1997

Animal memory processes for number and time: Pigeons, methamphetamine, and the internal clock model

James W. Coyle
Wilfrid Laurier University

Recommended Citation

Coyle, James W., "Animal memory processes for number and time: Pigeons, methamphetamine, and the internal clock model" (1997). *Theses and Dissertations (Comprehensive)*. 645.
https://scholars.wlu.ca/etd/645

INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

Animal Memory Processes for Number and Time:
Pigeons, Methamphetamine, and the Internal Clock Model

By

James W. Coyle

Bachelor of Arts (Honours), Queen's University, 1995

THESIS

Submitted to the Department of Psychology

in partial fulfilment of the requirements

for the Master of Arts degree

Wilfrid Laurier University

1997

0-612-21876-7

Abstract

The mode-control model of counting and timing (Meck & Church, 1983) suggests that discriminations based on number and time may be controlled by the same internal clock mechanism. In Experiment 1, two groups of pigeons were initially trained to perform delayed symbolic matching-to-sample (DSMTS) at a 5s fixed baseline delay, with sample stimuli that consisted of sequences of flashing light. Testing was conducted with a range of delays (0, 2.5, 5, 7.5, and 10s). In the Number Group, control by number was established by varying the number of flashes while holding time constant. In the Time Group, control by time, or number, was established by varying the sample duration while holding the number of flashes constant. In Experiment 1, data from the Number Group supported the mode control model, while analysis of the Time Group's performance failed to identify whether these birds used either temporal or numerical aspects of their stimuli to control their choice of comparison. In Experiment 2, the pigeons received injections of methamphetamine (1.5 mg/kg) or saline under delay testing conditions identical to Experiment 1 in an attempt to determine if methamphetamine speeds up the internal clock and if the same theoretical pacemaker mechanism is responsible for memory for time and number. Data from both groups failed to support the notion that an increase in dopamine levels results in an increase in the rate of an internal pacemaker mechanism. Rather, Experiment 2 further supported the notion that amphetamine may affect attention to temporal/numerical samples in a general manner.

Acknowledgements

Unless I grow senile, I doubt that I will ever forget the time and effort I have put into the creation of this document. I am pleased with the final copy of my thesis, but my greatest satisfaction comes from the opportunity to thank a select number of people who have helped guide, inspire, and support me during my "Masters experience".

As with anything I have worked hard to earn, I owe great thanks to my mother father and sister for their continual support and encouragement. Very special (and very different!) personal thanks also go to Sarah and my pigeons. To Sarah for the kind of support that only she could provide, and to my birds for the kind of data that only they could provide!

I would like to thank Dr. Linda Parker, Dr. Keith Horton, and Dr. Bill Roberts for their participation on my thesis committee. I am pleased to have received your professional input and helpful suggestions regarding this study. I would also like to thank Marion for doing an incredible job in her assistance with the animals, Yolanda for her patience in answering any questions about SPSS, and Dave for two years of crucial computer assistance.

Finally, I would like to extend my greatest thanks to my advisor Dr. Angelo Santi. I would like to thank Angelo for his constant financial support as well as his professional and personal guidance regarding my studies. Without a doubt, my scientific apprenticeship under him has been the highlight of my time at Wilfrid Laurier.
I have learned a lot from you, and I have had fun learning with you.

Table of Contents

List of Figures

Although psychology and its ties with philosophy are centuries old, the field of psychology has affirmed its independence over the past century in its study of the mind. In the last quarter of the twentieth century, two paths of research have been influential in shaping the discipline of psychology. One path, advocated most notably by J. B. Watson, B. F. Skinner, and K. Spence, was the strict study of behaviour (Schultz, 1973; Wertheimer, 1979). The second path, and perhaps currently more popular, emphasizes psychology's study of the mind's cognitive processes (Hothersall, 1984). Both paths, however, often work in concert with one another. In the field of animal cognition, researchers examine aspects of cognitive processing by attempting to understand the way that animals code various types of information. Cognitive theories examine flexible and active information processes by analysing a variety of animal behaviours and performance on many different tasks similarly studied in humans. An important process examined in the field of animal cognition is memory.

Two areas of interest, involving memory, examine how animals are able to make accurate discriminations based on time and number. Interest in animal memory has encouraged researchers to learn how to identify the type of processes that might exist for both time and number. Research suggests that the processing of time and number are not necessarily separate from one another. To study animal counting and timing processes, various theories and empirical techniques have been used in collaboration. The primary question that this study attempts to address is how time and number might both be recorded by the same clock mechanism through a similar accumulation of pulses according to the information processing model advanced primarily by Meck and Church

(1983). In order to understand the internal clock model, and the impact of others' proposed adjustments to the model, an overview of fundamental memory and coding processes and the typical methodologies used to study memory for event duration and counting is useful.

Over the past two decades, a distinction between working memory (WM) and reference memory (RM) in animal learning has generated a large amount of research. Working memory, developed initially in the field of human cognition, refers to a hypothetical repository for dynamic information, while reference memory is suggested to contain information regarding the strength of learned relationships that are of lasting relevance to the animal (Grant, 1993). Researchers suspect that the nature of memory coding processes is affected by several factors including the context of the task. The majority of recent research examining the coding of information in animals involves use of delayed matching-to-sample tasks (DMTS). Generally, accurate performance on this task requires animals to retain information obtained from a sample stimulus over a delay until a test response for a particular trial is required. In other words, the animal is typically presented with a sample stimulus that is followed by a choice of more than one comparison stimulus. The animal must then choose the correct comparison stimulus that corresponds to the sample stimulus that was presented on that trial. Given the nature of this task, WM can be regarded as the information relevant to the animal for a particular trial, while RM consists of information relevant to the animal for all trials (Honig, 1978). Grant (1993) examined the nature of coding in pigeons in a variety of studies concluding that the coding processes in these animals was flexible and dependent upon the task.

Of the types of coding argued to exist, retrospective and prospective coding are of primary interest in this study. For illustration purposes, consider a basic experiment using a one-to-one (OTO) mapping arrangement. Following a green key as the sample stimulus, a pigeon is required to peck a vertical comparison key in order to gain access to food. Similarly, following the presentation of a red sample key, the pigeon is required to peck a horizontal comparison key. Grant explained that either a "peck vertical code" or a "green code" may be activated by the green sample. At test, a "peck vertical" code established in WM could control responding without further inquiry of RM. Grant argues that this is an example of prospective coding. Alternatively, a "green code" in working memory (WM) could query reference memory (RM) regarding the appropriate response. This second possibility is considered an example of retrospective coding.

Memory for Time

The DMTS procedure has been used extensively to study memory for event duration in pigeons. Typically, an animal is trained to respond to the appropriate comparison stimulus after being exposed to either a short or long sample duration (for example, a 2s or 10s presentation of houselight). After learning this task at a zero (0) second delay between the offset of the sample presentation and the onset of the comparison, the animal is tested with the introduction of a delay (e.g., 2s, 5s, and 10s). Grant (1993) reported that, after the introduction of some delay, pigeons tended to respond to the long samples as though they were short. This result, known as the "choose-short effect", has been observed consistently under a variety of conditions (Kraemer, Mazmanian, & Roberts, 1985; Spetch & Rusak, 1989; Spetch & Wilkie, 1983). By contrast, when pigeons are trained with a delay (e.g., 10 s), they respond to shorter delays at test with a tendency to treat short samples as though they were long (Spetch & Rusak, 1989). This is known as a "choose-long effect". Grant (1993) suggests that short and long samples are believed to be coded in a retrospective and analogical fashion. In other words, Grant and Spetch (1993) explain that animals assess the sample "retrospectively" by considering the sample duration at the time of comparison by comparing it to reference memory values. The animals employ an "analogical" code such that they use the number of pulses produced by an internal pacemaker operating during the presentation of the sample. There is speculation that a subjective shortening process occurs such that the sample duration is perceived to be shorter as the time in which the event is absent increases (Grant, 1993; Grant & Spetch, 1993; Spetch & Wilkie, 1983).

It is interesting to examine how an information processing model advanced by Church (1984) has been used to account for results examining memory for temporal samples that used a DMTS procedure. A diagram of this model is shown in Figure 1. Church (1989) explains that when a switch is closed, a pacemaker transmits pulses to an accumulator at a fixed rate. These pulses are then transmitted to, and stored in, WM on a trial-by-trial basis. Once the pulses are in WM, a comparison between WM and RM is made. Responses by the animal are directed by rules stored in RM. If an animal learns a temporal discrimination between 2s and 8s for example, RM has representations of reinforced durations for each of these samples. RM representations will be compared to the representation of a duration sample in the accumulator or WM at the time of response. A response will be made to a comparison stimulus based on the closest match between the perceived RM duration and accumulator duration. The explanation of the subjective shortening process suggested by the internal clock model is that pulse counts stored in WM diminish, in an unspecified manner, over a period of delay. If pulse counts are lost from WM, then, at the time of comparison, the pulse counts for long samples in WM will resemble more closely the pulse count for the short sample stored in RM following training at a 0-s delay. Although pulse counts are also lost from the short sample in WM, the short sample will resemble more closely the pulse value for the short sample, compared to the long sample, following training at a 0-s delay. Therefore the comparison stimulus for the short sample will be an animal's preferred choice.

Memory for Number

A considerable amount of attention has been given to exploring animals' numerical abilities using the number of times a discriminative stimulus appears. For example, Davis and Albert (1986) found that rats were able to discriminate 3 (S+ or reinforced) auditory noise flashes from both 2 and 4 (S- or nonreinforced) noise flashes. A study such as this demonstrates that rats are capable of making intermediate numerical discriminations and are not only subject to making discriminations based on a simple many-versus-few dichotomy. Many experiments have also determined that animals are capable of accurately discriminating sequential samples based both on number and time. Modelled after work by Meck and Church (1983) with rats, Roberts and Mitchell (1994) found that pigeons were able to successfully discriminate between light flashes that simultaneously varied in duration as well as number of flashes. After presenting the birds with flashes which varied in duration or number, different colour side keys were used to direct the animals to make their comparison choice based on time or number. Temporal proficiency was assessed by presenting the animals with stimuli that varied in duration but not in the number of flashes, while numerical competence was assessed by presenting the birds with stimuli that varied in number of flashes but that were constant in duration of presentation. The right and left sides were correct for specific values of either time or number. For example, after training, red side keys might indicate a timing trial while green side keys would indicate a counting trial. Roberts and Mitchell concluded that the birds were capable of simultaneously processing temporal and numerical information since the subjects could selectively retrieve both number and time information from working memory, depending upon which was required, in order to determine the correct comparison stimulus.

Since animals can simultaneously process time and number information from a sample, a separate "event" mode for numerical processing, another switch and accumulator were added to the internal clock model (Meck & Church, 1983). The most current diagram of the internal clock model which also contains modifications to WM outlined by Roberts and Mitchell (1994) is shown in Figure 2. To account for how animals may process temporal and numerical information simultaneously, the "event" mode is assumed to have a switch (i.e., "count" switch) that stays closed for a brief period of time, "gating" or allowing a number of pulses through into a number accumulator every time a stimulus event occurs. Researchers have suggested that for rats this "event' mode switch remains closed for approximately 200 ms after the initiation of each stimulus in a sequence (Meck, Church, & Gibbon, 1985). Similar to temporal information, the pulse count in the numerical accumulator is transferred to WM and then compared with the numerical values stored in RM for numerical information in the "comparator" in order to direct the response.

Roberts, Macuda, and Brodbeck (1995) examined the possibility that the coding of temporal and numerical information in WM by pigeons made use of the same internal clock while using a separate numeric event mode. The stimuli used for their Time and Number groups can be seen in Figure 3. Using a 0-s delay at training, Roberts et al. predicted that, as the delay increases, a "choose-small" effect should be observed for a group of pigeons exposed to a number of light flashes (Number Group). This effect would be similar to a "choose-short" effect commonly observed for birds exposed to temporal stimuli during delay testing. This result was observed in the Number group. In addition, however, an unexpected "choose-long effect" for the Time Group was observed. Roberts et al. hypothesized, however, that the observed "choose-long effect" in the Time group, was actually a "choose-small effect" symptomatic of a numerical effect. In other words, Roberts et al. suggested that birds in the Time group were not attending to the total duration of the sample sequence but rather to the number of "recent" stimulus flashes.

To test this hypothesis, Roberts et al. (1995) used a consistent and inconsistent transfer contingency technique. These transfer tests switched both the Time and Number groups onto the opposite task. In addition to training the birds on new samples, the birds in each group were also assigned to two subgroups of birds. One subgroup was exposed to contingencies which were either consistent or inconsistent with the hypothesis that number was being attended to. Roberts et al. explained that the hypothesis held, for example, that a time group learned to choose the red comparison after 4f/2s because the birds remembered a relatively large number of flashes and learned to choose the green comparison after 4f/8s because they remembered a relatively small number of flashes. Therefore, Roberts et al. expected that these pigeons, in a "consistent" subgroup, would show positive transfer when transferred to number samples if the red comparison is correct after the "many" number sample, 8f/4s, and the green comparison is correct after the "few" number sample, 2f/4s. Negative transfer was expected, however, in an "inconsistent" subgroup, for those birds that experienced the same training if the colours were reversed from the above transfer comparisons. Similar predictions were also possible for transfer of the Number group to time stimuli. Subsequently, with chance performance being 50 percent (using two comparisons), both of the "consistent" subgroups were expected to perform above chance, while the "inconsistent" subgroups were expected to perform below chance. Results supported the hypothesis that the birds in the original Time group attended to the number of "recent" flashes. Specifically, the birds in both "consistent" subgroups displayed immediate positive transfer by performing above chance, indicating that when the transfer comparisons corresponded to the hypothesis that all birds were attending to the number of flashes, subjects performed accurately. As expected, birds in both "inconsistent" subgroups also showed negative transfer. The "inconsistent" group birds exhibited performance significantly below chance because their previous training encouraged them to select the comparisons which were incorrect with the transfer-test contingencies. After comparing the degree of transfer between the Time and Number groups, Roberts et al. also suggested that performance in the temporal group reflected an attentional recency effect in sequence processing. In other words the Time group focused on the number of flashes near the end of the sequence instead of considering equally the flashes presented over the whole sequence.

Recent work by Alsop and Honig (1991) supports Roberts et al.'s (1995) conclusion that a recency effect could have occurred in Roberts et al.'s study. Alsop and Honig examined pigeons' discriminative ability for the relative numerosity of flashes of blue and red light and found that stimuli that occurred later in the sequences exerted greater control than stimuli that appeared earlier. Considering Roberts et al.'s "choose-long" results for his Time group in the context of the internal clock model, it is possible that these birds used the number of flashes from the last 2 seconds of both the 2s and 8s samples, where the 2s sample contained 4 flashes and the 8s sample would contain 1 flash. It is possible that the birds may have done this if such a strategy was cognitively economical and resulted in sufficient reward over a session. If birds attended to the number of flashes in only the last 2 seconds of each trial, the accumulation of numerical "event" mode pulses in working memory would be greatest for the 2s sample, not the 8s sample. In turn, this predicts that over a delay during which pulses would be diminishing, the birds would respond to the 2s sample as if it were an 8s sample. Such responding would be expected since the "larger" number of pulses for the 2s sample would diminish, after some delay, and appear "small". Since the number of flashes over the last 2 seconds of the 8s sample would be regarded as "small", the comparison for the 8s sample would be the preferred choice over a delay. In addition Roberts et al. suggested that pulse counts may begin to diminish immediately after being transmitted. These findings may encourage future studies to examine more closely the accumulators and transmission of pulses to WM in an attempt to expand the internal clock model to account for recency effects. While a closer examination of attentional recency effects is appropriate, further validation, or refutation, of the notion that the processing of numerical and temporal information involves the same mental processes is also important.

Present Study

The first experiment attempts to determine if "choose-many effects" can be obtained similar to "choose-long effects" by training pigeons on a long baseline delay and subsequently presenting these animals with shorter delays during testing. Similar to Roberts et al.'s (1995) study, subjects were trained on a sequence of light flashes, holding time constant for one group while varying number (Number Group) and holding number constant for a second group while varying time (Time Group). Similar effects observed in number and event duration studies with pigeons would strengthen the argument that number and time are recorded by the same mechanism in general, and also highlight similarities between pigeons and rats. Dissimilar results would suggest that memory for number and time may not be recorded by the same general mechanism in the pigeon. Based on findings by Roberts et al. (1995), I did not expect, however, that the Time Group would attend to their stimuli as though they were temporal in nature. The

Time Group birds were expected to attend to the number of recent flashes.

Experiment 1

Studies by Mechner (1958) and Fetterman and MacEwan (1989) have attempted to examine the existence of counting and control by number, respectively. Both studies are inconclusive since time or duration was confounded with number. In other words, as the number of responses to be made by the animal increased, the time it took to perform the responses also increased. Following Roberts et al. (1995), the present experiment used sequences of sample stimuli that presented time and number in an unconfounded manner. To examine memory for number, one group of pigeons (Number Group) was trained to match sample stimuli based on the number of stimuli while time was held constant. These number samples consisted of 2 light flashes in 4s (2f/4s) or 8 flashes in 4s (8f/4s). To support Roberts et al.'s findings that their group designed to examine memory for time actually attended to number, a second group of pigeons was trained to match light-flash sample stimuli based on the duration of stimuli while the number of flashes was held constant (Time Group). These time samples consisted of 4 flashes in 2s (4f/2s) and 4 flashes in 8s (4f/8s). Following acquisition of these discriminations with a 0s fixed delay, subjects were shifted to a 5s fixed delay. When accuracy stabilized at this delay, subjects were tested at delays ranging from 0s to 10s.

When the birds were tested at delays longer than the 5s baseline, I hypothesized that a "choose-few" effect would be exhibited by the Number Group, resulting in a steeper retention curve for the 8f/4s sample stimulus than for the 2f/4s sample. In other words, accuracy for the "many" sample (8f/4s) was expected to drop off in a steeper fashion. In addition, when the Number birds were tested at delays shorter than the 5s baseline, a "choose-many" effect was expected for the Number Group, resulting in a steeper drop in accuracy for the 2f/4s sample stimulus than for the 8f/4s sample.

Given the findings by Roberts et al. (1995), I anticipated that the Time Group would be controlled by the number of flashes rather than by the time of the sample stimuli. If the Time Group's performance was controlled by number, as opposed to time, both a "choose-few" effect at delays longer than the 5s baseline and a "choose-many" effect at delays shorter than 5s was expected, similar to the Number group. Observing only one of these two effects for the Time Group, at either delays only shorter or only longer than the 5s baseline delay, might weaken the support for an attentional recency explanation by Roberts et al. for their Time Group's performance. Roberts et al.'s attentional recency account for their Time group might be invalid because it is reasonable to expect that subjects that attend to the number of flashes for a given period of time, for example the final 2s, should perform in a manner similar to the Number Group over delays both shorter and longer than the 5s baseline delay.

Experiment 1 attempted to further assess the notion that numerical processing by animals is related to their processing of temporal information. By employing techniques and procedures similar to those used by Roberts et al. (1995), Experiment 1 replicated Roberts et al.'s findings. Experiment 1 also tested animal numerical processes in a procedure which has only been used previously with temporal stimuli in order to test the mode-control model of timing and counting in an attempt determine whether temporal and numerical processing of sequential events can be accounted for by the same internal clock model.

Method

Subjects

The subjects were 12 experimentally naive adult White Carneaux pigeons obtained from Palmetto Pigeon Farm (retired breeders), and were approximately 5 years old at the beginning of the experiment. They were maintained at approximately 80% of free-feeding weight with constant access to grit and water, and postsession feedings of Purina Pigeon Chow were provided to maintain their target weights. Subjects were housed individually in a room kept at approximately 22°C. The colony room was illuminated on a 12:12 cycle by fluorescent light turned on at 8:00 a.m. each day. Testing was conducted for 5-6 days a week between 1000h-1400h.

Apparatus

Four Coulbourn modular operant test cages (Model #E10-10), housed individually in isolation cubicles (Model #10-20), were used. The cubicles were equipped with baffled air intake exhaust systems and ventilation fans. Each test cage was equipped with three horizontally aligned, clear plastic keys behind which projectors displayed stimuli (red, green, or white) onto a frosted rear projection screen (Coulbourn Model #E21-18). These keys required a force of approximately .25 N to operate. Directly below the centre key was a 5.7 X 5 cm opening that provided access to a hopper containing mixed grain, which was accompanied by illumination of a lamp in the feeder only during reinforcement (Coulbourn Model #E14-10 with bulb #S11819X). A houselight was located 6.5 cm above the center key such that it directed the light upward to reflect from the top of the cage (Coulbourn Model #E14-10). All experimental events and response measures were arranged and recorded by a microcomputer system in the same room.

Procedure

All birds were trained to eat mixed grain from the illuminated food hopper. After hopper training, key pecking was established through a standard autoshaping procedure similar to that of Brown and Jenkins (1968) to establish pecking at each of the side keys when illuminated with red or green light. The trial initiating stimulus and each side comparison was presented randomly and independently and remained on for 8s or until the key light was pecked. Following either 8s or a peck to the left or right side key when illuminated with a red or green light, the stimulus was turned off, resulting in 3s of access to grain. The houselight remained off throughout training and during the 45 second intertrial interval. Training began once all birds were reliably pecking the side keys on at least 85% of the trials. Any birds that did not peck the illuminated keylights by the end of the third session were manually shaped to peck the keylight for reinforcement.

Originally, the entire study involved 12 subjects, however two birds were removed due to illness. The 10 remaining pigeons were divided randomly into two groups of 5 subjects each; a Number and a Time Group. Both groups were then exposed to baseline DSMTS training modelled after Spetch and Rusak (1989) which consisted of two phases that differed only in terms of delay interval. During the first phase of training, a 0s delay between offset of the sample and onset of the comparison choice stimuli was in effect on all trials. Phase one training continued until each bird reached a criterion of at least 85% correct (overall) for at least 5 out of the last 6 sessions. The second phase was similar to the first phase except that the delay between the sample and choice was increased to 5s. Also, during phase 2, the criterion required for the birds to enter delay testing was lowered due to the difficulty of the task at the 5s baseline delay. Originally, during phase 2, the birds were required to reach the same criterion as in phase 1. At session 60, only 3 birds had managed to reach this criterion. Therefore, at session 60, the remaining 7 birds were then required to reach a criterion of 75% correct overall for 5 consecutive sessions, with no value being less than 70% on any given day. Finally, at session 66, one bird in the Number group was exposed to delay testing despite performing just below the level of the adjusted criterion (68% over the last 5 days).

During each of the two phases, the following procedure was in effect: All trials began with the projection of a white light with a small black dot in the center on the center key as a trial-initiating stimulus. A single peck to this stimulus resulted in its termination and the presentation of the illuminated houselight as the sample stimulus. The houselight flashed on and off throughout a sequence; each light flash lasted for 200 ms, with flashes spaced at equal intervals throughout a sequence. On each day of both phase 1 and phase 2 training, pigeons in the Number Group were presented with the 8f/4s sample and the 2f/4s sample for 24 trials each, with green being the correct choice after 8f/4s and red as the correct choice after 2f/4s (48 total). The left-right positions of the red and green keys were balanced within the trials devoted to each sample sequence. The sample sequences of light flashes are shown in Figure 3, with each sample sequence ending on the right side of the figure at the point where comparison stimuli would appear during training.

On each daily session of both phase 1 and phase 2 training, pigeons in the Time Group had the 4f/8s sample presented on 24 trials and the 4f/2s sample presented on the other 24 trials, with these trials randomly intermixed. Red and green lights appeared on the side keys as comparison stimuli after each sample, with green being the correct choice after 4f/8s and red being the correct choice after 4f/2s. The left-right positions of the red and green keys were balanced within the trials devoted to each sample sequence. Correct choices led to 3s access to grain from the food hopper followed by the initiation of the intertrial interval (ITI). The intertrial interval, spent in darkness, was 45s. An incorrect response resulted in a 3s blackout followed immediately by the presentation of the same sample stimulus and subsequent comparison stimuli (correction procedure). This correction was repeated continually until a correct response was made. A correct response during a correction trial resulted in 3s access to mixed grain, although only noncorrection trials were used in the analyses. All sessions ended upon completion of 48 trials, or after a maximum of 75 min.

After acquisition of matching at the 5s baseline delay was complete, pigeons in both groups were given 20 days of testing at several delays. Within a daily session of 48 trials, delays of 0, 2.5, 5, 7.5, and 10s were placed between the end of a sample sequence and the presentation of the comparison stimuli. Delay intervals were tested in random order, with delays 0, 2.5, 7.5, and 10s being tested on 2 trials with each of the two sample sequences. In addition testing at the 5s baseline delay was conducted on 16 trials with each of the two sample sequences. This distribution of delays (66% baseline delay, 33% other delays) was used so that the reference memory of temporal and numerical samples and their association with the comparison stimuli established during 5s baseline delay training would remain stable during testing (Spetch & Wilkie, 1983). As in training, correct responses were rewarded and incorrect responses were not rewarded. During delay testing, the correction procedure was only used for 5s baseline delay trials. Sessions ended upon completion of 48 trials, or after a maximum of 75 min. The level of significance used for all statistical tests was $p < .05$.

Results

Acquisition of Phase 1 (0s Baseline Delay)

Overall acquisition by birds in both groups proceeded from approximately 50% (chance) accuracy on Session 1 to over 90% accuracy by the final session of training, as illustrated in Figures 4 and 5 for the Number and Time groups, respectively. Analyses of the number of sessions to reach the Phase one criterion (of at least 85% correct for 5 out of the last 6 sessions) revealed that the Number group (M = 12.6 sessions) did not differ from the Time group (M = 11.6 sessions), $F < 1$. Using each bird's final day of acquisition, accuracy was 98.33% for the Number group and 91.25% for the Time group. After each groups' mean percent correct was collapsed across sample type, an ANOVA showed these group means to differ significantly, $F(1, 8) = 41.26$, $MS_e = 3.04$.

Separate analysis of the data for the Number group and Time group did not reveal any effect of sample type for either group, F's < 1. Therefore, as expected, at the end of Phase 1 training, the Number group's accuracy on 2f/4s (few) trials (M = 98.33%) was the same as accuracy on 8f/4s (many) trials (M = 98.33%), and also the Time group's accuracy of performance on 4f/2s (short) trials (M = 90.83%) was similar to accuracy on their 4f/8s (long) trials (M = 91.67%).

Acquisition of Phase 2 (5s Baseline Delay)

Overall acquisition for both groups proceeded from approximately 50% accuracy (chance) on the first session of 5s baseline training to over 85% accuracy during the final session of Phase 2 training, as illustrated in Figures 6 and 7. Figure 6 also illustrates that Bird 2 failed to acquire the discrimination to as high a level as the other Number birds, and for unknown reasons Bird 4 performed very poorly on one day during Phase 2 acquisition. On the final day of Phase 2 acquisition, the mean levels of accuracy were 86.67% correct for the Number group and 86.25% correct for the Time group. When the groups' percent correct was collapsed across sample type for both groups, an ANOVA did not show the group means to differ significantly, F < 1.

Separate analysis for the Number group and Time group did not reveal any effect of sample type for either group, F's < 1. Therefore, as expected, at the end of Phase 2 training, the Number group's accuracy on 2f/4s (few) trials (M = 85.84%) was similar to accuracy on 8f/4s (many) trials (M = 87.5%), and also the Time group's accuracy on 4f/2s (short) trials (M = 89.16%) was similar to accuracy on 4f/8s (long) trials (M = 83.33%).

Additional Analyses

In order to help determine whether the birds were attending to the number of samples or were timing some element of the samples performance was considered when both groups were shifted from the 0s to the 5s baseline delay. Figures 8 and 9 illustrate the percent correct for each sample type for the five days before and the five days after the shift to the 5s baseline delay, for the Number group and Time group, respectively. Although a general decrease in accuracy might be expected for both groups following the shift, it is also expected that a sudden shift in training from no delay to a baseline delay longer than previous should produce a significantly larger drop in accuracy for one of the samples relative to the other. Specifically, if both groups were attending to the number of flashes comprising the sample, as originally hypothesized, the Number group's accuracy should initially drop significantly more on its "many" (8f/4s) sample and the Time group's accuracy should decline more on its "many", referred to here as "short", (4f/2s) sample. The predictions for both groups' would be in accordance with the internal clock model since the numerical samples would shorten due to the loss of pulses from working memory over the 5s delay, in contrast to their usual 0s delay, causing both groups to judge both of their samples to be "few". Upon inspection of Figures 8 and 9, these hypotheses appear to be supported for the Number group, but not for the Time group.

A phase X sample type analysis (ANOVA) revealed a highly significant effect of phase for both the Number and Time groups, *F*'s (1, 16) = 468.58 and 254.23, MS_e's = 15.82 and 21.53, respectively, and a significant main effect of sample type for the Number group, *F* (1, 16) = 5.46, MS_e = 15.82, but no significant main effect of sample type for the Time group, *F* < 1. More importantly, analyses did reveal a significant phase X sample type interaction for the Number group, *F* (1, 16) = 10.71, MS_e = 15.82, but not for the Time group, F < 1. In other words, performance of both groups dropped when they were shifted from the 0s to the 5s baseline. However, only for the Number group was there a significantly greater drop in accuracy for one sample compared to the other. Thus accuracy for the "few" (2f/4s) sample dropped less (32.69% decrease) than accuracy for the "many" (8f/4s) sample (44.33% decrease), when shifted from the 0s baseline to the 5s baseline delay.

Delay Testing at the 5s Baseline Delay

Retention curves based on data from the 20 test sessions are shown for the Number group in Figure 10. As anticipated, these curves show evidence of a "choose-few" effect at delays longer than the baseline. Responding to both samples began at a high level of accuracy at the 5s baseline delay. At longer delays, however, the 2f/4s curve shows a slight increase in accuracy to above 90% while the 8f/4s curve drops steeply to less than 70% correct at the 10s delay. These curves also show some evidence of the hypothesized "choose-many" effect at delays shorter than the baseline. Moving in a leftward direction away from the 5s baseline, at shorter delays than the baseline, the 2f/4s curve shows a decrease in accuracy to below 75% while the 8f/4s curve remains at approximately 85% correct, at the 0s delay.

A sample type X delay analysis of variance (ANOVA) performed on the Number group's data yielded nonsignificant effects of sample type, F(1, 40) = 2.21, MS_e = 121.57, and delay, F < 1, but did produce a significant sample type X delay interaction, F(4, 40) = 4.31, MS_e = 121.57. Simple main effects were conducted to determine if any differences existed in accuracy between sample types at each delay. Although the percent accuracy for the "many" sample (8f/4s) was greater than the accuracy for the "few" sample (2f/4s) at both the 0s and 2.5s delays, which was predicted, the means for the two samples did not differ significantly at the 0s or 2.5s delay probes, *F*'s (1, 8) = 2.58 and .30, MS_e's = 139.69 and 208.12, respectively. Although the results appear to fall in the predicted direction, strictly speaking, the anticipated "choose-many" effect was not observed. Analyses did, however, support the hypotheses for the Number group's performance at the 5s, 7.5s, and 10s delays. Simple main effects revealed no significant difference at either the baseline (5s) delay, *F* < 1, or the 7.5s delay, *F* (1, 8) = 4.19, MS_e = 116.87, but did reveal a significant difference at the 10s delay, *F* (1, 8) = 18.81, MS_e = 76.56. As can be seen in Figure 10, higher accuracy for the "few" numerical sample (2f/4s) at delays longer than the baseline demonstrate the expected "choose-few" bias.

Retention curves based on data from the 20 test sessions are shown for the Time group in Figure 11. Unexpectedly these curves show no clear evidence of any response bias. In general, the accuracy for both sample types appears to be similar at each delay, with the possible exception at the 2.5s delay. Delays both shorter and longer than the 5s baseline do not appear to decrease the accuracy of performance as accuracy for both types of samples drops only just below 80% correct at the two extreme delays (0s and 10s). A sample type X delay analysis of variance (ANOVA) yielded nonsignificant effects of sample type, delay, and no sample type X delay interaction, *F*'s < 1.

Discussion

In general, the results from Experiment 1 supported the notion of the mode control model of counting and timing. When the Number group was shifted from training at a 0s baseline delay to a 5s baseline delay, an interaction of sample by phase demonstrated the predicted immediate "choose-few" effect. Therefore, at the time of shift, the birds in the Number group appeared to be counting the stimuli in accordance with the mode control model of counting and timing. The interaction term was not, however, significant for the Time group. Therefore, we were unsure how the birds in the Time group coded their sample information.

As expected, delay testing data conducted at the 5s baseline delay for the Number group demonstrated a clear "choose-few" bias at the 7.5 and 10s delays. Testing at these delays may have resulted in fewer pulses in working memory at the time of comparison, causing the birds to incorrectly perceive the "many" sample to be "few" more often. This replicates a "choose-few" bias in pigeons at test delays longer than baseline recently observed by Roberts et al. (1995) who used similar stimuli. Also as predicted, accuracy is similarly high for both "few" and "many" samples at the 5s baseline delay. In this respect, our findings are analogous to previous research on timing in pigeons by Spetch and Rusak (1989) that showed that a "choose-short" bias at delays longer than baseline was eliminated with continued training at the longer baseline delay. The model also predicts a "choose-many" bias at the 0s and 2.5s delays since these delays were shorter than the baseline delay and the number of pulses in working memory had not yet had a chance to decrease before being compared with reference memory values. This lack of usual decrease might have caused the pigeons to incorrectly perceive the "few" samples as though they were "many" more often, especially at the 0s delay. This predicted effect occurred in the expected direction, but only marginally, and was not statistically significant at either the 0s or 2.5s delays. It is possible that this study lacks the necessary power and that a less variable "choose-many" bias might have been obtained with a larger number of subjects. Perhaps more importantly, the overall trend for performance across delays for both Number samples is identical to pigeons' performance with temporal samples under similar baseline training and test delays (Spetch & Rusak, 1989). A replication of the same functions across all delays is the most compelling piece of new evidence that supports the notion that discrimination of numerical and temporal information uses similar underlying processes.

As mentioned, delay testing data at the 5s baseline delay for the Time group were less conclusive. The birds' performance produced no definitive patterns which might suggest that they attended to either temporal or numerical components of the stimuli. It is possible that the Time birds were overtrained on their task and that test delays ranging from 0s to 10s were not a large enough deviation from the 5s baseline to elicit systematic errors to the samples indicative of either timing or counting.

Experiment 2

Church (1989) outlines how investigations of timing behaviour in animals have involved biological explanations that include, in part, neuropharmacological manipulations. Empirically driven research initiated by Meck and Church (1983) encouraged Church (1989) to suggest that manipulations of the dopaminergic system produce phasic shifts in timing functions, such that an increase in the level of dopamine results in an increase in the rate of the pacemaker. In the context of the internal clock model, Church suggested that the administration of various dopaminergic drugs such as amphetamine, may result in a phasic shift by increasing or decreasing the rate of pulses emitted from the pacemaker resulting in phasic leftward and rightward shifts in responding, respectively, given that responses to the "long" comparison are recorded. Specifically, after rats, for example, have been trained on temporal samples (e.g., 2s and 8s houselight), they experience test sessions that include probe trials which present temporal samples that fall between 2s and 8s. The recording of animals' percentage of responses to the "long" (8s) stimulus during testing results in an ogive function of the duration values 2s through 8s, where responding to the 2s stimulus is lowest and responding to the 8s stimulus is highest. The dopaminergic system and the effect of amphetamine administration are of specific interest in this study.

Some researchers have suggested that administration of amphetamine to animals increases the speed of the internal pacemaker mechanism (Meck, 1983; Meck & Church, 1983; Spetch & Treit, 1984). Moreover, delay testing under the influence of amphetamine has been suggested to generate a perceived lengthening of time in the animals (Spetch & Treit, 1984). Although a study by Santi, Weise, and Kuiper (1995) found an effect of amphetamine on memory for event duration, they did not, however, observe evidence suggesting that d-amphetamine increased the speed of the internal clock. Instead Santi et al. found that administration of amphetamine yielded a general disruption of attention to temporal samples for both pigeons and rats. Specifically, both pigeons and rats were trained to discriminate 2s and 8s sample durations. If amphetamine simply speeds up the pacemaker, then administration of the drug would yield a reduction in the magnitude of the "choose-short" effect typically observed over delays greater than the 0s baseline delay. Santi et al. did not observe this effect. Rather, amphetamine reduced the accuracy of temporal memory even at the 0s delay suggesting a general disruptive effect of the drug. The failure to observe an increase in perceived duration can also be seen in two other amphetamine studies (Rapp & Robbins, 1976; Stubbs & Thomas, 1974) that used different test paradigms and examined different species (rats and pigeons, respectively). Results from these studies also suggested that d-amphetamine appeared to markedly disrupt performance on temporal discrimination tasks in perhaps a more general manner, including an increase in the latency to respond.

There is a lack of agreement regarding conclusions about amphetamines' impact on the speed of the theoretical pacemaker. Similar to Experiment 1, Experiment 2 tested the adequacy of the mode control model's prediction that the manipulation of a variable should affect memory for the number of events in the same manner as memory for time. Such findings would support the notion that memory for number of events in a sequence in pigeons is coded in a retrospective and analogical fashion which is mediated by the same pacemaking mechanism. The notion that time and number processes are controlled by the same pacemaking mechanism allows predictions about both groups' performance during delay testing after the administration of methamphetamine (METH) (1.5 mg/kg). However, predictions about how methamphetamine will affect the Number group can be tested more effectively, given the inconclusive results regarding the Time Group observed in Experiment 1.

If methamphetamine causes an increase in the speed of the pacemaker, and if time in other studies, and number in the present study, are controlled by the same pacemaking mechanism, METH was predicted to produce an immediate "choose-many" effect in the Number group at the delays shorter than the 5s delay, at the 5s baseline delay and perhaps at longer delays. Although the hypothesized "choose-many" effect at delays shorter than the 5s baseline was not reliable in Experiment 1, the anticipated increase in the pacemaker under the influence of methamphetamine was expected to induce this effect. This "choose-many" effect at delays shorter than the baseline delay and at the 5s baseline delay (and perhaps at longer delays) was hypothesized if administration of METH speeds up the internal clock since this would result in a greater number of pulses than usual being present in WM at the time of comparison. This greater number of pulses was expected to lead the animals to judge the "few" sample stimulus as though it was the "many" sample, resulting in a lower accuracy for the "few" (2f/4s) sample when compared to the "many" (8f/4s) sample, at the 5s baseline delay. If a "choose-many" effect was not found at delays longer than 5s, it was hypothesized that, at least, a decrease in the magnitude of the "choose-few" effects (observed in Experiment 1) for the Number Group will occur on METH test days but not on saline test days. It is plausible that the "many" (8f/4s) samples anticipated to be judged to be "few" at the 7.5s and 10s delay, due to a dwindling of pulses over delay, may be counterbalanced by a pharmacologically induced increase in the speed of the pacemaker that may dispense pulses more rapidly. For example, if a "many" sample were to lose "x" number of pulses by a 7.5s and 10s delay, under saline, making it appear to be "few", it is possible that a METH-induced increase in the speed of the pacemaker may result in a sample being represented in WM with a high enough number of pulses such that a dwindling of "x" number of pulses would not be sufficient for the sample to be remembered as "few".

Experiment 1 yielded no conclusive evidence as to whether the Time group was attending to the temporal components of their samples or to the number of flashes comprising their samples. It may be that the Time group was attending to the number of flashes during Experiment 1, but that the birds had overlearned the task, or that the measurements were not sufficiently sensitive to detect any effect of delay. If the birds were attending to the number of flashes over the final 2s of each sample, as the pigeons in Roberts et al.'s (1995) work did, and methamphetamine does increase the speed of the pacemaker, it was anticipated that the results for the Time group would be similar to the Number group. In such a case, an immediate "choose-many" effect would be observed at delays shorter than the 5s baseline delay, at the 5s baseline, and perhaps at longer delays. Results for delay testing under saline control were expected to be similar to results from Experiment 1 for both groups.

Method

Subjects and Apparatus

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

Procedure

Due to a break between Experiment 1 and 2, the pigeons in the Number and Time groups were given 10 additional sessions of further training on DSMTS at the 5s baseline delay, ensuring stable performance in all birds before delay testing. Each sample stimulus and correct comparison stimulus contingency was the same as in Experiment 1 and the correction procedure was operative. Analysis for Experiment 2 includes the data for all birds with the exception of one subject in the Number group. Only the first 10 days (of 20) of testing were analysed for this bird due to his loss of the discrimination under saline during the final 10 days of testing. The reason for this bird's poor performance is unknown.

In each testing session, the pigeons were given either an injection of 1.5 mg/kg of methamphetamine or an injection of saline. While other studies (Santi et al., 1995; Spetch & Treit, 1984; Stubbs & Thomas, 1974) have used d-amphetamine in research similar to these experiments, the use of methamphetamine here was based both on its previous use with rats examining its impact on counting and timing (Meck & Church, 1983; Santi et al., 1995) and on the paucity of research involving this drug's effect on memory for time and number in pigeons. The dose of methamphetamine chosen was based on previous research that showed that it is below the dosage range that typically produces motoric side-effects on DMTS procedures (LeSage, Clark, & Poling, 1993).

Each test session was otherwise identical to the delay testing sessions and the delay interval manipulations used in Experiment 1. Similar to research conducted by Santi et al. (1995), all injections were administered intramuscularly (im) into the pectoral muscle 10-15 min before each test session in a volume of 1.0 ml/kg of body weight. Modelled after studies by Spetch and Treit (1984), Santi et al. (1995), and Meck and Church (1983), each subject received injections of methamphetamine and saline on alternate days. Injections were such that half of the birds received drug or saline on any given test session and that either 2 or 3 of the 5 subjects from both groups received drug on alternate test days. A total of 20 test sessions (10 saline, 10 METH) were conducted.

Results

Retraining

On the tenth session of retraining, accuracy was 83.33% for the Number group and 90% for the Time group. Analysis (ANOVA) revealed that the groups' mean percent correct, collapsed across sample type, did not differ significantly, $\underline{F}(1, 8) = 2.15$, $MS_e = 29.08$. Separate analyses for the Number and Time groups did not reveal any effect of sample type for either group, $\underline{F}$'s < 1. Therefore, as expected, at the end of retraining, the Number group's accuracy on 2f/4s (few) trials (M = 83.33%) was the same as accuracy on 8f/4s (many) trials (M = 83.33%), and the Time group's accuracy on 4f/2s (short) trials (M = 89.17%) was similar to accuracy on 4f/8s (long) trials (M = 90.83%).

Delay Testing with Saline and Methamphetamine at the 5s Baseline Delay for Number Group

Retention curves based on data from the 20 test sessions are shown for the Number group in Figure 12. As anticipated, the saline curves resemble those obtained in Experiment 1 (Figure 10), although the effects under saline are less defined. The saline curves show some evidence of a "choose-few" effect at delays longer than the 5s baseline delay. Response accuracy to both samples remained high at the 5s baseline delay. At longer delays, however, the 2f/4s curve maintains the same level of accuracy (above 80%) while the 8f/4s curve drops slightly to 73% correct at the 10s delay. The saline curves also show some evidence of a "choose-many" effect at delays shorter than the baseline. Moving in a leftward direction away from the 5s baseline, at shorter delays than the baseline, the 2f/4s curve shows a decrease in accuracy to 65% while the 8f/4s curve remains higher at 76% correct, at the 0s delay. A sample X delay X drug analysis of variance (ANOVA) did not yield a significant 3-way interaction, $\underline{F} < 1$, did reveal a significant sample effect, $\underline{F}$ (1, 80) = 9.46, $MS_e = 133.73$, but more importantly, yielded a sample X delay interaction, $\underline{F}$ (4, 80) = 3.64, $MS_e = 133.73$. Simple main effects analysis revealed that this sample X delay interaction was due to a significant effect of delay for the "few" (2f/4s) samples only, $\underline{F}$ (4, 40) = 5.12, $MS_e = 87.26$.

The sample X delay X drug analysis of variance (ANOVA) also yielded a significant sample X drug interaction, $\underline{F}$ (1, 80) = 14.19, $MS_e = 133.73$. Figure 13 illustrates this interaction. In general, it appears that METH tends to affect performance on "many" (8f/4s) trials to a greater extent than on "few" (2f/4s) trials. Specifically, it can be seen that performance is marginally higher on "few" (2f/4s) trials under METH (M = 80.98%), relative to saline (M = 76.3%), and performance is dramatically lower on "many" (8f/4s) trials under METH (M = 65.15%), relative to saline (M = 77.9%). A simple main effects analysis indicated that performance on "many" (8f/4s) trials was significantly lower than performance on "few" (2f/4s) trials under the influence of METH, $\underline{F}$ (1, 40) = 18.48, $MS_e = 169.39$. In addition, a significant effect of condition on "many" (8f/4s) trials indicated that performance on "many" (8f/4s) trials was lower on METH days when compared to saline days, $\underline{F}$ (1, 40) = 11.23, $MS_e = 180.21$.

Delay Testing with Saline and Methamphetamine at the 5s Baseline Delay for Time Group

Retention curves based on data from the 20 test sessions are shown for the Time group in Figure 14. The saline curves show no evidence of any response bias, replicating observations in Experiment 1. Responding under methamphetamine was also surprisingly unbiased in any manner. In general, the accuracy for both sample types, under either saline or METH, appears to be similar. Delays both shorter and longer than the 5s baseline do not appear to decrease the accuracy of performance under saline or METH. Examination of Figure 14 does suggest, however, that the administration of METH slightly reduced the overall mean percent correct responding to both samples at the 0s, 2.5s, and 5s delays, relative to saline. A sample type X delay X drug analysis of variance (ANOVA) performed on these data yielded only a significant effect of drug condition, $\underline{F}$ (1, 80) = 4.21, MS_e = 183.51. Therefore, METH generally decreased the Time birds' accuracy relative to saline trials.

Discussion

In general, the saline test results from Experiment 2 tended to support the mode control model of counting and timing. As expected, the saline data for both groups resemble their delay data obtained in Experiment 1. The Number group's saline data again demonstrate delay functions on both sides of the 5s baseline delay which are similar to those functions found by Spetch and Rusak (1989) with temporal stimuli. Although the Number group's saline functions are similar to the group's results in Experiment 1, they are not however identical. The "choose-few" tendency at the 7.5s and 10s in Experiment 2 appears to have been attenuated on saline days, when compared with the magnitude of the bias from Experiment 1. The reason for the reduction in the tendency to "choose-few" at the 7.5s and 10s delays under saline is uncertain. The decrease in the magnitude of the "choose-few" tendency at the 7.5s and 10s delays under saline could be due to an improvement in the animals' ability over time to discriminate between their samples at delays longer than baseline, thus causing a decrease in the "choose-few" tendency at the longest delays. The saline data for the Time group are, again, inconclusive in implicating temporal or numerical control by samples. More importantly, considering both groups' data, Experiment 2 did not suggest that methamphetamine simply speeds up the rate of the pacemaker.

For the Number Group, at the 5s baseline delay under METH, there appears to be a "choose-few" bias as opposed to the predicted "choose-many" bias. The tendency for METH to enhance the "choose-few" trend at the 7.5s and 10s delays was also observed. In addition, METH also appeared to eliminate the slight "choose-many" bias at the 0s delay. These tendencies at each delay, however, were not examined due to the absence of the three-way interaction, so in general it may only be concluded that METH generally decreased performance on the "many" trials relative to saline, and decreased performance on the "many" trials relative to the "few" trials under METH. Therefore, it is still reasonable to conclude that the data did not support our hypothesis that the drug would simply increase the rate of the pacemaker since general performance on the "many" trials decreased, exactly contrary to predictions based on the internal clock model. Although METH administration did not generate a performance bias for response to either sample in the Time group, it is also interesting that METH appeared to generally decrease performance to both samples in the Time group.

Although the METH data, especially for the Number group, are inconsistent with the notion that METH simply speeds up the rate of the pacemaker, these data are somewhat consistent with other findings which suggest that amphetamine may cause a general disruption of attention (Lejeune, Hermans, Mocaër, Rettori, Poignant, & Richelle, 1995; Rapp & Robbins, 1976; Santi et al., 1995; Stubbs & Thomas, 1974). Inattention to some of the samples at any delay may result in an increase in the birds' tendency to "choose-few" on trials in which they were presented with the "many" sample since the pulse count in working memory might more closely resemble "few" trials. For example, a bird who only attends to part, or none, of a sample is liable to have few, or no, pulses in WM at the time of comparison. Few or no pulses in WM would be closer to the value of "few" in RM, causing the bird to perceive some of the "many" samples as though they were "few" and incorrectly select the comparison key associated with the "few" sample. Moreover, administration of METH to the Number Group appears to cause a deficit in WM leading to a loss of sample control at delay intervals longer than 0s. The point of equivalent discriminability to both samples for the Number Group seems to have shifted from the 5s baseline delay to the 0s delay.

General Discussion

Many animal studies have contributed to the current form of Church's (1983) information processing model of timing, known as the Internal Clock Model. We were interested in testing a variation on this model, most recently updated by Roberts et al.

(1994), known as the Mode Control Model of counting and timing. The latter model suggests that many of the mental processes used in timing tasks may be similar to those processes used for making judgements about the number of events presented in a sample sequence. We were interested in examining the validity of this theory of time and number. Particularly, we were interested in pigeons' ability to discriminate between time or number using different sequences of flashing lights in two different experiments to test the notion of a common pacemaking mechanism for Time and Number discrimination, and if methamphetamine (1.5 mg/kg) speeds up the rate of this hypothetical pacemaker.

Using stimuli already employed by Roberts et al. (1995), we extended his tests of numerical discrimination in Experiment 1 by shifting pigeons to a 5s baseline delay, analogous to procedures used by Spetch and Rusak (1989) to test timing in animals. After examining the birds' performance at the time of shift to the 5s baseline delay, and during delay testing using delays ranging from 0s to 10s, the Number group's data suggested that the birds were indeed counting the number of flashes in their stimuli, and that the Mode Control Model of counting and timing was consistent with the group's performance across the range of delays. The Time group's performance at both the time of shift to the 5s baseline delay and during delay testing was inconclusive. Unlike Roberts et al.'s (1995) birds, we could not conclude that our Time pigeons coded the samples numerically. In Experiment 2, administration of methamphetamine (METH) did not simply appear to speed up the rate of the pacemaker in the Number group or in the Time group. Instead, in the Number group, the administration of METH appeared to affect attention to the samples such that performance on the "many" trials was generally decreased. For the Time group, administration of METH failed to elicit any differences in drug/non-drug performance which might explain how these birds were processing the stimuli. However, if we are to assume that the birds are processing the stimuli in either an analogically temporal or numerical manner in accordance with the Mode Control Model of counting and timing, it is important to note that we did not obtain any evidence to suggest an increase in the rate of the pacemaker, but rather, METH resulted in a general decrease in performance. Therefore, the METH results from Experiment 2 contribute to a growing body of research that does not support the notion that amphetamine simply increased the rate of the pacemaker in the internal clock by increasing the level of dopamine in the brain (Lejeune et al., 1995; Rapp & Robbins, 1976; Santi et al., 1995; Stubbs & Thomas, 1974). This evidence is in sharp contrast to animal timing work which first suggested that amphetamine could be used as a "tool" to tease apart various components of the internal clock, by speeding up the pacemaker and having no other significant effects on other components in the internal clock model (Maricq, Roberts, & Church, 1981; Meck, 1983; Meck & Church, 1983; Spetch & Treit, 1984).

Originally, this experiment was designed to extend our knowledge about pigeons' ability to discriminate numerical or temporal sequences of light flashes in order to test Church's (1983) Mode Control Model of counting and timing, as modified by Roberts et al. (1994). One extension of testing was the shift of pigeons to a 5s baseline delay in order to test for a "choose-many" bias at delays shorter than the 5s baseline, analogous to the “choose-long” bias found in the timing literature (Spetch & Rusak, 1989). Although our non-drug functions were very similar in nature to the functions found in the timing literature, strictly speaking, we did not obtain the “choose-many” bias at the 0s delay. There are a number of possible reasons, but the most plausible ones involve our small sample size in each group (n = 5) and the use of a 5s baseline delay. As mentioned, the results fall in the predicted direction, but a high amount of variance may have obscured any effect. However, without simply increasing the number of birds in the group to possibly obtain significance, a larger number of test probe trials per session may be appropriate. We gave our birds 48 trials in each session of training and testing, but our pigeons could conceivably have performed up to three times as many trials on each session. We chose 48 trials/session in order to parallel previous work by Roberts et al. (1995) and Spetch and Rusak (1989). By increasing the number of trials overall, we could have had a much larger number of probe trials at each delay over the same number of delay sessions and decreased the variability at these delays. Alternatively, it is possible that the magnitude of our non-drug delay effects would have been larger if we had used a 10s baseline similar to Spetch and Rusak (1989). By using a 10s baseline instead of a 5s baseline, the distance between the baseline delay and the 0s probe would have been much larger, and may have been more effective at teasing out an obvious systematic “choose-many” bias at the 0s delay. In addition, testing could have included probe trials of 15s, 20s, again, similar to Spetch and Rusak (1989). Training at a 10s baseline delay, however, was not feasible for the birds in either of our groups. Both groups of birds had a great deal of difficulty maintaining stable and accurate performance at the 5s baseline until 60 sessions of training was given. Therefore, it seems likely that a much larger number of sessions would be required to train our birds to a high level of accuracy at a 10s baseline delay.

We presume the task of acquiring a high level of accuracy at a 10s baseline would be extremely difficult for birds in both of our groups since Spetch and Rusak (1989) were able to train their birds up to a 10s baseline by 60 sessions. Clearly, both of our groups had a more difficult task. It is possible, however, that a change in the signal carrier of the sample sequence of flashes would facilitate better performance in our birds. In order to parallel Roberts et al.'s (1995) work, our study employed an overhead bulb in the bird's chamber as the carrier of the light flashes. Instead, Spetch and Rusak (1989) used the feeder light as the carrier of the light stimulus. It is quite probable that the feeder light is more salient to pigeons, relative to an overhead bulb, due to the feeder light's association with the presentation of food. Therefore, future use of baseline delays longer than 0s in timing/number experiments should consider using the most salient carrier of information in order to train pigeons and other animals to a baseline of 5s quickly and effectively.

By conducting additional tests with the birds used in this study, it would be interesting to determine more about the Time group's strategy. The assumption in future testing of the Time birds is that they will continue to use strategies that they employed in the previous experiments. Given the current ambiguity of their strategy, any changes in procedure could also lead to a change in strategy that might go undetected. Given this possible confound, only the most basic of changes in procedure might lead to definitive conclusions regarding this group's strategy. The most obvious test would involve drug free testing at delays longer than 10s. Inspection of Figure 14 reveals that the group's performance at the 10s delay is still equally accurate at approximately 80% for both samples. This suggests that there is room for performance to decrease over longer delays, perhaps giving us more insight to their processing strategy. As suggested earlier, it is possible that the birds' in this group were overtrained in their discriminations, in which case temporal/numerical processing predicted by the Mode Control Model might only be identified at delays of 15s, 20s, or even 25s. Determining if the birds' in the Time group were attending to the temporal or numerical elements of their stimuli would be useful in further replicating Robert's et al.'s (1995) unexpected finding that the bird's attended to the number of flashes, rather than the stimulus duration, and in our case replicate this result at a baseline delay longer than 0s. Similar tests with the Number group, at delays longer than 10s, might also prove useful. Performance by the Number birds under saline in Experiment 2 observed at the 7.5 and 10s delays suggests a decrease in the magnitude of the "choose-few" bias found in Experiment 1, although the shape of the functions were generally consistent. If the birds were merely improving in their ability to discriminate their stimuli at delays longer than baseline, as suspected, testing at delays of 15s and 20s should likely tease out the original "choose-few" effect found at a shorter probe delay. If, on the other hand, the "choose-few" effect is not observed at delays longer than 10s, then the effect found in Experiment 1 might be regarded as an artifact, rather than the result of a dwindling of pulses in WM over a delay. Following these tests, training the Number pigeons with the same stimuli, but using the feeder light as the carrier of the sample information, would be interesting in an attempt to increase the birds' training to a 10s baseline delay in order to provide a potentially stronger test of the "choose-many" bias at the 0s delay.

In light of the results obtained in Experiment 2 and research by others (Lejeune et al., 1995; Rapp & Robbins, 1976; Santi et al., 1995; Stubbs & Thomas, 1974), future studies of animal timing and related numerical competence will have to be more cautious in their conclusions about the ability of amphetamine to simply increase the rate of the internal pacemaker. It is possible that future research may be more successful in finding a more specific biological explanation for an increase in the rate of the hypothetical pacemaker. One avenue of such research involves the testing of drugs that have a high binding affinity for particular receptors in the dopaminergic system. Meck (1986), for example, has suggested that particular dopamine receptors may function in relatively larger or smaller ways to increase or decrease the rate of the pacemaker. More recent research by Frederick and Allen (1996), however, has underscored the continuing need to conduct more detailed and exhaustive analyses of different drugs and doses in an attempt to understand the specific nature of the dopaminergic system's relation to the internal clock. After surveying the timing literature involving dopamineric manipulations of the internal clock, Stanford (1996) came to the same conclusion as Frederick and Allen (1996) since discrepancies between studies were probably not based on differences in procedural measures and/or methods of data analysis. Specifically, Stanford explains that prior exposure to drugs affecting the dopamine system does not seem crucial. Stanford also concluded that it is not necessary to use a psychophysical function procedure to examine aspects of the internal clock, and that correction in data analyses for response latencies in animals' performance does not account for discrepancies between studies.

Our non-drug results from Experiment 1 and our Saline data from Experiment 2 lend further support to the notion that representations of time and number may be related, and in our case mediated by the same processes of an internal clock. This exciting relation has had, and seems destined to continue having, an impact on experimental psychology and the study of both animal and human cognition. Many evolutionary uses of numerical competence and its relation to time may be found in optimal foraging for prey (Church & Meck, 1984; Fetterman, 1993). For example, in order to forage successfully, animals might keep track of the number of prey caught over a particular time spent searching in a particular area. Such a strategy might result in an animal's decision to remain and continue foraging, or instead to leave in search of richer areas of food. In research more directly tied to humans, Gallistel and Gelman (1992) have discussed interesting evidence of the rapid, but inexact, preverbal counting mechanism in animals (such as that studied here with pigeons), which may have been a necessary precursor to the development of the more accurate human verbal and written counting. Therefore, future research examining the relationship between time and number processes appears to be an interesting and fruitful avenue in filling in crucial gaps in our understanding regarding different aspects of species' evolutionary development and cognition in general.

References

Alsop, B., & Honig, W. K. (1991). Sequential stimuli and relative numerosity discriminations in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 17,* 386-395.

Bridson, S. (1990). *Evidence for common coding of temporal and nontemporal information in pigeons.* Master of Arts Thesis, Wilfrid Laurier University.

Brown, P. L., & Jenkins, H. M. (1968). Autoshaping of the pigeon's keypeck. *Journal of the Experimental Analysis of Behavior, 11,* 1-8.

Church, R. M. (1984). Properties of the internal clock. In J. Gibbon & L. G. Allan (Eds.), *Timing and time perception.* (Annals of the New York Academy of Sciences, Vol. 423, pp. 566-582). New York: New York Academy of Sciences.

Church, R. M. (1989) Theories of timing behavior. In S. B. Klein & R. R. Mower (Eds.), *Contemporary learning theories: Instrumental conditioning theory and the impact of biological constraints on learning* (pp. 41-71). Hillsdale, NJ: Erlbaum.

Church, R. M., & Meck, W. H. (1984). The numerical attribute of stimuli. In H. L. Roitblat, T. G. Bever, & H. S. Terrace (Eds.), *Animal cognition* (pp .445-464). Hillsdale, NJ: Erlbaum.

Davis, H., & Albert, M. (1986). Numerical discrimination by rats using sequential auditory stimuli. *Animal Learning & Behavior, 14,* 57-59.

Fetterman, J. G., & MacEwan, D. (1989). Short-term memory for responses: The "choose-small" effect *Journal of the Experimental Analysis of Behavior, 52,* 311-324.

Fetterman, J. G. (1993). Numerosity discrimination: Both time and number matter. *Journal of Experimental Psychology: Animal Behavior Processes, 19,* 149-164.

Frederick, D. L., & Allen, J. D. (1996). Effects of selective dopamine D_1- and D_2-agonists and antagonists on timing performance in rats. *Pharmacology, Biochemistry and Behavior, 53,* 759-764.

Gallistel, C. R., & Gelman, R. (1992). Preverbal and verbal counting and computation. *Cognition, 44,* 43-74.

Grant, D. S. (1993). Coding processes in pigeons. In T. R. Zentall (Ed.), *Animal cognition: A tribute to Donald A. Riley. Comparative cognition and neuroscience* (pp. 193-216). Hillsdale, NJ: Erlbaum.

Grant, D. S., & Spetch, M. L. (1993). Analogical and nonanalogical coding of samples differing in duration in a choice-matching task in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 19,* 15-25.

Honig, W. K. (1978). Studies of working memory in the pigeon. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior* (pp. 211-248). Hillsdale, NJ: Erlbaum.

Hothersall, D. (1984). *History of psychology.* New York, NY: Random House.

Kraemer, P. J., Mazmanian, D. S., & Roberts, W. A. (1985). The choose-short effect in pigeon memory for event duration: Subjective shortening versus coding models. *Animal Learning & Behavior, 13,* 349-354.

Lejeune, H., Hermans, I., Mocaër, E., Rettori, M., Poignant, J., & Richelle, M. (1995). Amineptine, response timing, and time discrimination in the albino rat. *Pharmacology, Biochemistry and Behavior, 51,* 165-173.

LeSage, M., Clark, R., & Poling, A. (1993). MDMA and memory: The acute and chronic effects of MDMA in pigeons performing under a delay-matching-to-sample procedure. *Psychopharmacology, 110,* 327-332.

Maricq, A. V., Roberts, S., & Church, R. M. (1981). Methamphetamine and time estimation. *Journal of Experimental Psychology: Animal Behavior Processes, 7,* 18-30.

Mechner, F. (1958). Probability relations within response sequence maintained under ratio reinforcement. *Journal of the Experimental Analysis of Behavior, 1,* 109-121.

Meck, W. H. (1983). Selective adjustment of the speed of internal clock and memory processes. *Journal of Experimental Psychology: Animal Behavior Processes, 9,* 171-201.

Meck, W. H. (1986). Affinity for the D_2-receptor predicts neuroleptic potency in decreasing the speed of an internal clock. *Pharmacology, Biochemistry and Behavior, 25,* 1185-1189.

Meck, W. H., & Church, R. M. (1983). A mode control model of counting and timing processes. *Journal of Experimental Psychology: Animal Behavior Processes, 9,* 320-334.

Meck, W. H., Church, R. M., & Gibbon, J. (1985). Temporal integration in duration and number discrimination. *Journal of Experimental Psychology: Animal Behavior Processes, 11,* 591-597.

Rapp, D. L., & Robbins, T. W. (1976). The effects of d-amphetamine on temporal discrimination in the rat. *Psychopharmacology, 51,* 91-100.

Roberts, W. A., Macuda, T., & Brodbeck, D. R. (1995). Memory for number of light flashes in the pigeon. *Animal Learning & Behavior, 23,* 182-188.

Roberts, W. A., & Mitchell, S. (1994). Can a pigeon simultaneously process temporal and numerical information? *Journal of Experimental Psychology: Animal Behavior Processes, 20,* 66-78.

Santi, A., Weise, L., & Kuiper, D. (1995). Amphetamine and memory for event duration in rats and pigeons: Disruption of attention to temporal samples rather than changes to the speed of the internal clock. *Psychobiology, 23,* 224-232.

Schultz, D. P. (1973). *A history of modern psychology.* New York, NY: Academic Press.

Spetch, M. L., & Rusak, B. (1989). Pigeons' memory for event duration: Intertrial interval and delay effects. *Animal Learning & Behavior, 17,* 147-156.

Spetch, M. L., & Treit, D. (1984). The effect of d-amphetamine on short-term memory for time in pigeons. *Pharmacology, Biochemistry and Behavior, 21,* 663-666.

Spetch, M. L., & Wilkie, D. M. (1983). Subjective shortening: A model of pigeons' memory for event durations. *Journal of Experimental Psychology: Animal Behavior Processes, 9,* 14-30.

Stanford, L. E. (1996). *Specific dopaminergic manipulation of the internal clock mechanism.* Master of Arts Thesis, Wilfrid Laurier University.

Stubbs, D. A., & Thomas, J. R. (1974). Discrimination of stimulus duration and d-amphetamine in pigeons: A psychophysical analysis. *Psychopharmacologia, 36,* 313-322.

Wertheimer, M. (1979). *A brief history of psychology: Revised.* Toronto: Holt, Rinehart and Winston.

Figure Captions

Figure 1. Information processing model of timing.

Figure 2. Information processing model of timing and number.

Figure 3. Sample sequences of light flashes (Roberts et al., 1995).

Figure 4. Acquisition for the Number group at the 0-sec baseline delay.

Figure 5. Acquisition for the Time group at the 0-sec baseline delay.

Figure 6. Acquisition at the 5-sec baseline delay (Number group).

Figure 7. Acquisition at the 5-sec baseline delay (Time group).

Figure 8. Mean percent correct for the five days before and five days after shift to 5-sec baseline delay (Number Group)

Figure 9. Mean percent correct for the five days before and five days after shift to 5-sec baseline delay (Time Group)

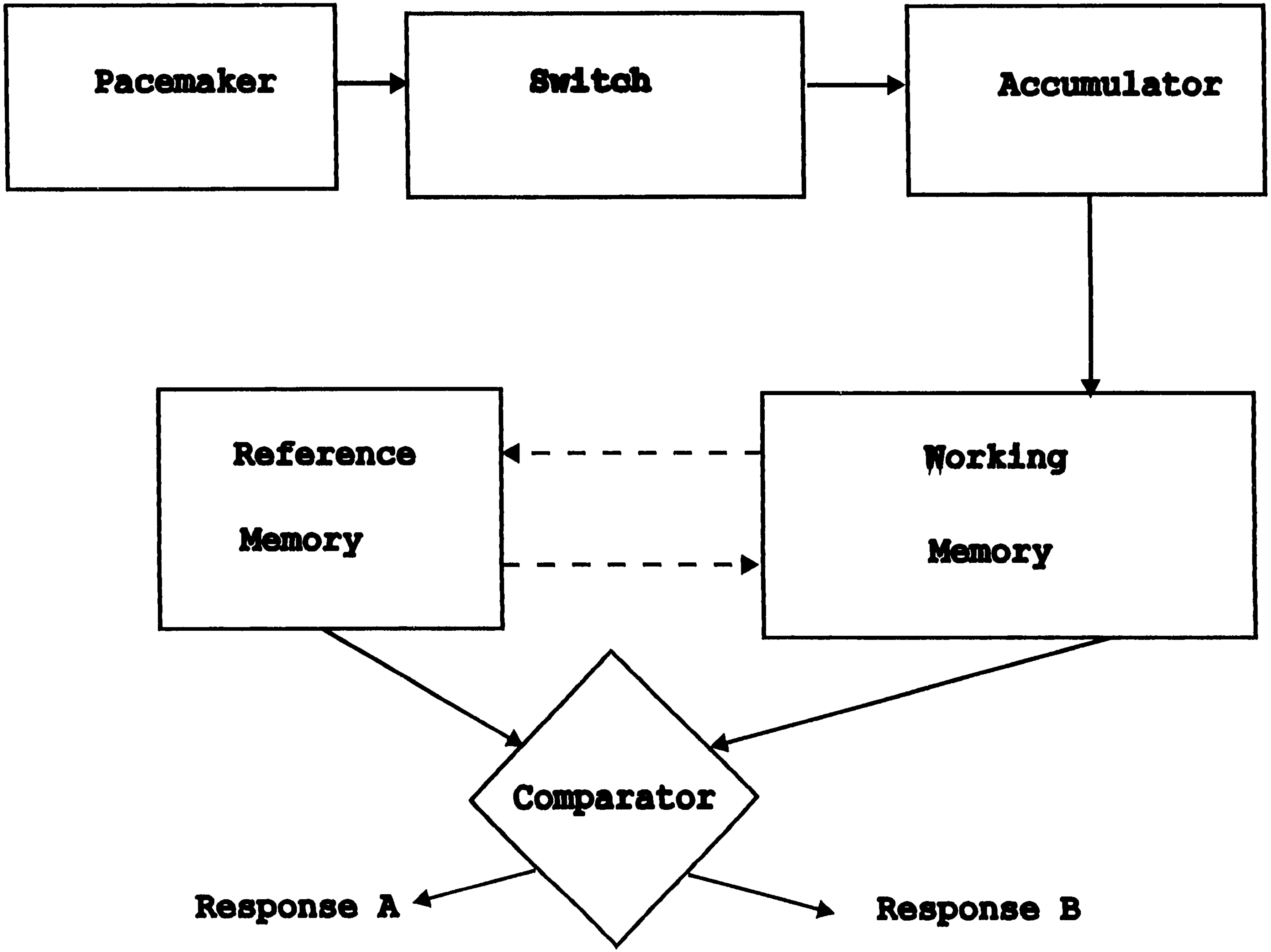
Figure 10. Mean percent correct over delay testing for Experiment 1 (Number Group).

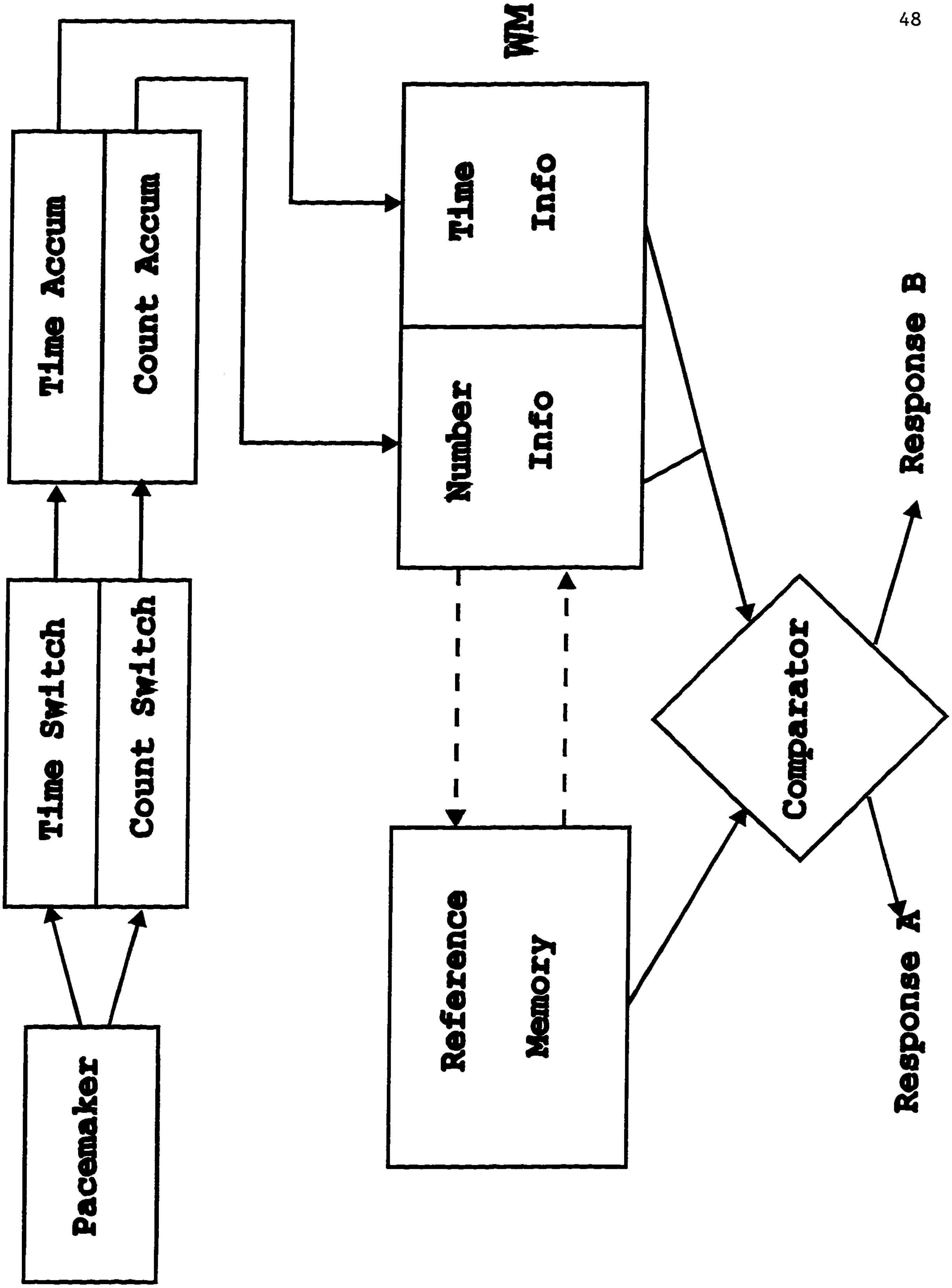
Figure 11. Mean percent correct over delay testing for Experiment 1 (Time Group).

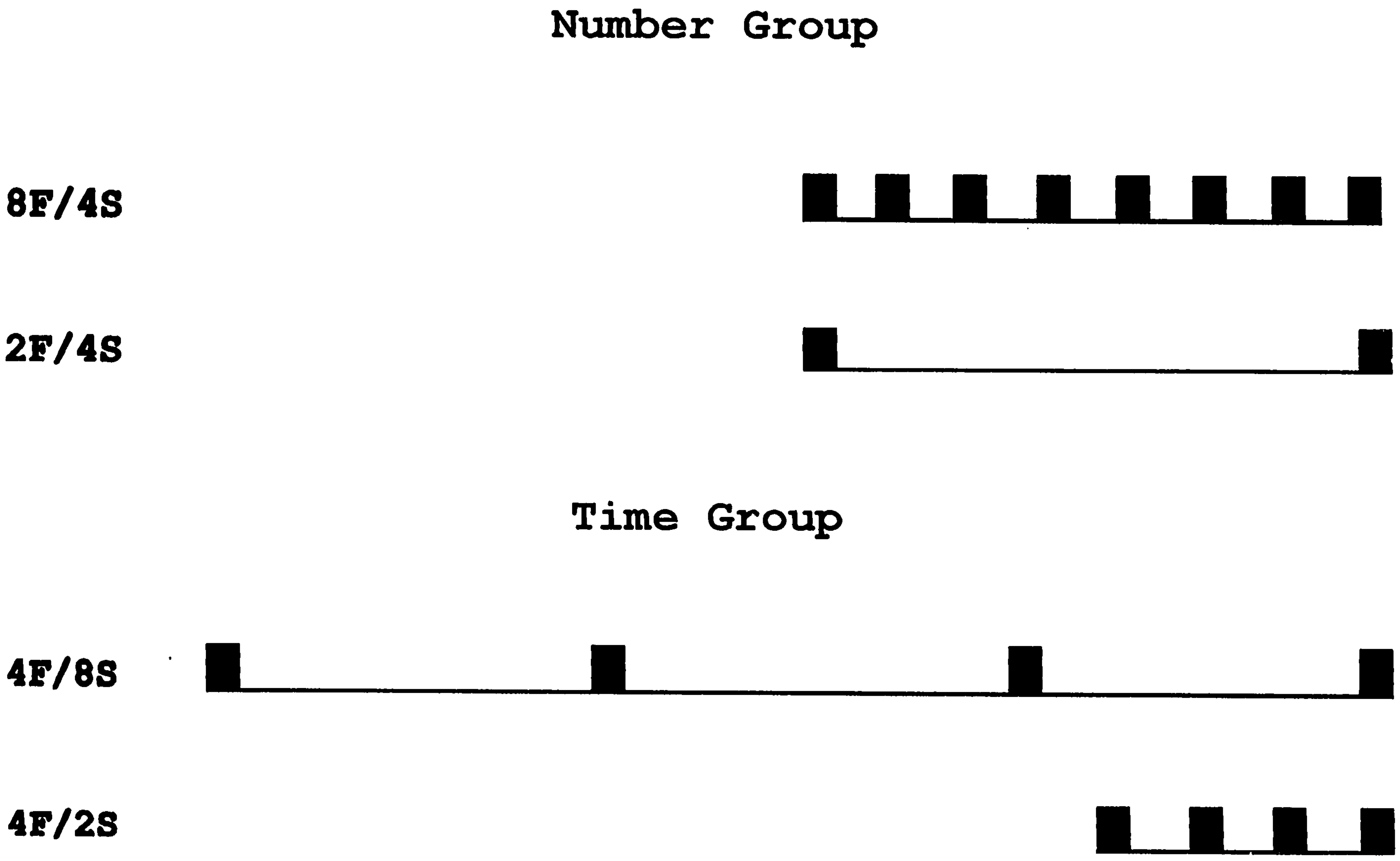
Figure 12. Mean percent correct over Drug delay testing for Experiment 2 (Number Group).

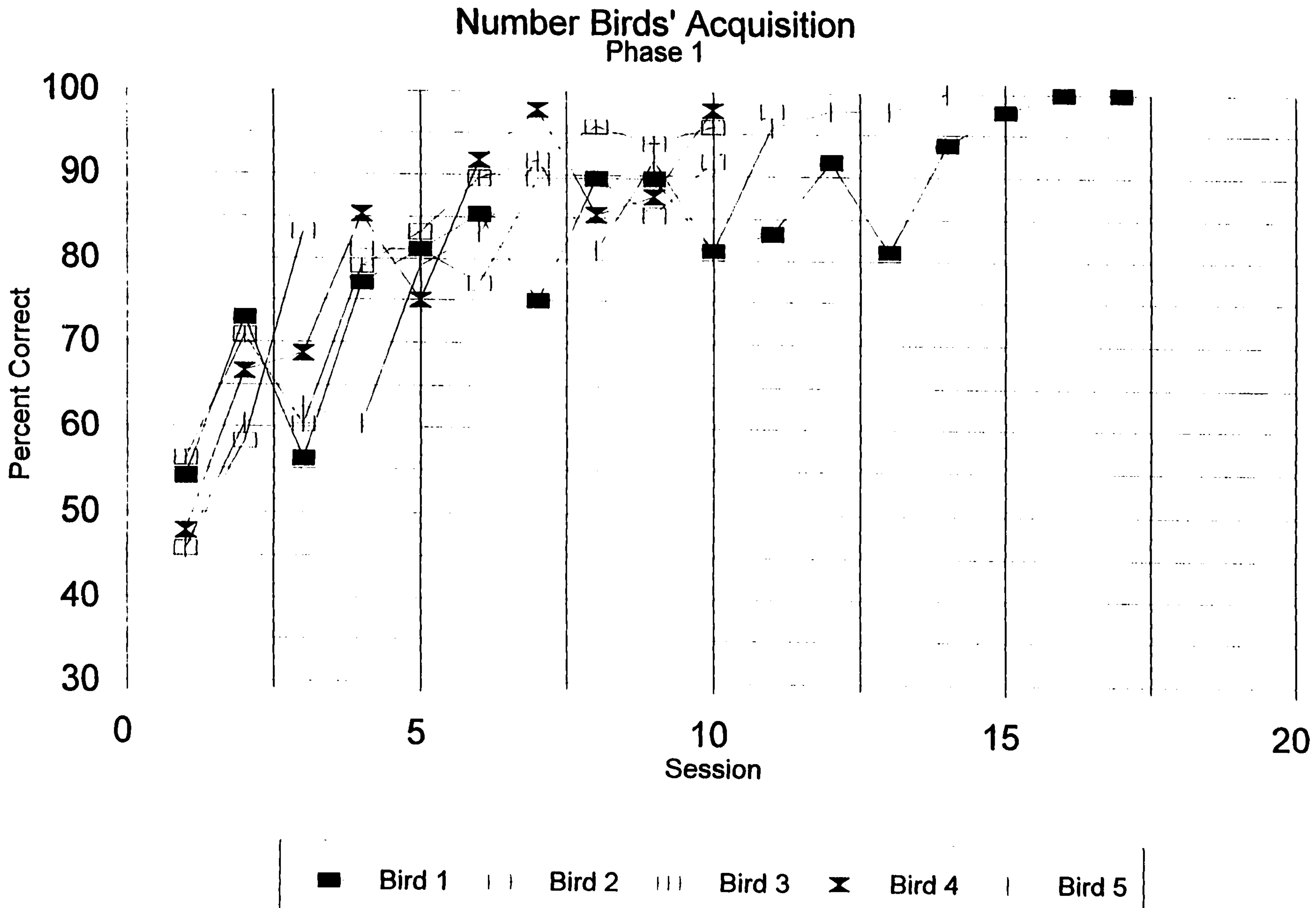
Figure 13. Sample X Drug Interaction over Drug delay testing for Experiment 2 (Number Group).

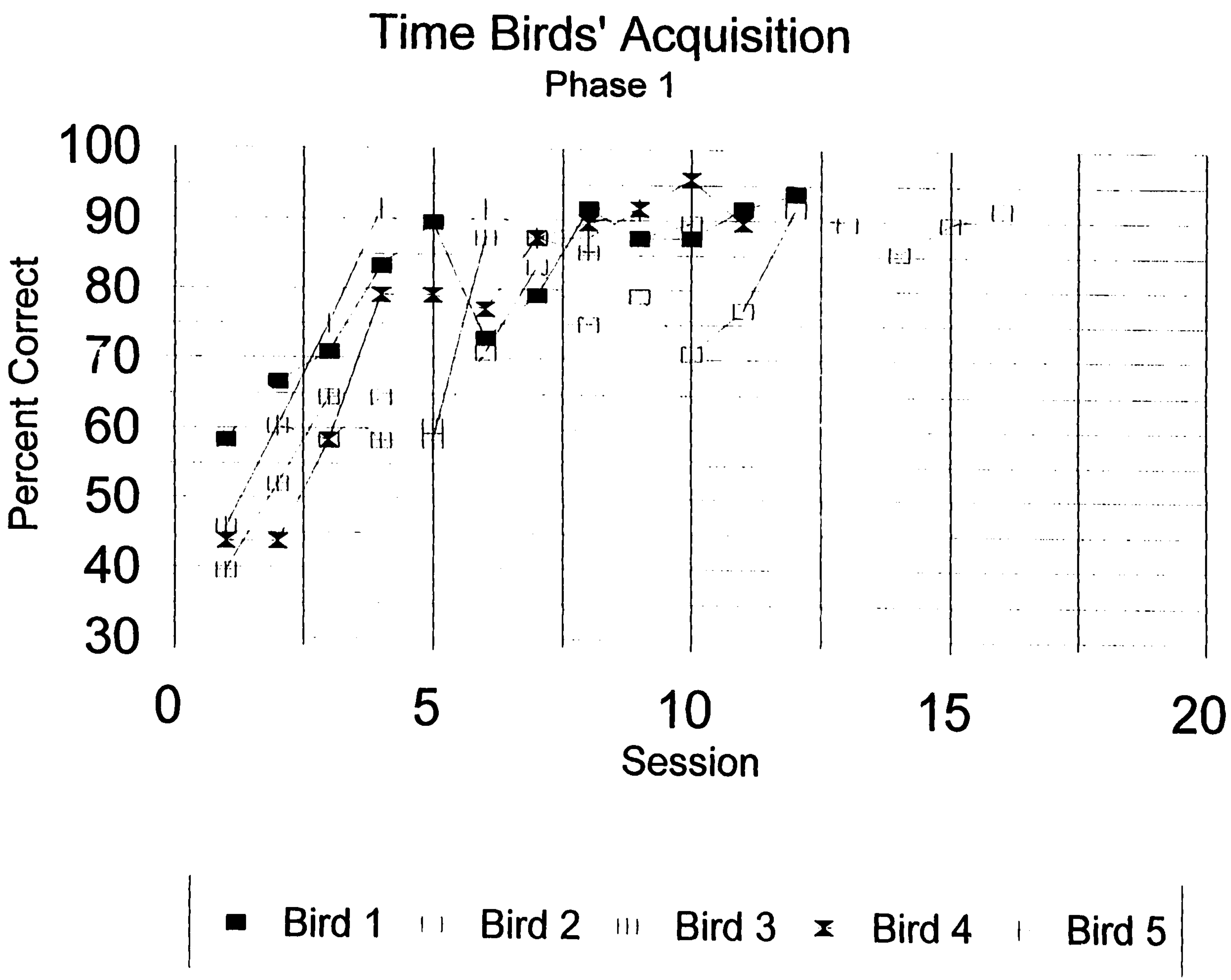
Figure 14. Mean percent correct over Drug delay testing for Experiment 2 (Time Group).


Pacemaker
Switch
Accumulator
Reference
Memory
Working
Memory
Comparator
Response A
Response B


Pacemaker
Time Switch
Count Switch
Time Accum
Count Accum
WM
Time Info
Number Info
Reference Memory
Comparator
Response A
Response B

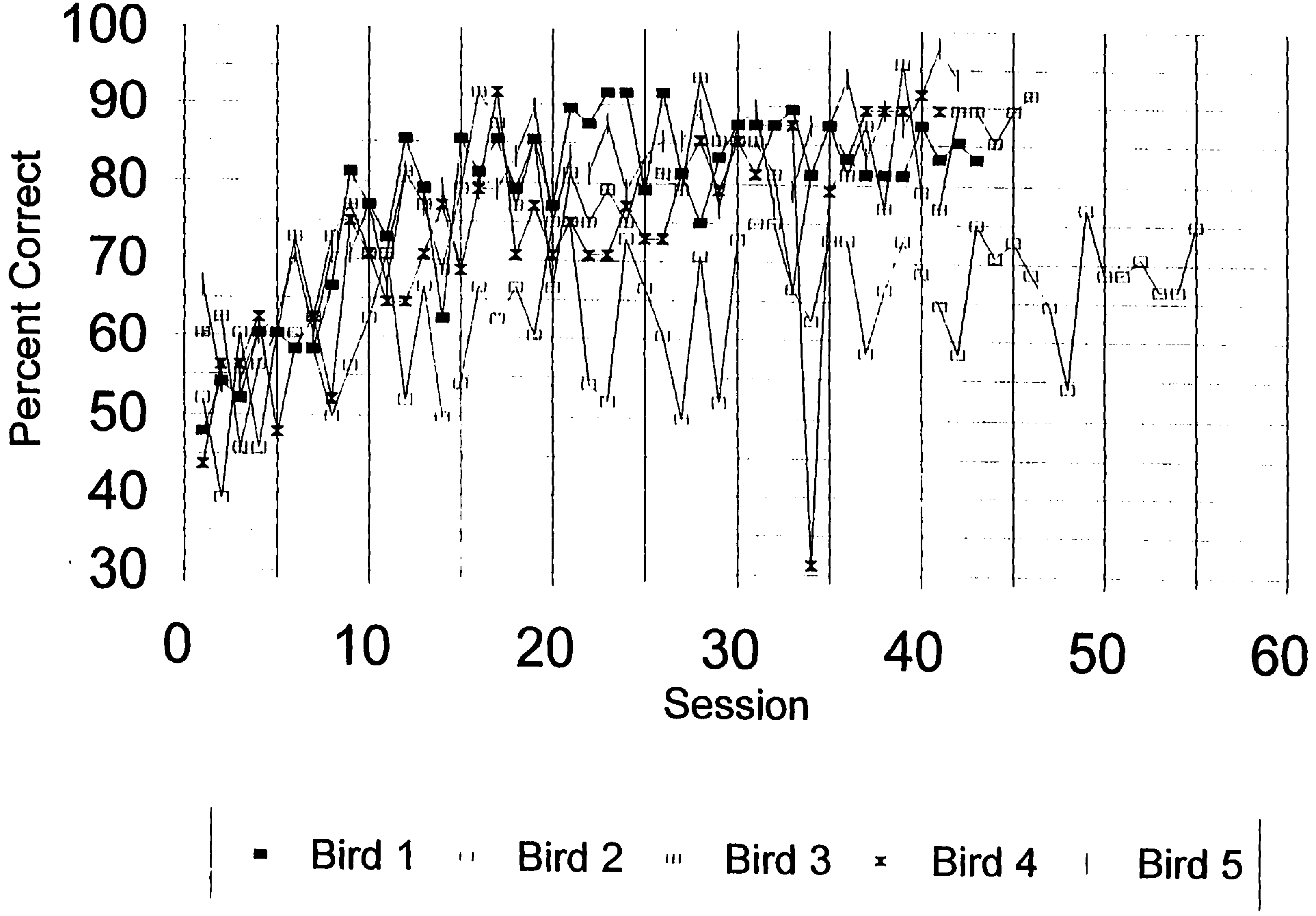

Number Group
8F/4S
2F/4S
Time Group
4F/8S
4F/2S


Number Birds' Acquisition
Phase 1
Percent Correct
100
90
80
70
60
50
40
30
0
5
10
15
20
Session
Bird 1
Bird 2
Bird 3
Bird 4
Bird 5


Time Birds' Acquisition
Phase 1
Percent Correct
100
90
80
70
60
50
40
30
0
5
10
15
20
Session
Bird 1
Bird 2
Bird 3
Bird 4
Bird 5

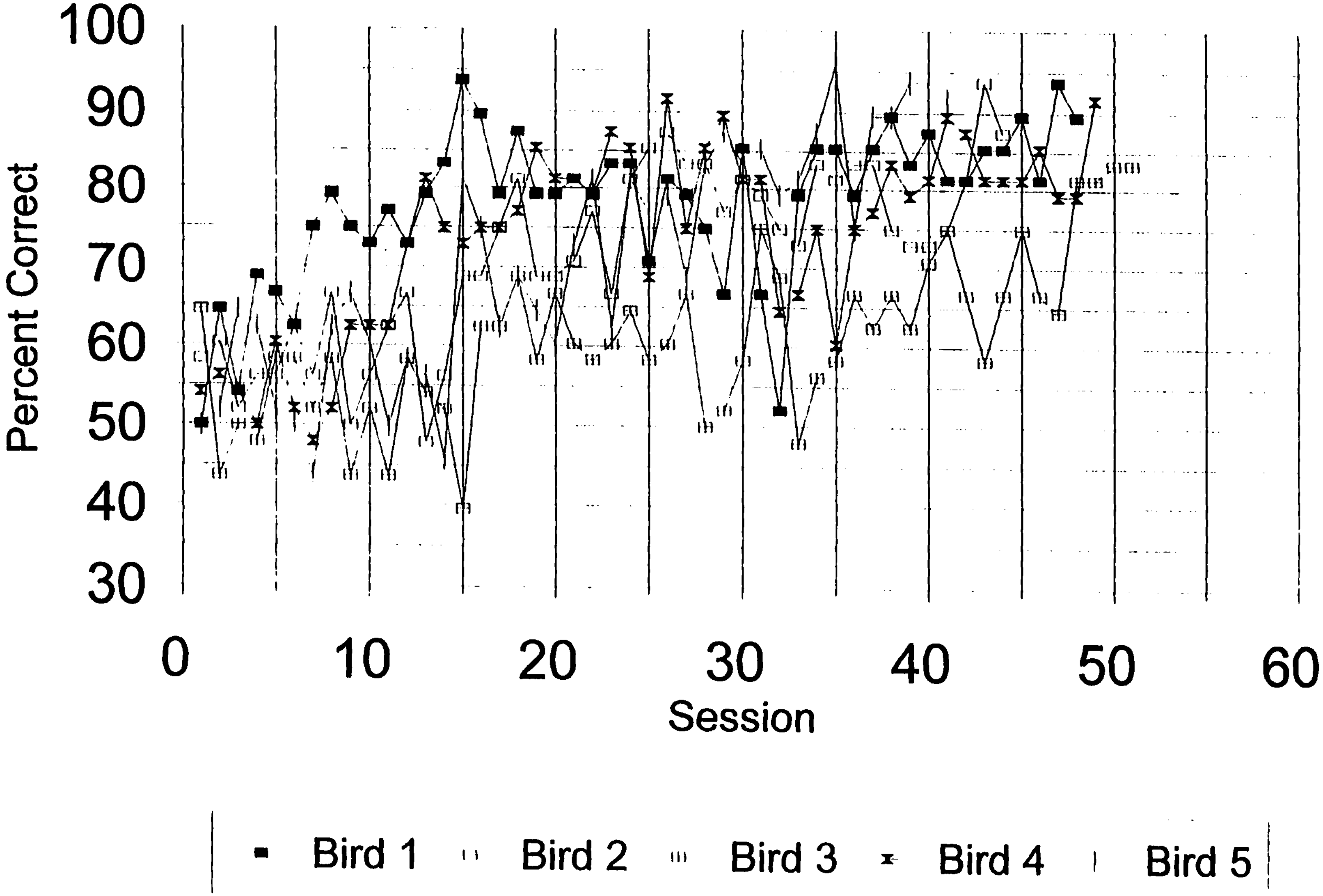
Number Birds' Acquisition

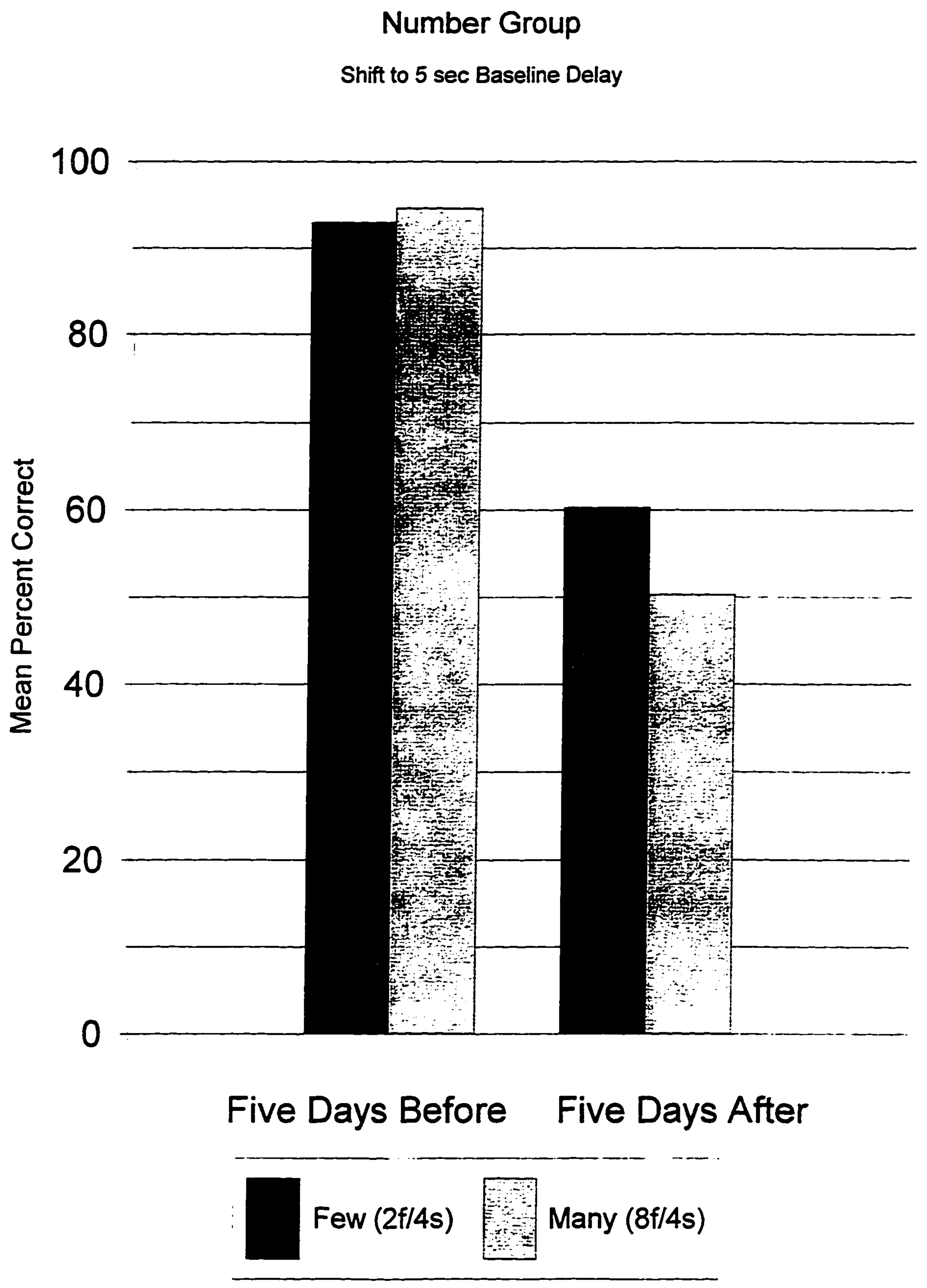
Phase 2

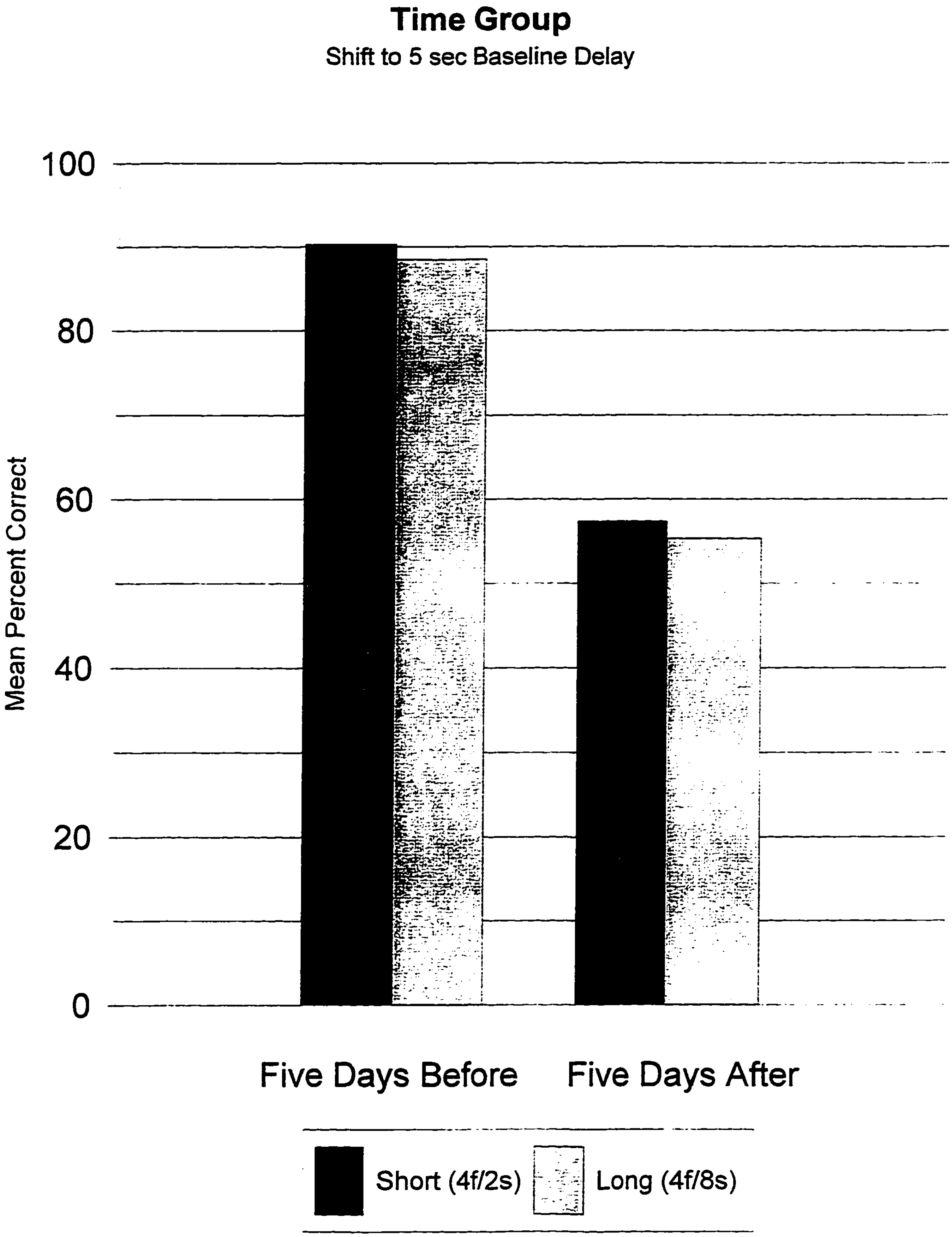


Time Birds' Acquisition

Phase 2




Number Group
Shift to 5 sec Baseline Delay
100
80
60
40
20
0
Mean Percent Correct
Five Days Before
Five Days After
Few (2f/4s)
Many (8f/4s)

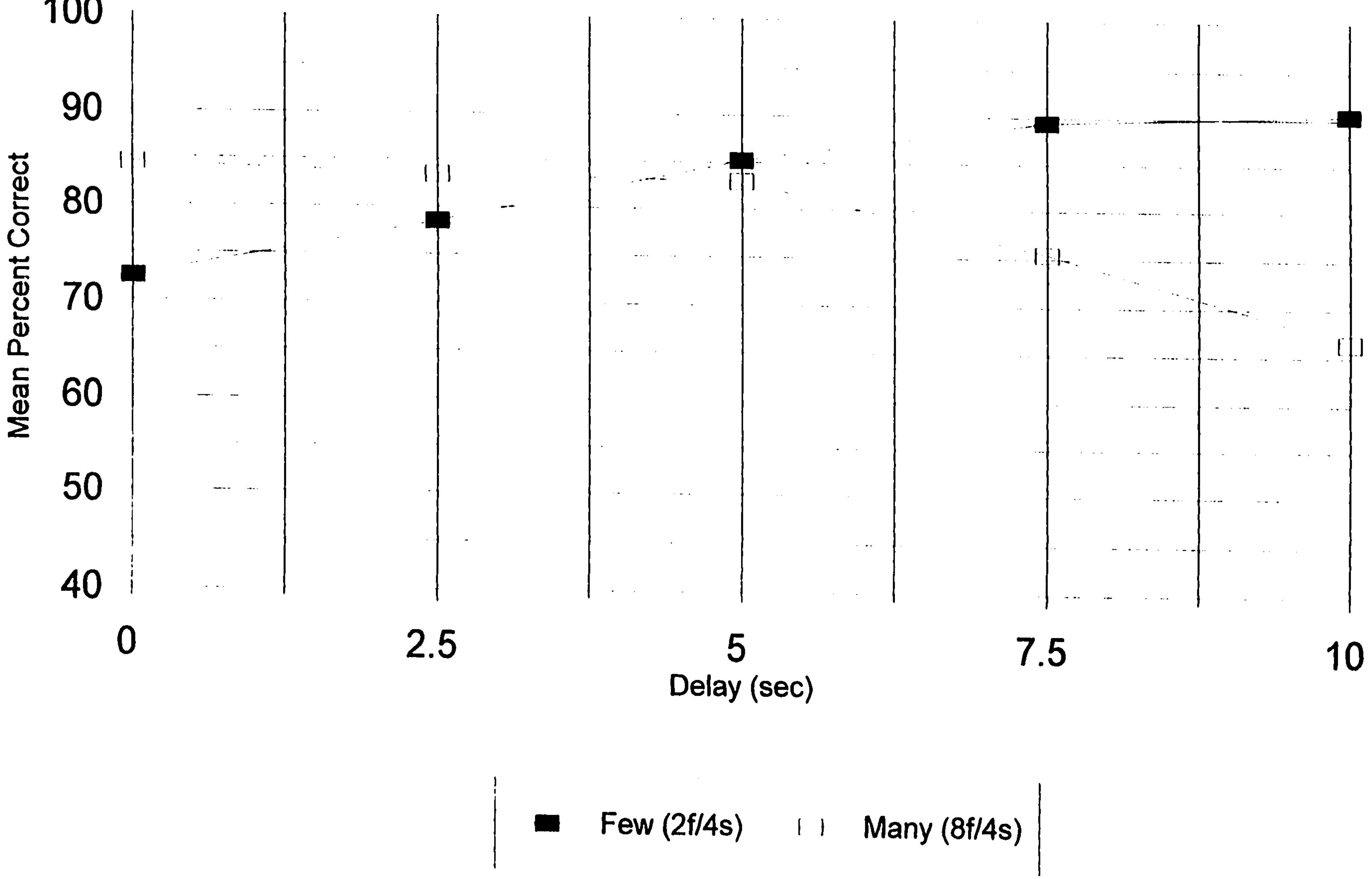


Time Group

Shift to 5 sec Baseline Delay

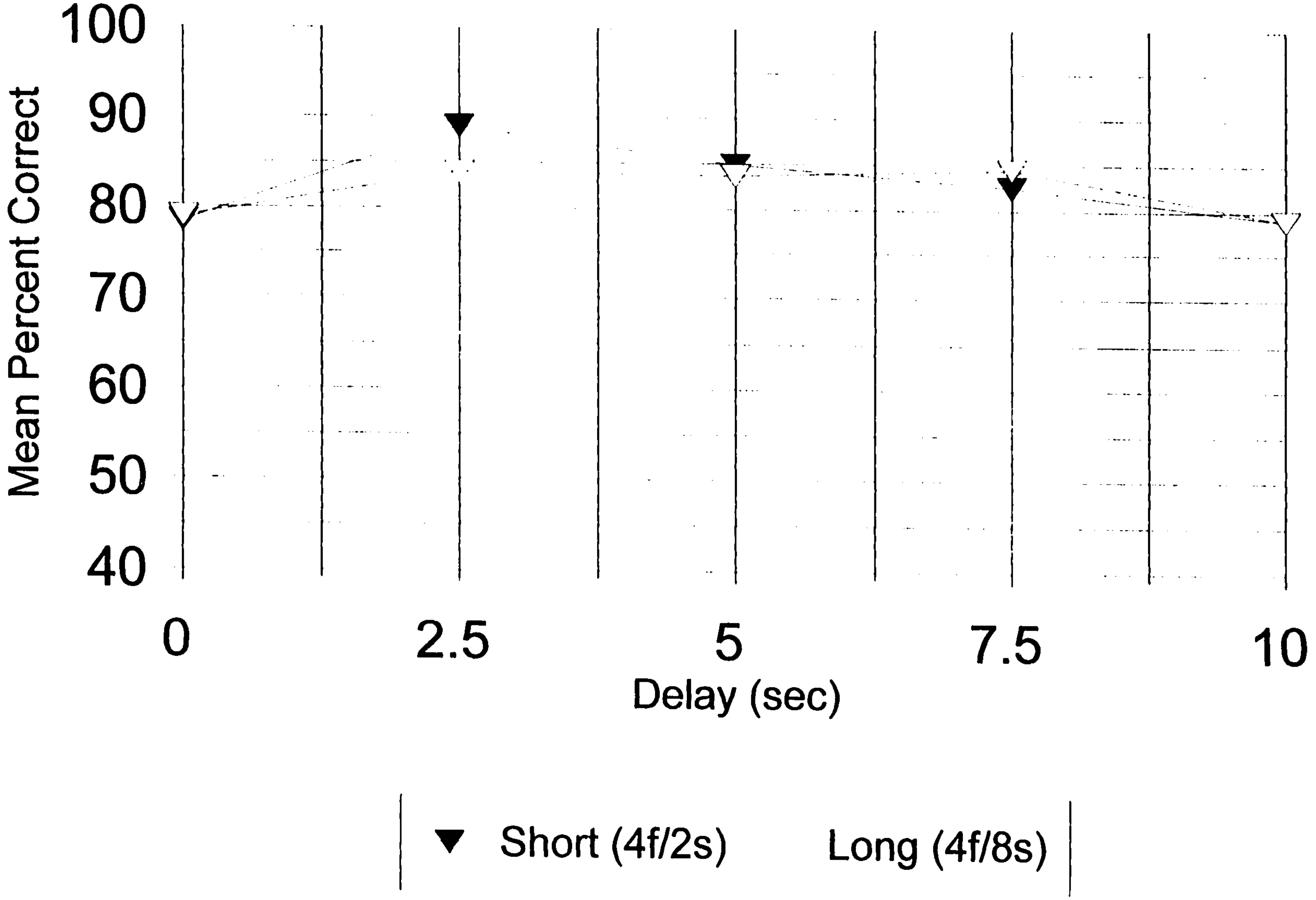
Number Group

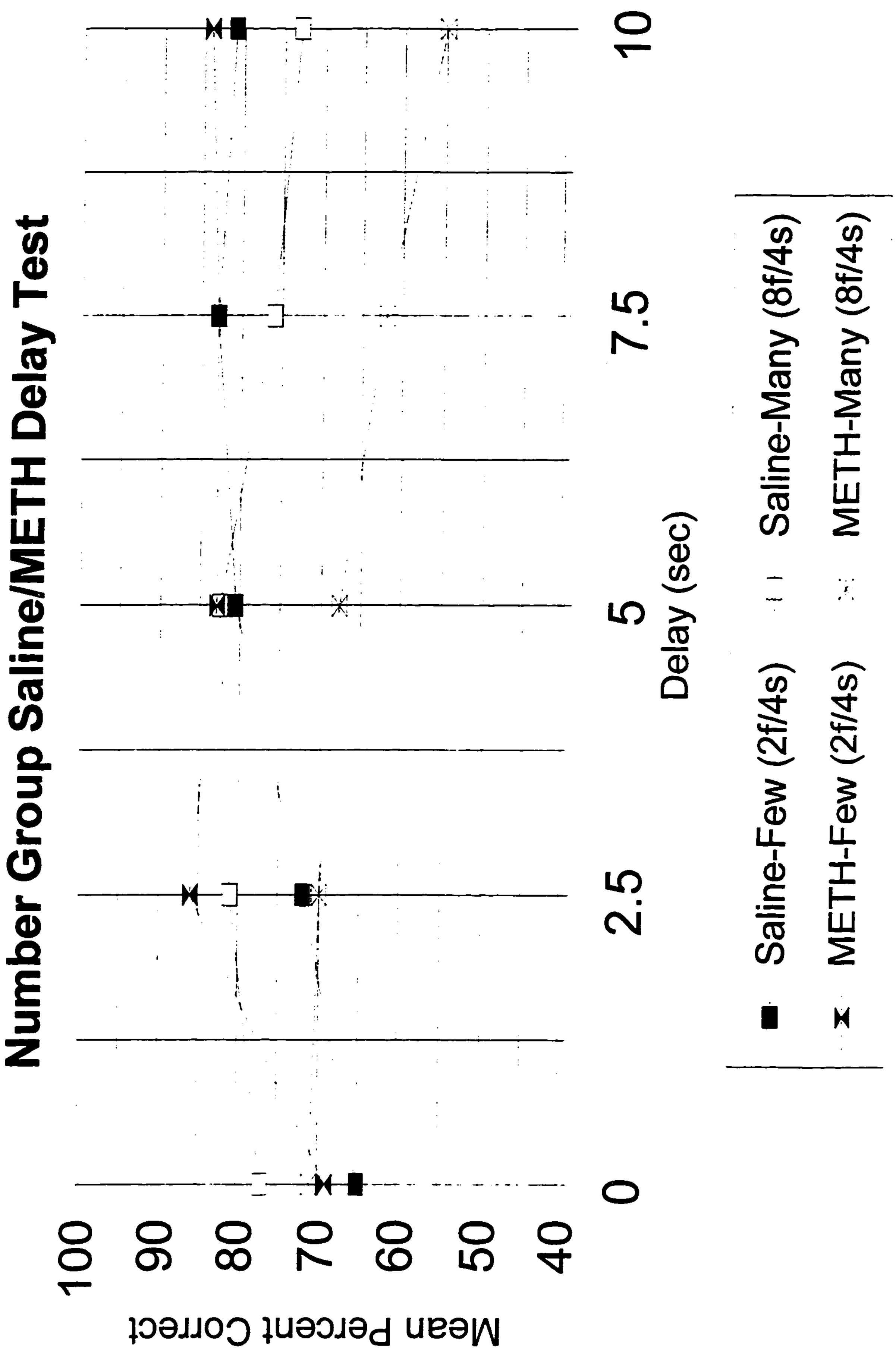
Delay Testing (5-sec Baseline)

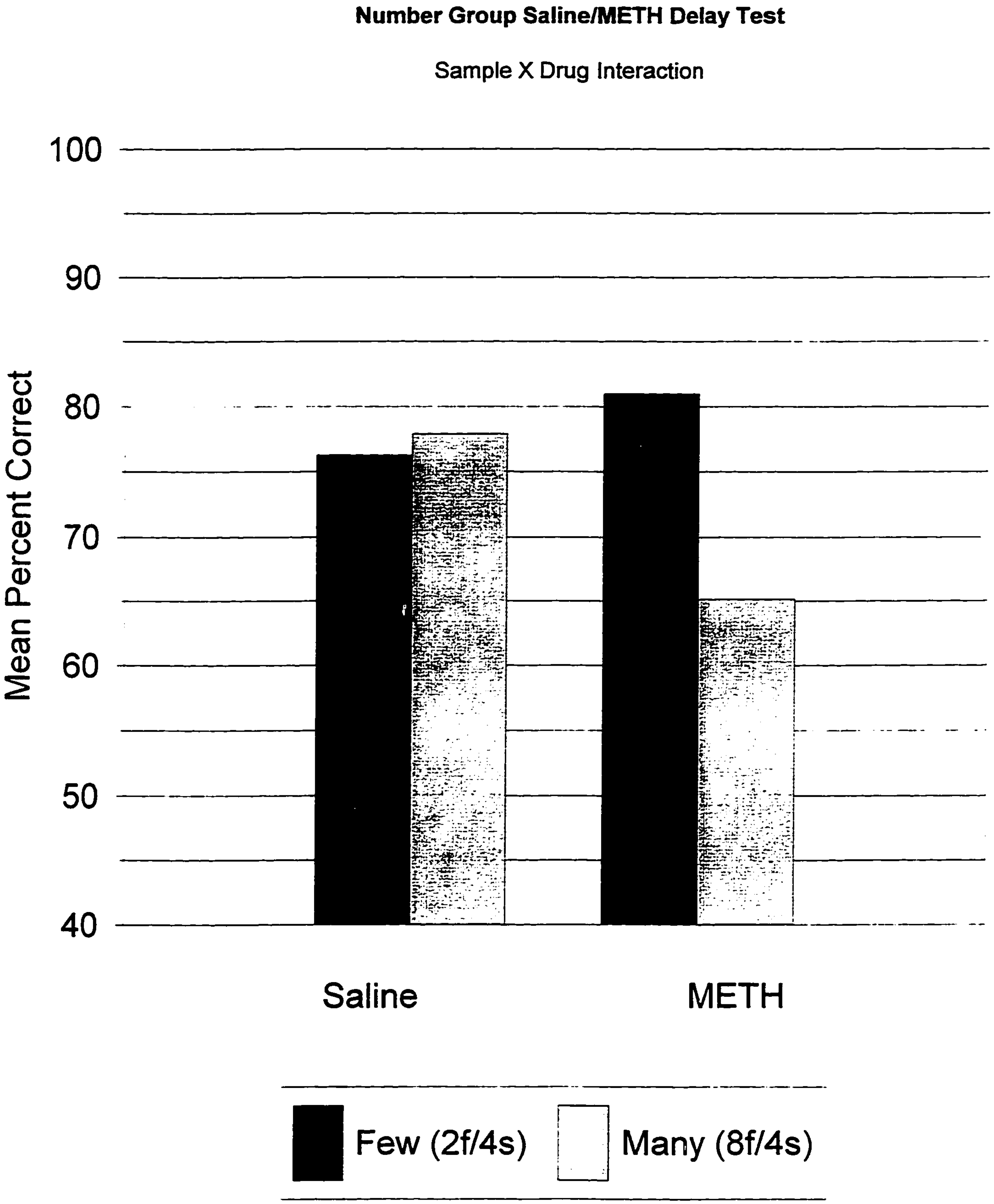


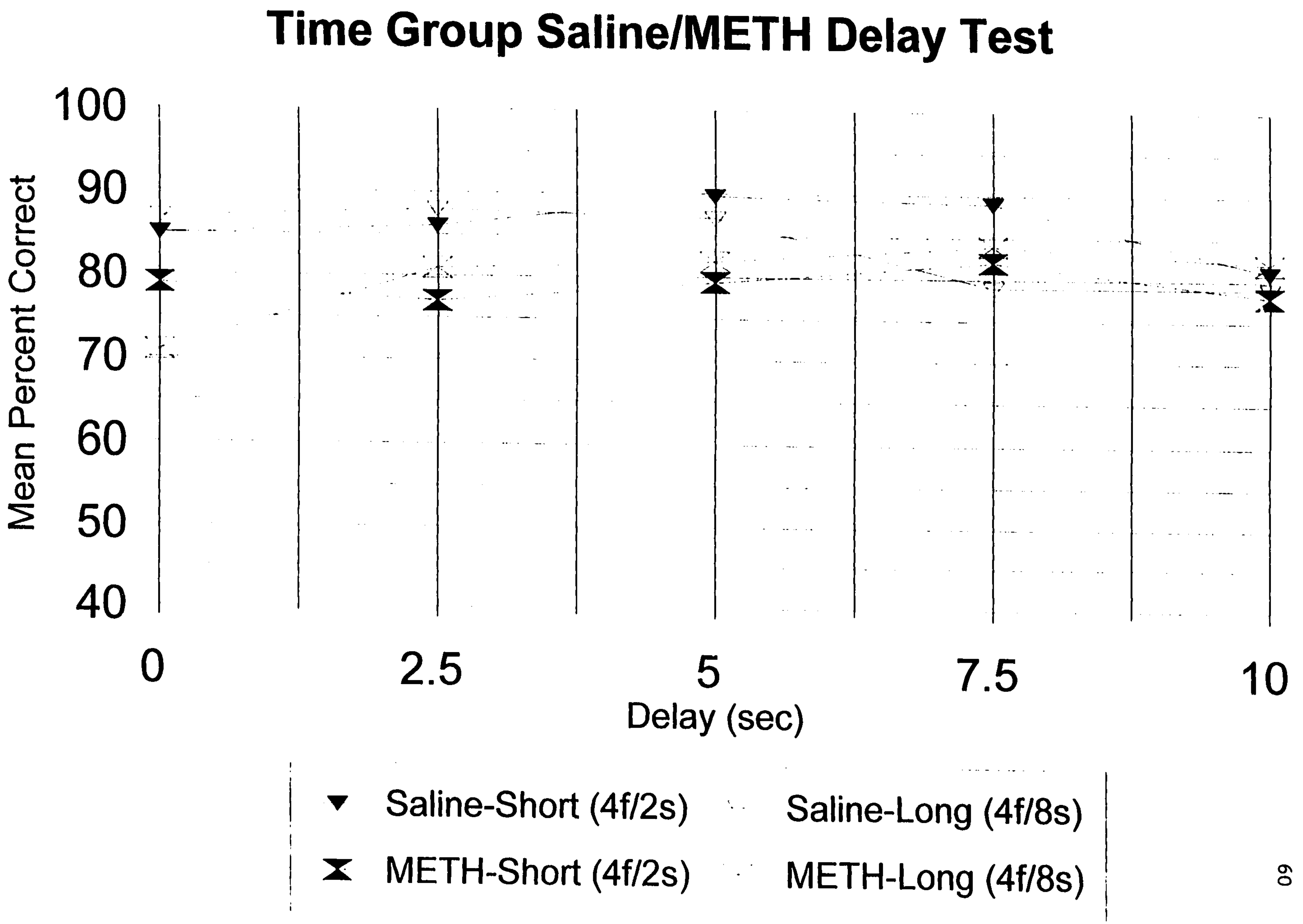
Time Group

Delay Testing (5-sec Baseline)




Number Group Saline/METH Delay Test
Mean Percent Correct
100
90
80
70
60
50
40
0
2.5
5
7.5
10
Delay (sec)
Saline-Few (2f/4s)
Saline-Many (8f/4s)
METH-Few (2f/4s)
METH-Many (8f/4s)


Number Group Saline/METH Delay Test
Sample X Drug Interaction
Mean Percent Correct
100
90
80
70
60
50
40
Saline
METH
Few (2f/4s)
Many (8f/4s)


Time Group Saline/METH Delay Test
Mean Percent Correct
100
90
80
70
60
50
40
0
2.5
5
7.5
10
Delay (sec)
▼ Saline-Short (4f/2s)
Saline-Long (4f/8s)
⧗ METH-Short (4f/2s)
METH-Long (4f/8s)