and Church (1982) and Meck and Church (1983) found evidence in favour of an event switch in rats, the same tests have not been conducted on pigeons. A simple test to clarify whether the pigeons in this study were using an event switch or not would be to extend the duration of the events in the small sample to equal the total overall duration of the events in the large sample. If the pigeons respond as though the sample is large then the pigeons would have to be operating a switch in stop mode and summing the durations of the flashes. If the pigeons are operating an event switch, then extending the duration of the events in the small sample should have no effect on accuracy. Until a test of this nature has been conducted it should not be assumed that pigeons apply the use of an event counter in procedures such as the one used here.

The results presented here clearly adhere most closely to the predictions of the subjective shortening hypothesis and the use of an analogical code for the memory of temporal stimuli. Controlling for the possibility of confusion between the ITI and the DI did not eliminate the choose-small bias. Furthermore, the choose-large biases found for both groups is a direct prediction of this hypothesis. However, the contention that the subjective shortening hypothesis can be extended to include the subjective shrinking of number remains in question. Experiment 3 suggested that the pigeons might be making the discriminations on the basis of the total duration of light presented on a particular trial instead of the number of light flashes occurring in the sample. Thus, while it was clear

that the pigeons were using an analogical code, whether they were actually discriminating

on the basis of the number of flashes requires further testing.

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Figure Captions

Figure 1. Dual-mode model of time and number processing.

Figure 2. ITI and DI conditions for Group Light and Group Dark in Experiment 1.

Figure 3. Sample stimuli used throughout Experiments 1, 2, and 3.

Figure 4. Comparison between last day of baseline training with dark ITI's and first day of training with lit ITI's.

Figure 5. Acquisition data at the 0 sec baseline delay for Group Light and Group Dark on the small and the large samples.

Figure 6. Interaction between group and delay in Experiment 1

Figure 7. Interaction between sample type and delay during delay testing in Experiment 1.

Figure 8. ITI and DI conditions for Group Dark-Dark and Group Light-Dark in Experiment 2.

Figure 9. Comparison between last day of 0 sec delay training and first day of 5 sec delay training.

Figure 10. Acquisition data at the 5 sec baseline delay for Group Light-Dark and Group Dark-Dark on the small and the large samples.

Figure 11. Interaction between sample type and delay during delay testing in Experiment 2.

Figure 12. ITI and DI conditions for Group Light-Light and Group Dark-Light in Experiment 3.

Figure 13. Comparison between last day of training with dark DI's and first day of training with lit DI's.

Figure 14. Acquisition data for Group Dark-Light and Group Light-Light on the small and large samples.

Figure 15. Interaction between sample type and delay during delay testing in Experiment 3.
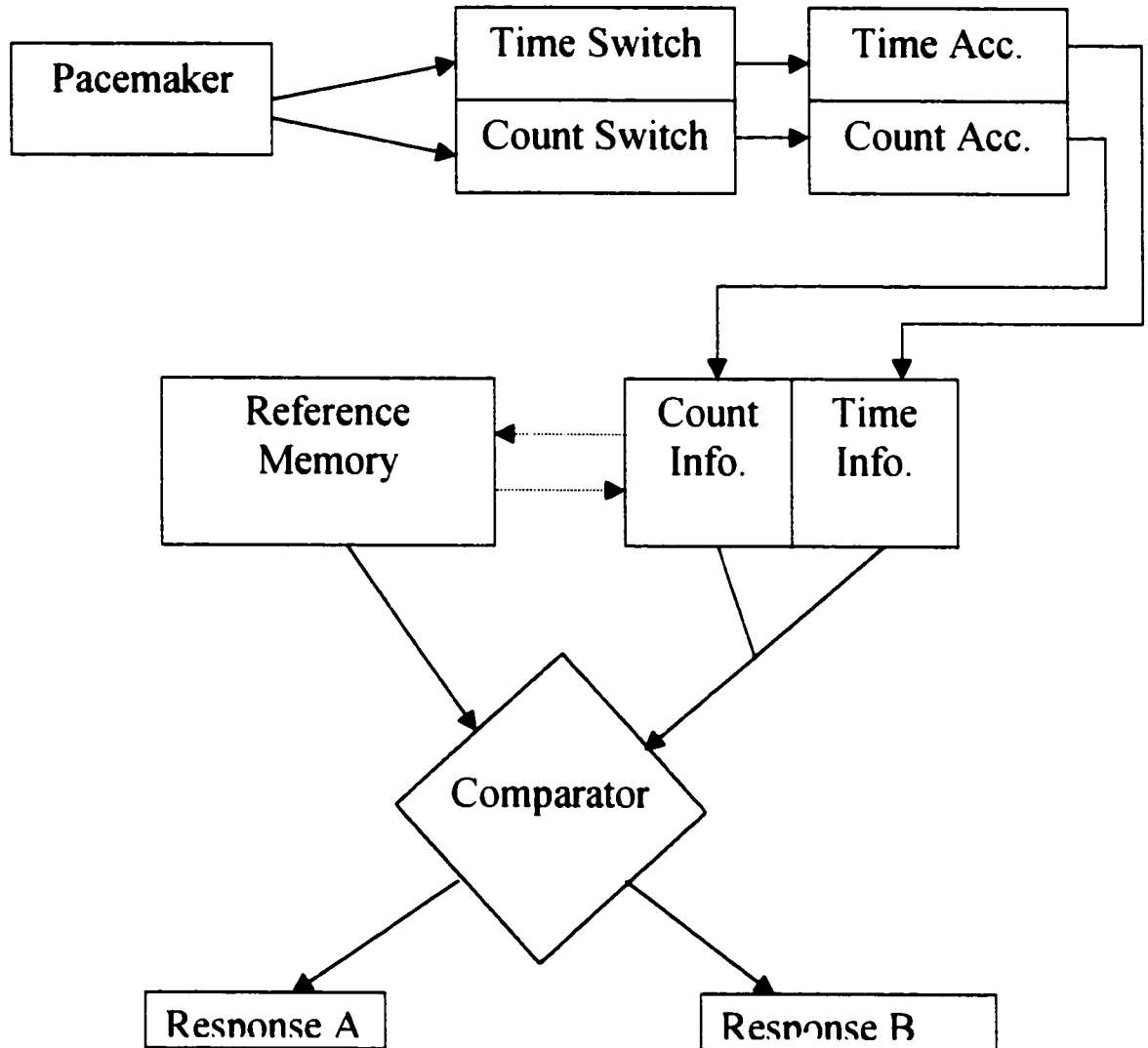
Figure 1

Figure 2

Experiment 1 – ITI, DI Conditions

Group	ITI	DI	Training Delay	Test Delays(sec)				
Dark	Dark	Dark	0sec	0	5	10	15	20
Light	Lit	Dark	0sec	0	5	10	15	20

Figure 3

Sample Stimuli

2f/4s (small)

8f/4s (large)

Figure 4

Introduction of lit ITI

Figure 5

Acquisition - Baseline 0 sec

Figure 6

Group X Delay Interaction
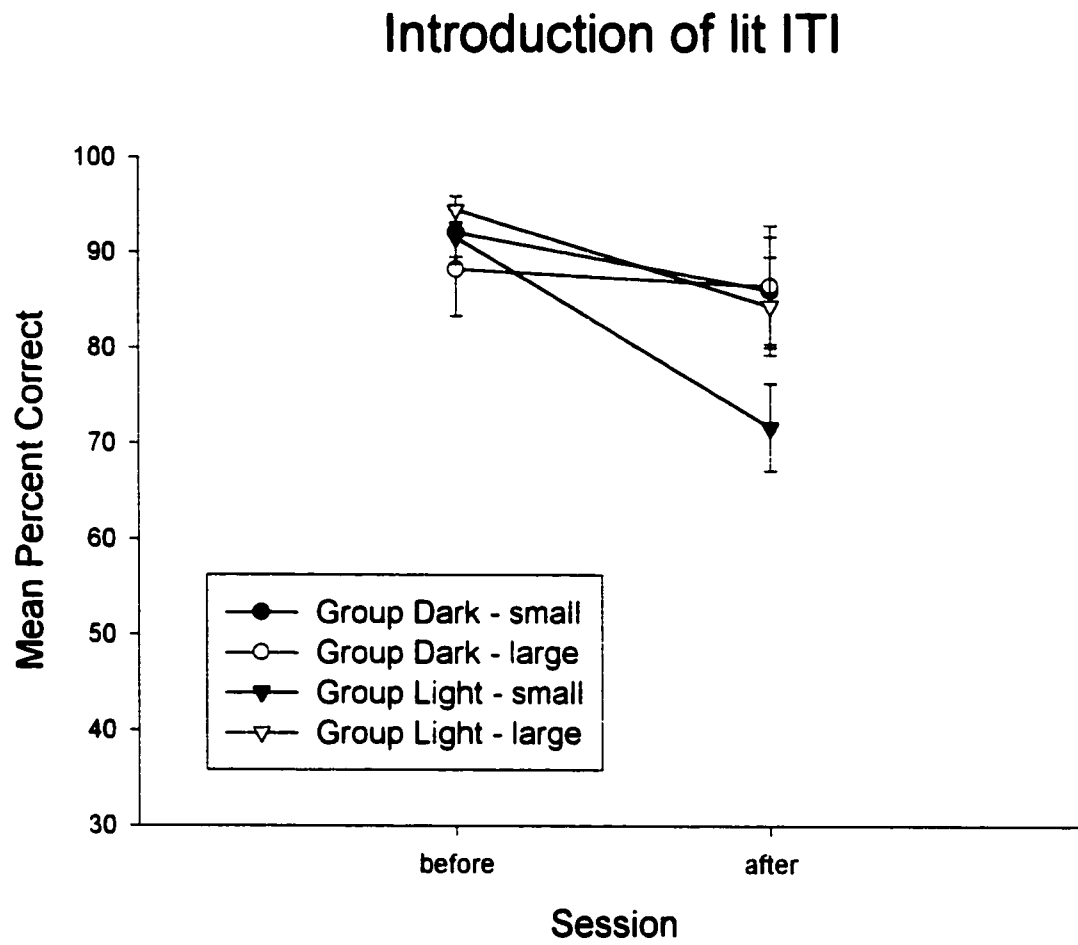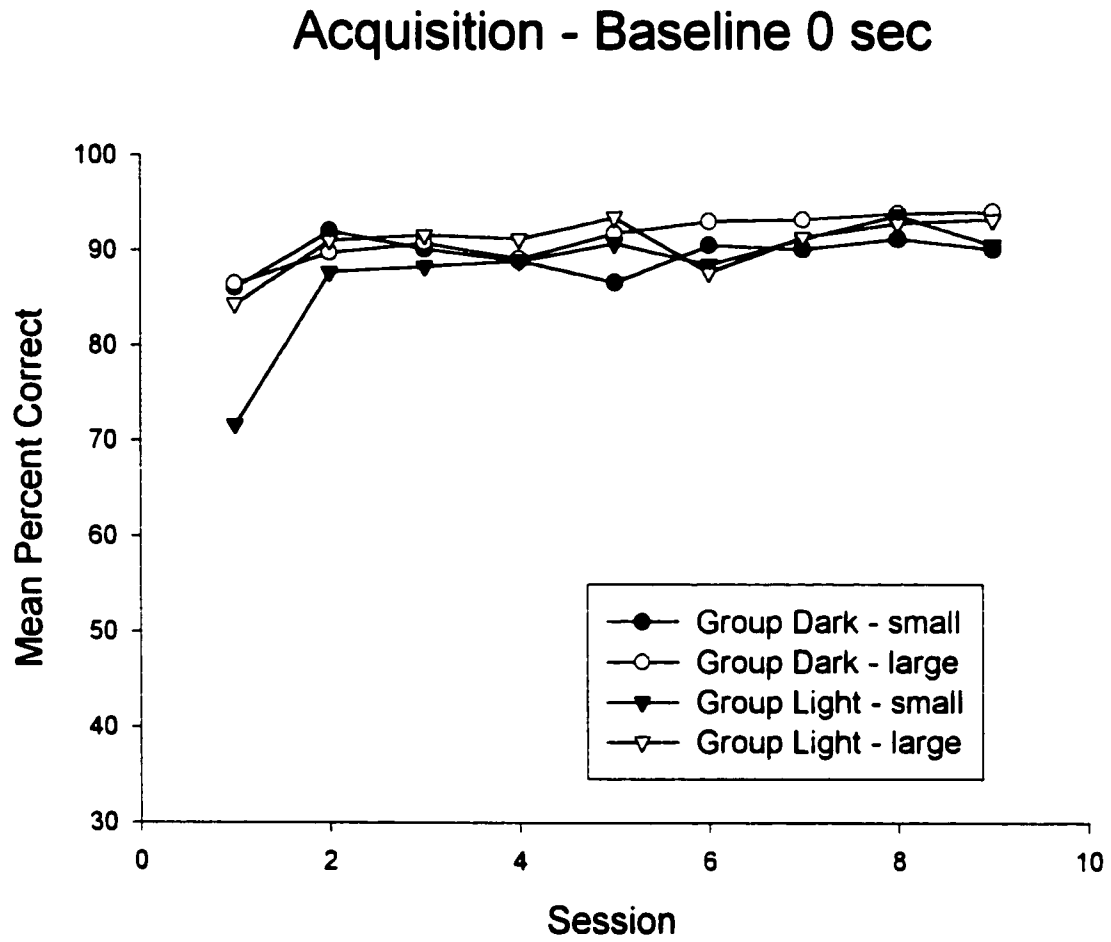
Figure 7
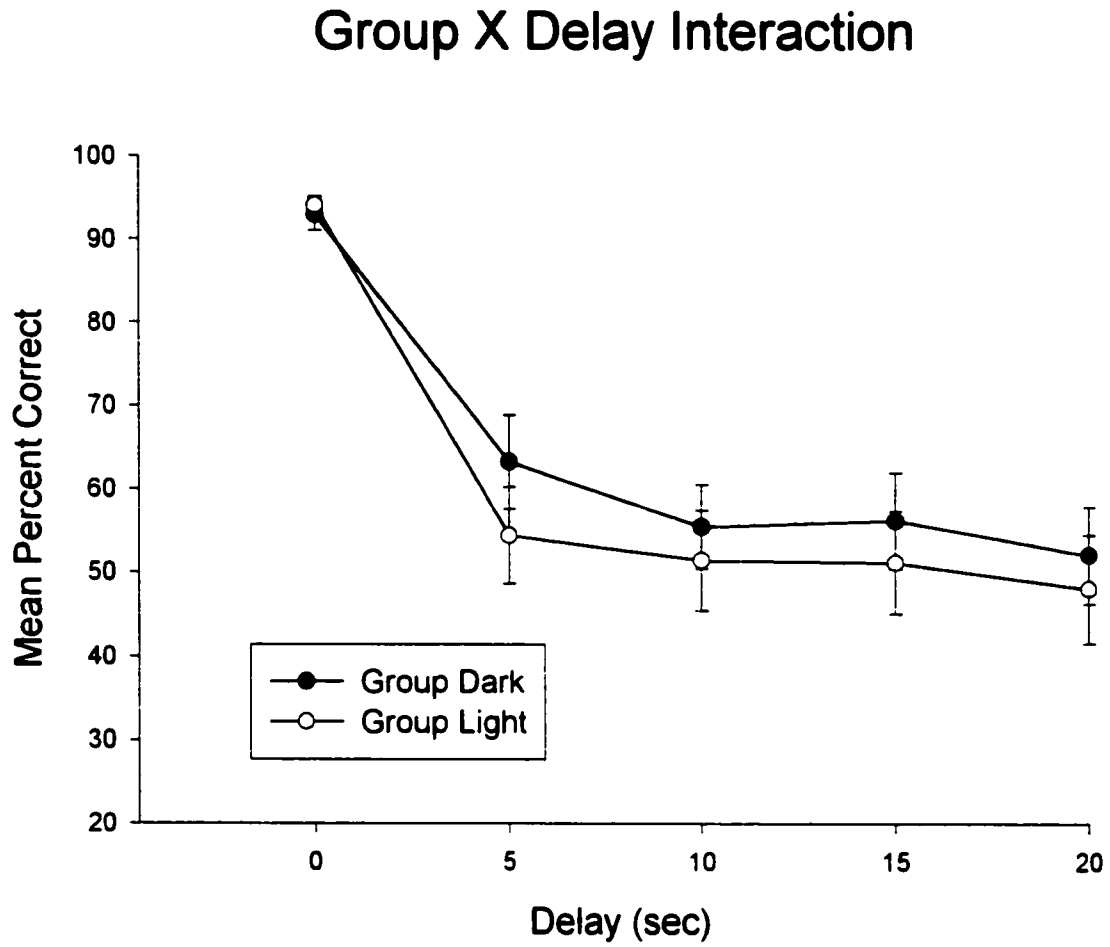
Baseline 0 sec - Delay test
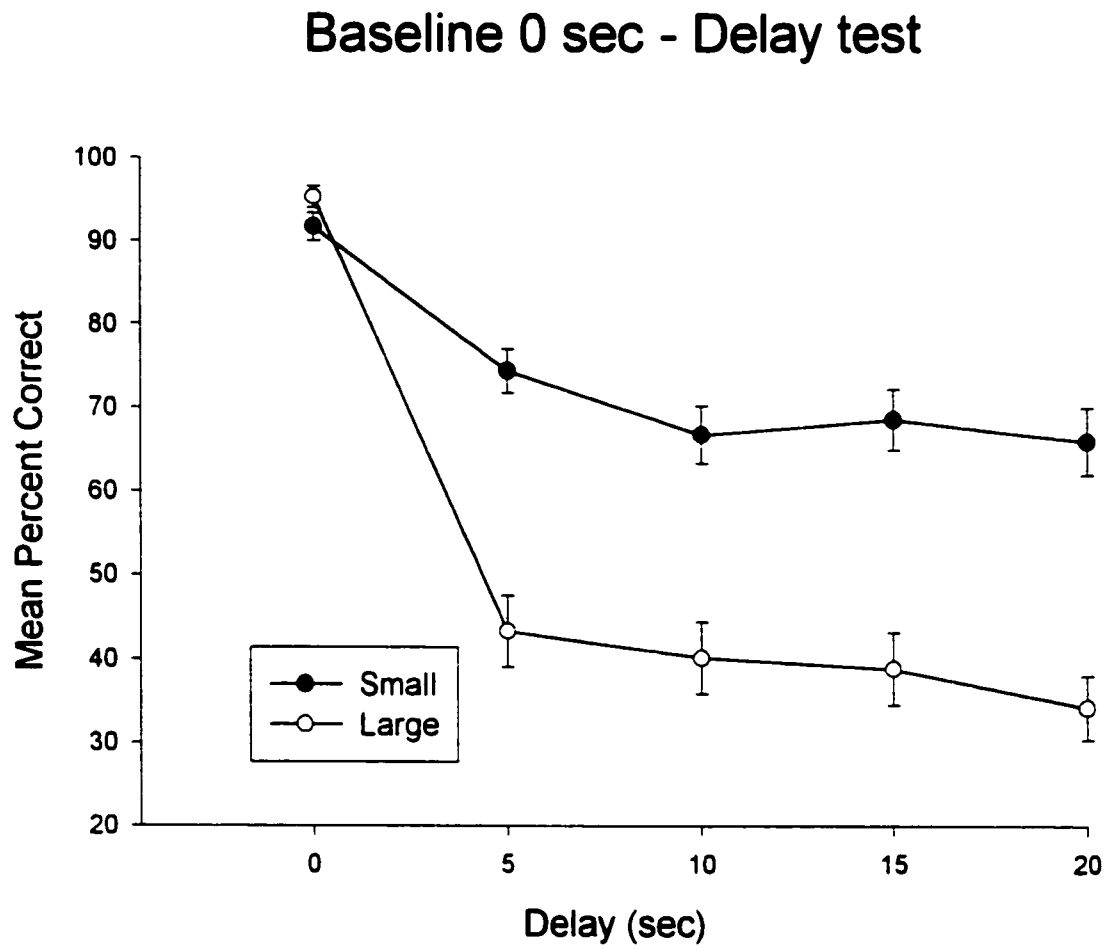
Figure 8

Experiment 2 – ITI, DI Conditions

Group	ITI	DI	Training Delay	Test Delays(sec)				
Dark-Dark	Dark	Dark	5sec	0	5	10	15	20
Light-Dark	Lit	Dark	5sec	0	5	10	15	20

Figure 9
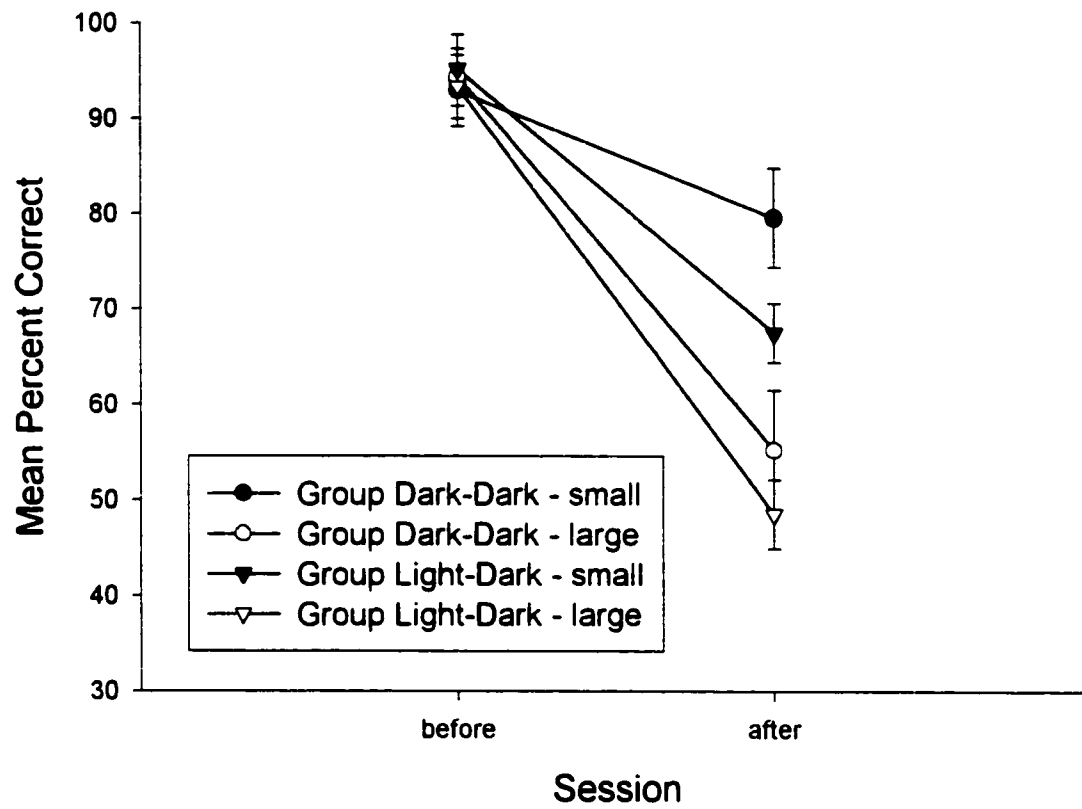
Figure 10

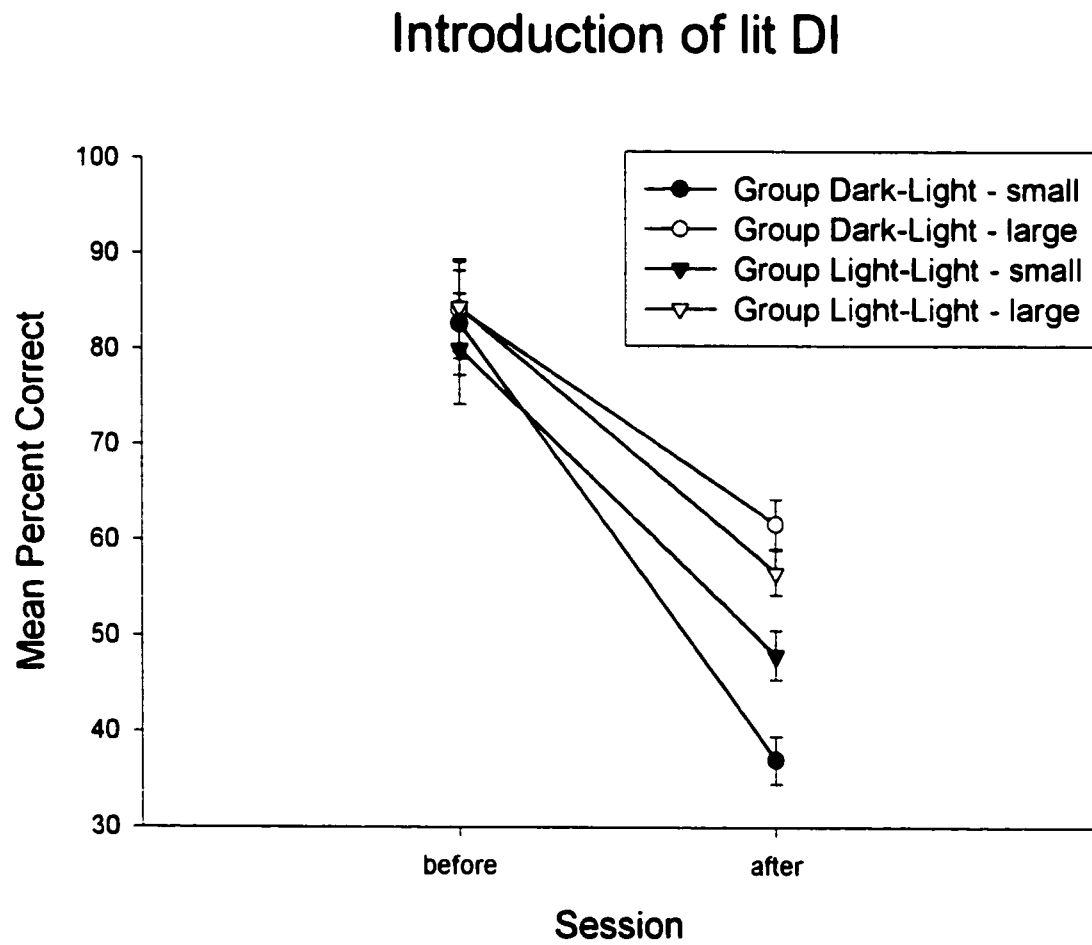Acquisition - Baseline 5 sec

Figure 11
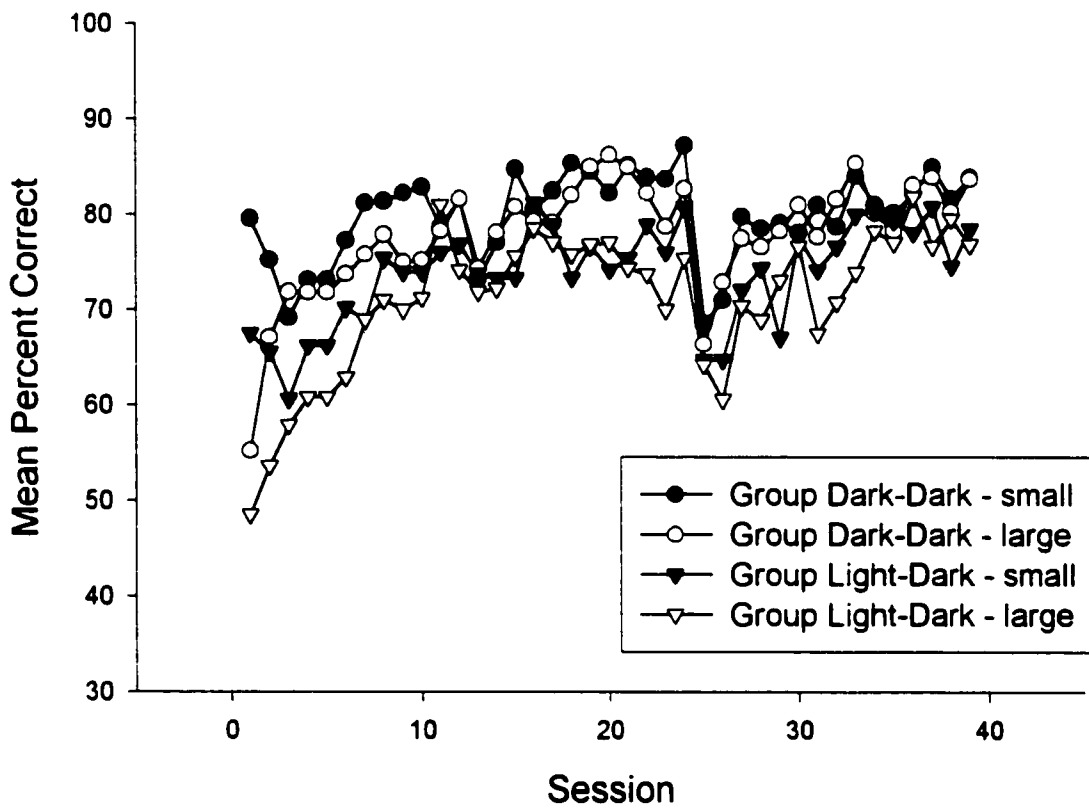
Baseline 5 sec - Delay test
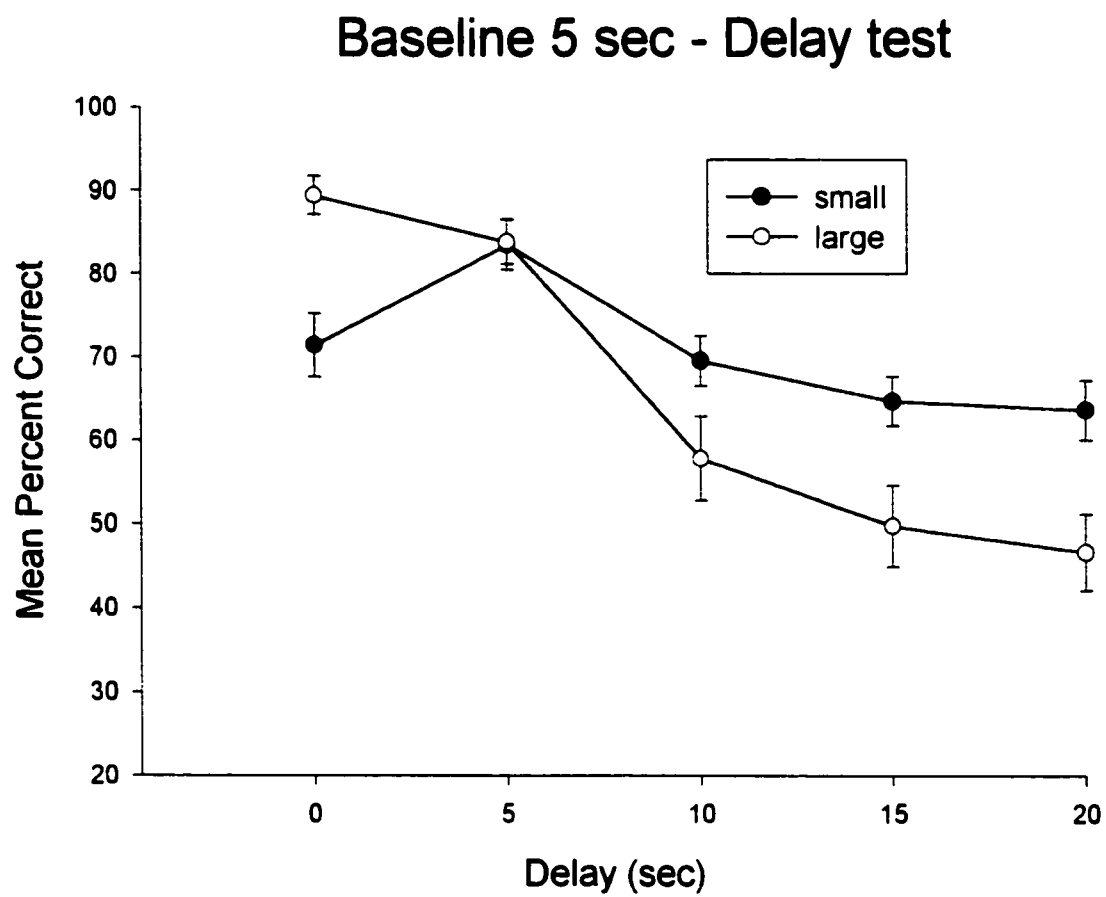
Figure 12

Experiment 3 – ITI, DI Conditions

Group	ITI	DI	Training Delay	Test Delays(sec)				
Dark-Light	Dark	Lit	5sec	0	5	10	15	20
Light-Light	Lit	Lit	5sec	0	5	10	15	20

Figure 13

Introduction of lit DI

Figure 14

Acquisition - Baseline 5 sec lit DI

Figure 15

Baseline 5 sec - Lit DI - Delay test