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THE UNIVERSITY OF ALBERTA

SHORT-TERM MEMORY FOR ITEM AND ORDER INFORMATION IN PIGEONS

SUZANNE E. MACDONALD

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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(Student's signature)

15107 Rio Terrace Dr.
Edmonton, AB T5R 5M6
(Permanent address)

Date: January 6, 1989

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Short-term Memory for Item and Order Information in Pigeons submitted by Suzanne E. MacDonald in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

....
(Supervisor)

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Jan O Murie

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Date: January 2, 1989

Abstract

The series of experiments reported here explored short-term memory for item and order information in pigeons using a delayed matching-to-successive-samples task (DMTSS). As demonstrated in Experiments 1 and 2, pigeons can accurately report both the identity and the order of presentation of two successively-presented samples. Experiments 3, 4 and 5 specifically addressed the representation of order information in short-term memory. Experiment 3 involved a manipulation of sample duration. When the duration of the first sample (S1) was very long, or the duration of the second sample (S2) was very short, an increase in order errors was observed, relative to baseline (S1 and S2 of equal duration). Experiment 4 involved a manipulation of interstimulus interval (ISI). The interpolation of an interstimulus delay did not systematically affect either first- or second-choice DMTSS accuracy. In Experiment 5, a series of retention intervals were introduced. First-choice accuracy decreased as delay increased, but second-choice accuracy was unaffected by delay. The decline in first-choice accuracy was accompanied by an increase in order errors. The results of Experiments 3 through 5 suggested that memory strength has an important role in the order-relevant DMTSS task. The results were discussed in terms of a two-process model of order-relevant DMTSS performance.

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I. Introduction

Most studies of visual short-term memory in animals employ tasks which assess memory for a single item. The delayed matching-to-sample procedure has been used extensively in this regard. In this paradigm, a sample stimulus is presented for a fixed duration, followed by a retention or delay interval which may vary in length. Following the retention interval, a test is presented. The retention test may involve a choice between two comparison stimuli, as in the two-choice delayed matching-to-sample procedure, and a response to the comparison which matches the sample is reinforced (e.g., Roberts & Grant, 1976). Alternatively, in the successive or go/no go version of matching, a single comparison stimulus may be presented at the time of test. In this case, comparison responses are reinforced only if the comparison matches the sample (e.g., Nelson & Wasserman, 1978). Typically, matching accuracy increases as sample stimulus exposure is lengthened and matching accuracy decreases as the retention interval is lengthened.

An important variation on the delayed matching task is the delayed matching-to-successive-samples procedure (DMTSS), introduced by Devine and Jones (1975). As the name implies, two samples are presented successively to the animal in this task. Following sample sequence presentation, three comparison stimuli are presented. The animal must choose the two comparisons that are identical with the previously presented samples, in the same order as the samples were presented. Consider, for example, a sequence consisting of a red sample followed by a green sample. After the second sample has been extinguished, comparison stimuli are presented simultaneously on three keys. To obtain reinforcement, the animal must initially choose the comparison corresponding to the first sample (in this case, red), and then must choose the comparison corresponding to the second sample (in this case, green). The third comparison stimulus serves as a distractor. Any responses to this distractor stimulus result in trial termination.

The DMTSS paradigm requires subjects to a) discriminate the particular sample sequence presented on each trial and b) produce or recall the sequence at the time of testing. To perform accurately, subjects must remember which samples were presented and the order in which the samples were presented. The DMTSS task, then, can be used to assess short-term memory for order information.

Until recently, there has been very little research on the temporal processing of events by animals, although the temporal sequence of events is a factor in most, if not all, experiments on animal learning and memory. Recently, some research has been directed specifically at the processing of sequences of events and has shown that animals can learn to discriminate and produce sequences of temporally ordered stimuli. Sequence discrimination experiments require animals (typically pigeons) to discriminate a particular sequence of stimuli from several possible alternative sequences.

Responding after only one of many possible sequences is reinforced. The results of sequence discrimination studies have shown that animals can accurately discriminate two- and three-element sequences (e.g., Weisman & DiFranco, 1981; Weisman, Duder & Von Konigslow, 1985; Weisman, Gibson & Rochford, 1981; Weisman, Wasserman, Dodd & Larew, 1980). Sequence production studies require animals (again, typically pigeons) to respond to a set of stimuli in a particular order. The reinforced order remains constant across trials, and the configuration of stimuli is varied randomly from trial to trial. A considerable amount of research has shown that pigeons can learn to produce a sequence of up to 5 elements with no explicit intratrial feedback, and can generalize this production to novel stimulus configurations (e.g., Straub, Seidenberg, Bever & Terrace, 1979; Straub & Terrace, 1981; Terrace, 1986a; Terrace, 1986b). In addition, pigeons can perform quite accurately on subsequences of the training sequence, which implies that birds do not learn chains of stimulus-response reflexes in the sequence production task. Taken together, the results of sequence discrimination and production studies suggest that birds may learn something about the relative order of elements in a sequence, and may use a representation of this order to perform accurately on these tasks (for further discussion of these experiments, see Appendix A).

Experiments addressing short-term memory for recent behavior also support the notion that animals can retain and utilize order information. The results of numerous studies confirm that pigeons, rats and monkeys can accurately "report" on their temporally-ordered recent behavior (Grayson & Wasserman, 1979; Jitsumori & Sugimoto, 1982; Kramer, 1982; Shimp, 1976a; 1976b; Shimp & Moffit, 1974; Wasserman, Deich & Cox, 1983; Wasserman, Nelson & Larew, 1980). In a representative study, Parker (1984) demonstrated that pigeons could reproduce sequences of two responses. The "sample" was two successively illuminated pecking keys. The birds were required to peck the keys as they were illuminated. Four spatial arrangements were possible (e.g., left-left, right-right, left-right and right-left). At the time of test, the birds were required to respond to simultaneously presented stimuli in the same order as they had responded to the successive elements of the sample. The birds in Parker's study were quite accurate at reproducing the orders they had seen and pecked. Further, accuracy remained at levels above chance when a retention interval was interpolated between the end of the sequence and testing.

Several researchers (e.g., Grayson & Wasserman, 1979; Shimp, 1976a) have suggested that a short-term memory concept is valuable in accounting for the results of these studies. According to their view, animals retain in short-term or working memory information about the pattern of their recent behavior, and use this memory to guide their performance at the time of testing. Implicit in this view is the assumption that the memory includes information regarding the two response elements, and the relative temporal order of these elements.

The DMTSS task is ideally suited for assessing short-term memory of order information. Unlike sequence discrimination and production studies, the DMTSS paradigm assesses short-term memory for a unique sample sequence on each trial. In discrimination and production experiments, responding to only one sequence is reinforced. It has been suggested that animals solve discrimination/production problems by comparing a short-term memory representation of the current sequence with a reference or long-term memory representation of the reinforced sequence (e.g.,Terrace, 1986a; Weisman, Gibson & Rochford, 1984). In discrimination studies, the animal will respond at the time of test if the current representation matches the reference representation. In production experiments, the animal uses its reference representation to guide its responses to a set of stimuli. In DMTSS, memory for sample items and the order of presentation of the items of a different sample sequence is tested on every trial. In this way, DMTSS is analogous to studies with humans in which short-term memory for item and order information is assessed.

Most memory research with human subjects has traditionally dealt with memory for the items in a list; that is, memory for specific content. Research on order information is directed at memory for the order in which specific items are presented. Obviously, memory for order is usually dependent upon memory for items: the items in a list must necessarily be remembered if their order is to be recalled.

The experimental separation of item and order information has generated much interest in the area of human memory (e.g., Donaldson & Glathe, 1969; Rohrman & Janke, 1965; Zimmerman & Underwood, 1968). Healy (1974; 1982) studied the recall of order information independent of recall of item information. In the "order only" conditions, item information was irrelevant to performance. The same four stimulus items were presented on every trial and the subject had to remember only the order of the items. In the "item only" conditions, order information was irrelevant to performance. Subjects were given order information in advance of each trial, so that only item information had to be learned. Serial position curves from the order-only conditions were consistently bowed or U-shaped when accuracy was plotted against serial position. Serial position curves from the item-only conditions, however, were not bowed, suggesting that the processes underlying the retention of item and order information may be independent. This finding has been replicated by other researchers (Bjork & Healy, 1974; Fuchs, 1969; Murdock, 1968).

The item/order information independence issue has been the subject of some controversy, with no clear resolution (e.g., Angiolillo-

Bent & Rips, 1982; Conrad, 1965; Crowder, 1979; Drewnowski, 1980; Lee & Estes, 1977). The results of some research indicate that item and order information may be processed independently; other research findings suggest that the two types of information may be interdependent. Regardless of the final outcome of the debate, this research has highlighted the usefulness and the theoretical significance of the item/order distinction (for further discussion of the item/order distinction, see Appendix A).

Several models of memory now incorporate both item and order information. Drewnowski (1980) has proposed an attribute model in which the sensory attributes of items are retained in short-term memory. Order information is one of the attributes of items, and functions as an important retrieval cue. This model, and others similar to it, distinguishes between item and order information, but assigns order information to a secondary role in memory. In keeping with this secondary role, most models assume that item and order information are encoded separately, but order information is lost from memory (or becomes unavailable) first, followed by loss of item information (Fozard, Myers & Waugh, 1971; Murdock, 1977; 1983; Murdock & vom Saal, 1967; Sperling & Melchner, 1976).

The hypothesis that order information is lost from memory before item information has received some support from research with animals. Devine, Burke and Rohack (1979) suggested, on the basis of error data analyses, that their rhesus monkeys remembered the sample stimulus items that had been presented on a trial even at long delays, but that the order of presentation of the samples was forgotten. Maki, Beatty and Clouse (1984), using a spatial memory task with rats, found that a long post-list delay impaired performance on an order discrimination more than performance on an item discrimination.

In the experiments reported here, short-term memory for item and order information in pigeons was explored using a DMTSS task. In Experiment 1 pigeons' retention of item information on a two-sample order-irrelevant DMTSS task was assessed. Experiment 2 examined retention of order <u>and</u> item information using an order-relevant DMTSS paradigm. Experiments 3, 4 and 5 specifically addressed the representation of order information in short-term memory using an order-relevant DMTSS task. In Experiment 3, the effect of varying sample stimulus duration on DMTSS accuracy was tested. In Experiment 4, the interval between successive sample presentations (ISI) was manipulated. The retention of order and item information across several delay values was assessed in Experiment 5.

II. Experiment 1

This experiment assessed pigeons' ability to match accurately in an order-irrelevant DMTSS task. Two sample stimuli were presented successively on the same pecking key, followed by a very brief retention interval. After the short delay, three keys were illuminated simultaneously and the bird was required to peck the two keys that corresponded to the samples. The addition of a third comparison stimulus at the time of test ensured that the birds did not simply remember one of the two samples, peck the corresponding key at the time of test and, by default, peck the remaining key. The task was essentially a modification of the DMTSS procedure introduced by Devine and Jones (1975). In their task, monkeys were required to discriminate two samples from three comparisons, but in addition, the animals were required to reconstruct the order of sample presentation. In the present experiment, pigeons were required to discriminate the two samples regardless of their order of presentation. This task, then, assesses pigeons' ability to retain multiple-item information.

Method

Subjects. Eight experimentally naive Silver King pigeons served as subjects. They were reduced to and maintained at 85% of their free-feeding weight. They were individually housed under 24-h illumination. Water and grit were continously available in the home cages.

Apparatus. The birds were tested in eight identical chambers. Three pecking keys were mounted horizontally in a row 20 cm above the grid floor in each chamber. An Industrial Electronics, Inc. in-line projector was mounted behind each pecking key and projected stimuli onto the pecking keys. A 28-v houselight was mounted directly above the center key, with the housing adjusted so that the light emitted was directed toward the ceiling. The houselight remained illuminated throughout every experimental session, except for brief (3 s) timeout periods following an incorrect test response. A grain feeder was mounted below the center pecking key, allowing brief (3 s) access to mixed grain after correct test responses. Each test chamber was enclosed in a sound- and light-attenuating enclosure. Masking noise was provided by an exhaust fan within the enclosure and by white noise delivered through a speaker in the testing room. The presentation of events within the chambers and the recording of data were controlled by microcomputers located in an adjoining room.

Procedure. The birds received preliminary magazine training and autoshaping with red, green and yellow stimuli presented on the center pecking key. Training on simultaneous delayed matching with single samples began after each bird was responding reliably.

Simultaneous matching-to-sample: Sessions consisted of 96 trials. Trials were separated by an intertrial interval of 20 s. Each trial began with the illumination of the center key by the preparatory stimulus (black dot on a white background). The preparatory stimulus was presented on the center key for 5 s, or until a response to the stimulus occurred. Termination of the preparatory stimulus was followed immediately by presentation of the sample (a red, green or yellow colored field) on the center pecking key. After 5 s of sample presentation, independent of responding, the two side pecking keys were illuminated by the comparison stimuli. One comparison was identical with the sample stimulus and the other comparison was randomly chosen from the remaining two colored fields. Thus, the sample and comparisons were illuminated simultaneously (simultaneous matching-to-sample). A single response to the matching comparison resulted in 3-s access to grain; a single response to the nonmatching comparison resulted in a 3-s timeout period during which the houselight was extinguished. Each sample was presented 32 times during each session, and position of the comparison stimuli was balanced for each sample type.

After 24 sessions of simultaneous matching, the birds were responding reliably and accurately, and zero-delay matching was introduced. The procedure was identical with that of simultaneous training, except that the sample was extinguished immediately prior to presentation of the comparison stimuli. Performance on the zero-delay task stabilized at a high level of accuracy after 20 sessions (mean accuracy for the final four-session block = 96.5 %, range = 93.2

to 99.1). Following these sessions, the birds received an additional 20 sessions of training with a short (0.5 s) delay interpolated between the offset of the sample and onset of the comparison stimuli. Mean accuracy for the final four-session block with the short delay was 93.5 % (range = 85.9 to 97.4).

Three-choice matching-to-sample: During the next stage of training, single samples continued to be presented, but the number of comparison stimuli presented on a trial was increased to three. Sessions consisted of 90 trials and were identical with those of earlier training, except that an additional stimulus was presented at the time of test, and the intertrial interval was increased to 30 s. As before, the comparison stimuli were illuminated following sample presentation and the short (0.5 s) delay. Now, however, the three colored fields (red, green and yellow) were presented as comparisons on every trial. The position of the colored comparisons was randomly determined and counterbalanced across the session. Each of the six possible stimulus configurations ((R)ed-(Y)ellow-(G)reen, R-G-y, G-R-y, G-Y-R,,Y-R-G, Y-G-R) was presented after each sample stimulus five times during the session. After 32 sessions of three-choice matching, performance stabilized at a high level of accuracy (mean accuracy for final four-session block = 93.2%, range = 85.5 to 98.0). The birds were then introduced to the matching-to-successive-samples task.

Order-irrelevant matching-to-successive-samples: In this version of the DMTSS task, the birds were required to respond to the two comparison stimuli that corresponded to the two sample stimuli on each trial, regardless of the order of presentation of the two stimuli (order-irrelevant MTSS). Sessions consisted of 72 trials. Trials were separated by an intertrial interval of 40 s, and began with the presentation of a black dot on a white background as a preparatory stimulus. The preparatory stimulus was presented on the center key for 5 s, or until a response to the stimulus occurred. Termination of the preparatory stimulus was followed immediately by presentation of the first sample on the center pecking key. After 5 s, the first sample was extinguished, followed immediately by the presentation of the second sample, also on the center key, for 5 s. A short (0.5 s) delay followed termination of the second sample. After the delay, all three pecking keys were illuminated by the choice stimuli. A single response to a comparison that corresponded to one of the two samples extinguished that keylight, leaving a choice between two remaining comparison stimuli. A single response to the comparison which corresponded to the remaining sample extinguished the remaining two keys, and resulted in 4-s access to grain. An incorrect comparison response at any time (first or second choice) extinguished the pecking keys and resulted in a 4-s timeout during which the houselight was turned off.

The two-sample sequence presented on a particular trial was randomly determined and counterbalanced across the session. Each of the six possible sample sequence combinations (R-G; R-Y; G-R; G-Y; Y-R; Y-G) was presented on 12 trials during a session. The position of the colored comparisons was randomly determined and counterbalanced across the session. Each of the six possible stimulus configurations (R-Y-G; R-G-Y; G-R-Y; G-Y-R; Y-R-G; Y-G-R) was presented after each sample sequence two times during each session. Statistical significance in this experiment, and in the following experiments, was set at the .05 level.

Results

Accuracy data

In this initial experiment, the birds were not required to peck the comparison stimuli in the order that corresponded to stimulus presentation. Reinforcement was obtained for pecking the two comparison stimuli that corresponded to the two samples, regardless of the order in which the samples were presented. The DMTSS task involves two distinct stages. The first stage involves a choice among three comparison stimuli. The chance probability of a correct first choice in this order-irrelevant task is 2/3, or .667. If, and only if, the bird responds correctly at the time of its first choice will the opportunity to make a second choice arise. The chance probability of a correct choice at the second stage is 1/2, or .50. The calculation of correct second-choices took into account the number of opportunities to make a second choice. Second-choices could only occur on trials on which a correct first-choice had been made. It is important to break down the data in this way, because overall accuracy rates (combining first and second choice accuracy) may obscure low levels of accuracy on one stage of the task. For example, a relatively high overall accuracy level may result from an extremely high accuracy rate on first choices, combined with a chance level of accuracy on second choices.

The mean percentage of correct first and second choices is shown in Figure 1 (p. 16). Mean first-choice accuracy during the final four-session block was 81.1%; mean accuracy on second choices (corrected for opportunity) was 83.9%. Both of these levels are significantly higher than chance (first choice, $t\ (7) = 4.82$, $p < .01$; second choice, $t\ (7) = 5.66$, $p < .01$). First-choice accuracy was significantly above chance (chi-square tests (1), all p's < .02) for six of the eight birds (333, 334, 335, 336, 337, 338) during the final four-session block. Second-choice accuracy was significantly above chance (chi-square tests (1), all p's < .01) for seven of the eight birds (all except 338) during the final four-session block.

In addition, a two-factor analysis of variance was performed on the combined acquisition data from all eight birds. Blocks (of four sessions) and Choice (first or second) were the factors. The main effects of Block and Choice were not significant. The Block by Choice interaction was highly significant, $F(8, 56) = 6.40$, $p < .001$, as

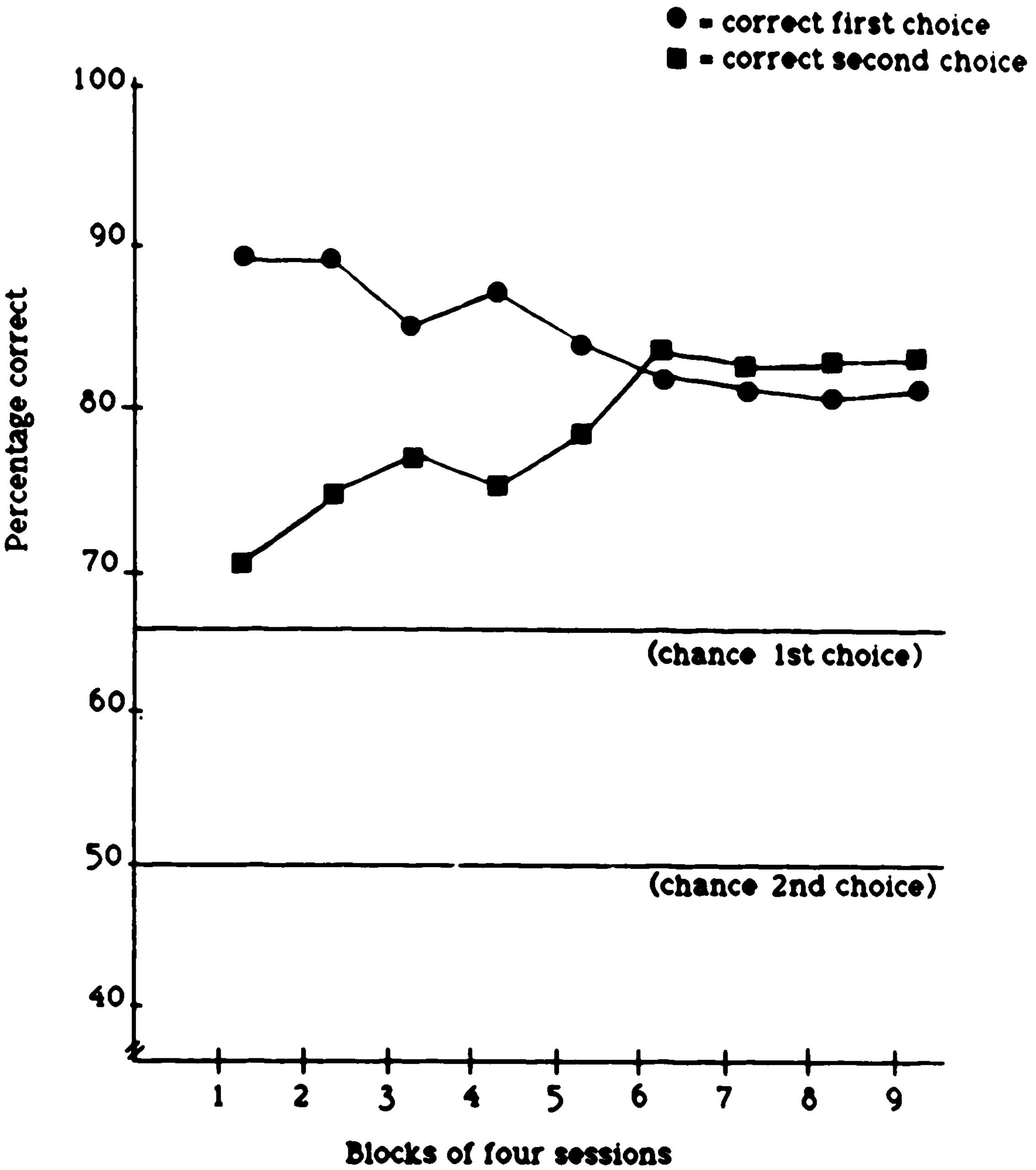

Figure 1. Mean percentage of correct first- and second-choices during order-irrelevant DMTSS in Experiment 1.

illustrated in Figure 1. Simple effects tests performed on the data indicated that the significant interaction was primarily a result of increased second-choice matching accuracy across blocks, F (8, 56) = 5.64, p< .001, combined with a decrease in first-choice matching accuracy across blocks, F (8, 56) = 4.61, p< .001.

Error data

There is only one type of error that can occur in this particular task. Because reinforcement is delivered for pecks to the comparisons corresponding to the samples, regardless of the order of the pecks, the only comparison choices that count as errors are to the comparison that does not match either of the two samples presented on that trial. These are classified as distractor errors. There are two opportunities for a distractor error to occur on each trial; the bird could respond to the distractor on its first comparison choice, or could respond to the distractor on its second comparison choice. For example, suppose the sample sequence on a particular trial is R-G, followed by a R-G-Y comparison configuration. A first-choice distractor error (D1) will be recorded if the bird responds to Y upon comparison presentation. The chance probability of a D1 error, then, is 1/3, or .33. If the bird responds instead to either R or G, it will be faced with a choice between the two remaining comparisons. A second-choice distractor error (D2) will be recorded if the bird responds to Y at this time. The chance probability of a D2 error is 1/2, or .50.

During the final four-session block, the mean percentage of D1 errors was 18.9 (range = 5.2 to 31.2, standard deviation = 8.39) and the mean percentage of D2 errors was 16.1 (range = 0.1 to 42.9, standard deviation = 16.96). The large range and standard deviation for D2 errors is primarily the result of the relatively low second-choice accuracy of three birds (335, 336 and 338). Excluding the data for these three birds results in a mean percentage of D2 errors of 4.3 (range = 0.1 to 12.1, standard deviation = 4.64).

The three birds with low second-choice accuracy received extended training on the order-irrelevant DMTSS task. Bird 335's accuracy increased to a level significantly above chance (chi-square (1) = 26.8, p < .001) over the extra sessions, and so training was terminated. Birds 336 and 338, however, continued to receive training. After an additional 48 sessions of order-irrelevant DMTSS, second-choice accuracy had improved to a level significantly above chance for both birds (chi-square tests, both p's < .001).

Discussion

As mentioned above, Birds 331 and 332 were not significantly more accurate than expected by chance for first-choice responding. However, the order-irrelevant DMTSS task provides a fairly high rate of reinforcement for chance levels of responding on first choices (66.7 %). Even if a bird guesses on its first choice, it will have the opportunity to make a second choice on almost 70 % of trials. All the birds, when faced with a second choice, responded at a level above chance (50 %). Birds 331 and 332 were 95.9 % and 99.9 % accurate, respectively, on their second-choices in the final block of training. Bird 338 (after extended training) was accurate on 88.0 % of second-choices in the final block of training. This highly accurate second-choice performance suggests that sample information was retained until the time of second choice. Overall, all eight birds responded at levels far above chance on second choices, and most birds responded above chance on first choices as well. This finding strongly suggests that pigeons can retain information regarding two sample items. The following experiment addressed the ability of pigeons to reproduce the order of sample presentation, in addition to reporting sample items.

III. Experiment 2

The purpose of the experiment was to determine whether pigeons can retain both item and order information, using the order-relevant DMTSS task developed by Devine and Jones (1975). The task [illegible] the present experiment was identical with that of Experiment 1, except that the birds were required to respond in a specified order to receive reinforcement. Accurate performance on this task indicates that pigeons can retain information about the order of presentation of two sample stimuli, as well as information regarding the identity of the two stimuli.

Method

Subjects and Apparatus. The eight birds from Experiment 1 served as subjects. The apparatus was the same as in Experiment 1.

Procedure. Order-relevant Matching-to-Successive-Samples: Order-relevant DMTSS trials were identical with the order-irrelevant trials of Experiment 1, except that the birds were required to peck the comparison stimuli in a particular order. Devine and Jones (1975) and Devine, Burke and Rohack (1979) required their rhesus monkeys to respond in a "forward" order to the comparison stimuli, i.e., a response to the comparison corresponding to the first sample (S1) followed by a response to the comparison corresponding to the second sample (S2) was reinforced. However, pilot testing revealed higher accuracy when the birds were required to respond in a "backward" S2-S1 order. It has been suggested by other researchers that animals may have an innate tendency to respond to the most recent of a series of stimuli (e.g., Roberts & Grant, 1976; Davis & Fitts, 1976). Accordingly, this order (S2-S1) was designated as correct for the order-relevant task.

Sessions consisted of 72 trials. Trials were separated by an intertrial interval of 40 s, and began with presentation of a black dot on a white background as a preparatory stimulus. The preparatory stimulus was presented on the center key for 5 s, or until a response to the stimulus occurred. Termination of the preparatory stimulus was followed immediately by presentation of the first sample (S1) on the center pecking key. After 5 s, the first sample was extinguished, followed immediately by the presentation of the second sample (S2), also on the center key, for 5 s. A short (0.5 s) delay followed termination of the second sample. After the delay, all three pecking keys were illuminated by the choice stimuli.

A single response to the comparison that corresponded to the sample presented second (S2) extinguished that keylight, leaving a choice between two remaining comparison stimuli. A single response to the comparison which corresponded to the sample presented first (S1) extinguished the remaining two keys, and resulted in 5-s access to grain. For example, if the sample sequence on a particular trial was red followed by green, reinforcement was only delivered if the bird first pecked the green comparison, followed by a peck to the red comparison. An incorrect comparison response at any time (first or second choice) extinguished the pecking keys and resulted in a 5-s timeout during which the houselight was turned off.

The chance probability of a correct first choice in this task is 1/3, or .33. If, and only if, the bird responded correctly at the time of its first choice did the opportunity to make a second choice arise. The chance probability of a correct second choice is 1/2, or .50.

After 24 sessions of order-relevant DMTSS, second-choice accuracy had not risen above a chance level for four of the birds. First-choice accuracy, however, was significantly above chance for each of the birds. This high first-choice accuracy combined with low second-choice accuracy suggested that the birds responded to the comparison corresponding to the most recent stimulus (S2) on their first-choice, and reverted to chance responding on second-choices. This low second-choice accuracy may have been a function of the DMTSS task. In the order-relevant task, S1 first-choice responses resulted in an immediate timeout. Thus, responding to S1 was often punished in the order-relevant task, and this may account for the low levels of responding to S1 on second choices. To alleviate this problem, a correction procedure was implemented after the initial 24 sessions of Experiment 2.

In the correction procedure, responses to the distractor stimulus on second-choices were recorded, but responses to this stimulus had no programmed effect. The bird was required to move away from the distractor stimulus and respond to the comparison corresponding to S1 before receiving reinforcement. In this way, the bird was forced to respond to S1 on every second-choice in order to receive reinforcement. This correction procedure remained in effect throughout Experiment 2, and in the experiments following. Training with the correction procedure continued for 68 sessions (4896 trials), for a combined total (noncorrection plus correction sessions) of 92 sessions (6624 trials).

Results

Accuracy Data. Two birds (336 and 338) performed at a chance level of accuracy on both first- and second-choices: a third bird (332) performed at a chance level on second-choices. Because these three birds failed to acquire the order-relevant task after 68 sessions, they were dropped from the present series of experiments. They were returned to training on the order-irrelevant task of Experiment 1 and eventually participated in another series of experiments, one of which is described in Appendix B.

Each of the remaining five birds performed at a level significantly above chance on both first- and second-choices (chi-square tests, all p's < .05). The mean percentage of correct first and second choices is shown in Figure 2 (p. 24). Mean first-choice accuracy during the final four-session block was 66.7 %; mean accuracy on second choices was 66.2 %. Both of these levels are significantly higher than chance (first choice, $t\ (4) = 8.02$, $p < .001$; second choice, $t\ (4) = 6.16$, $p < .01$).

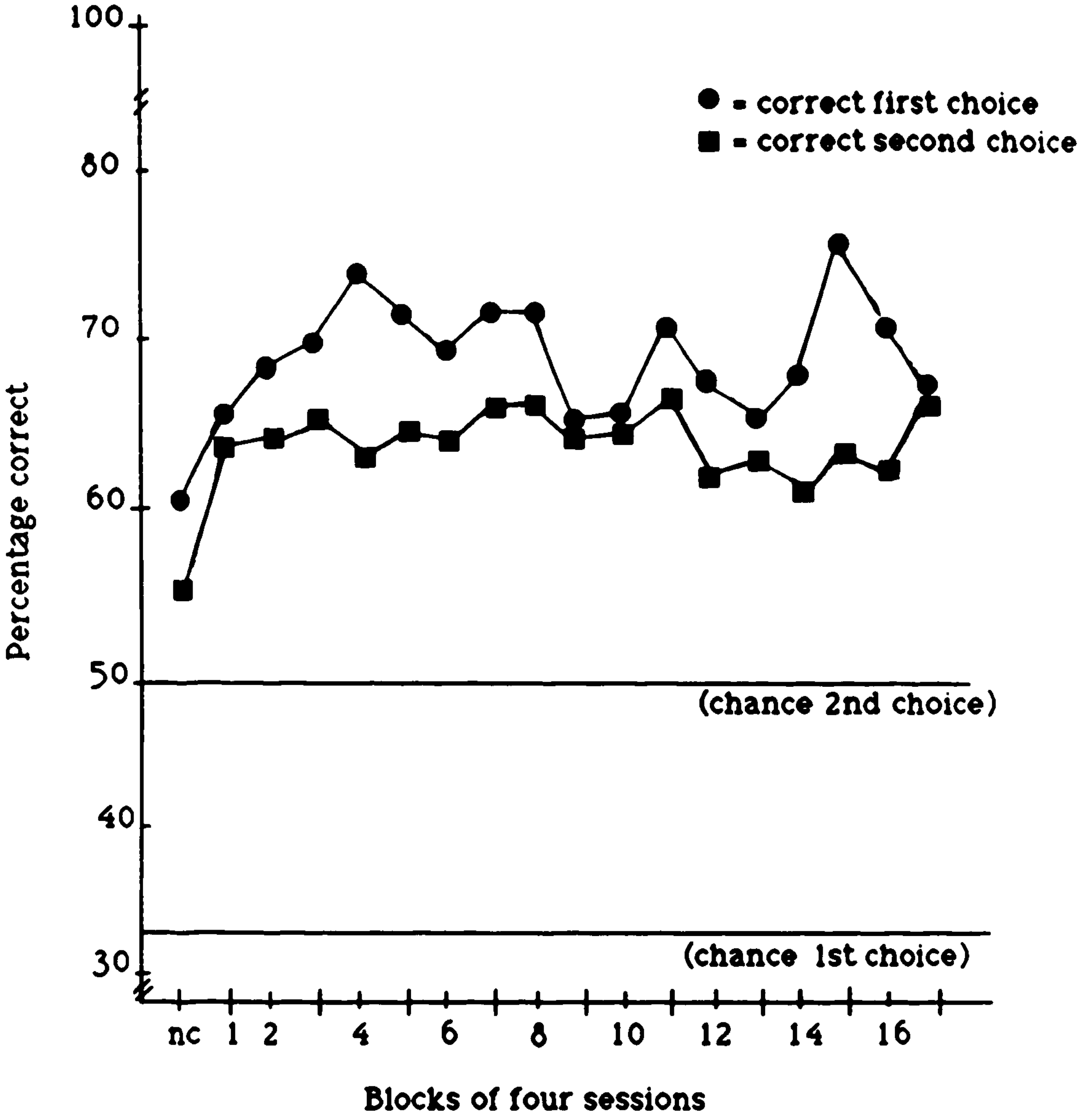

Figure 2. Mean percentage of correct first- and second-choices during order-relevant DMTSS in Experiment 2.

nc = final block of non-correction training

A two-factor analysis of variance was performed on the combined acquisition data from the five birds. Blocks (of four sessions) and Choice (first or second) were the factors. The Block main effect, the main effect of Choice, and the Block by Choice interaction were not significant.

Error Data. There are two types of errors that can occur in the order-relevant DMTSS task- distractor errors and order errors. As in Experiment 1, distractor errors occurred when a bird pecked a comparison that did not match either of the two samples. The chance probability of a first-choice distractor error (D1) in this task was 1/3, or .33; the chance probability of a second-choice distractor error (D2) in this task was 1/2, or .50. The mean percentage of D1 errors during the final four-session block (for the five remaining birds) was 10.7 (range = 8.3 to 17.7, standard deviation = 4.02) which is significantly lower than expected by chance ($t_{(4)} = 12.63$, $p < .001$).

The second error type in this task is order errors. Order errors occurred when a bird's initial choice was to the comparison corresponding to the first sample item. For example, consider a red (S1)-green(S2) sample sequence. If the bird's initial peck was to the red comparison, the trial terminated in nonreinforcement, and an order error was recorded. Assuming equiprobable responding to each of the three comparisons, the chance probability of an order error is .33. During the final four-session block of data collection, the mean number of order errors (for the five remaining birds) was 18.2

% (range = 14.2 to 22.2, standard deviation = 3.08). The number of order errors was significantly lower than that expected by chance (t (4) = 10.94, p < .001).

Discussion

The results of this experiment demonstrate that at least some pigeons can retain item and order information in the DMTSS task. First- and second-choice accuracy were consistently above chance for the majority of the eight birds. The DMTSS task is difficult, as evidenced by the lack of acquisition by three of the eight birds. Other animals also have difficulty mastering this task. Devine, Burke and Rohack's (1979) rhesus monkeys each required approximately 10,000 trials to reach the criterion level of accuracy, and that task was made easier for one monkey by omitting sample sequences containing two samples from the same dimension (i.e., two colors or two shapes). In the present task, the same three stimuli (all colors) were used as both samples and comparison stimuli throughout training and testing. This probably resulted in the build-up of considerable interference as trials progressed, and undoubtably made the task more difficult. Under different training conditions, (perhaps with a larger sample set containing samples from more than one dimension) the three birds that did not acquire the task may have showed improved accuracy. It may also be that the three birds may have eventually acquired the task with continued training on the current task. However, five of the eight pigeons did consistently perform at a reasonably high level of accuracy, indicating that at least some pigeons can retain order and item information in the DMTSS paradigm.

Although some pigeons can match accurately to successive samples when order and item information are tested, DMTSS accuracy is much higher when only item information is tested, as shown in Experiment 1. When the retention of order information is also tested, as in the present experiment, accuracy declines drastically. According to Hasher and Zacks' (1979) criteria of automaticity, the encoding of order information in this task may be characterized as an effortful, rather than an automatic, process. According to two of these criteria, a process or task is automatic if a) accuracy does not improve with practice and b) no reliable individual differences are observed. Although first- and second-accuracy did not improve significantly over the 24 sessions of noncorrection training, accuracy did improve considerably when the correction procedure was introduced. Thus, when pigeons receive appropriate practice, order-relevant DMTSS accuracy improves. In addition, as already noted, sizeable individual differences were found between birds. Taken together, these findings support the view that reporting the order of presentation of two samples in the DMTSS task involves an effortful process. It is interesting to note that, until recently, the representation of temporal order by humans was commonly thought to be the result of an automatic process (e.g., Hasher & Zacks, 1979;

Toglia & Kimble, 1976). However, Zacks, Hasher, Alba, Sanft & Rose (1984) found the encoding of temporal order information was not automatic in a list-learning task. The retention of order information improved with practice, and reliable individual differences were found between subjects. The similarity between the Zacks et al. (1984) findings and those of the present studies suggest that the processes underlying the encoding of order in humans and animals may be analogous in some situations. The representation of order information in the DMTSS task is addressed in the following experiments.

IV. Experiment 3

Experiment 3 assessed the effect of changes in sample stimulus duration on the retention of order information using the DMTSS task. The duration of S1 (with S2 duration held constant) and the duration of S2 (with S1 duration held constant) were manipulated. The purpose of this experiment, and the experiment following, was to determine how order information may be represented in short-term memory. There are two main ways that order information can be represented in memory: either relationally or absolutely (e.g., Ebenholtz, 1963; Shiffrin & Cook, 1978). The implications of each view for the present experiment are discussed below.

First, order information may be represented relationally in the DMTSS task. The two samples in the sequence may be connected by an order relation in memory, e.g., "red followed by green". In this example, the statement "followed by" expresses the order relation. The identity of the sample items and the relation between them are both maintained in memory. Sample duration changes should not affect the strength of the order relation, but instead should only affect the extent to which individual sample items are retained. Under the relational view, order information is represented as a "link" between adjacent sample items. Sample duration manipulations will affect item encoding, but will not directly affect order encoding. The encoding of order information is dependent on the extent to which sample items are processed. Assuming that duration is directly correlated with sample processing, increasing sample duration (either S1 or S2) should a) have no effect on the number of order errors observed, and b) decrease the number of distractor errors, relative to baseline accuracy. When the duration of S2 is increased, a reduction in the number of D1 errors should be observed; when S1 duration is increased, a decrease in D2 errors should be observed. Similarly, decreasing the duration of S1 or S2 should have no effect on the number of order errors observed, but should result in an increase in the number of distractor errors, relative to baseline accuracy. When S1 duration is decreased, an increase in D2 errors should be observed; when S2 duration is decreased, an increase in D1 errors should be observed.

Alternatively, order information may be represented "absolutely" in memory. According to this view, S1 and S2 establish separate memory representations. Order information in this case is part of the memory representation of each item. There are two main ways that order information could be represented absolutely in memory: by"time tags", or by relative strength differences.

One method of determining the relative recency of events is to "tag" memories as to their time of presentation (e.g., Yntema & Trask, 1963). On this view, temporal attributes are appended to representations of events as the events occur. Recency judgments depend on accessing the temporal tags attached to each representation. Manipulations of sample duration should not affect the time-tagging of sample items, and should not affect the recall of order information in the order-relevant DMTSS task. Under the time-tag hypothesis, similar to the relational hypothesis, sample duration manipulations should only affect the extent to which the sample items are encoded. Increasing sample duration (either S1 or S2) should result in a decrease in distractor errors relative to baseline levels (if S1 duration is increased, a decrease in D2 errors should be observed; if S2 duration is increased, a decrease in D1 errors should be observed). Decreasing sample duration should result in an increase in distractor errors relative to baseline levels (if S1 duration is decreased, an increase in D2 errors should be observed; if S2 duration is decreased, an increase in D1 errors should be observed). Manipulations of sample duration should not affect the number of order errors observed.

Another way that order may be represented absolutely in memory is through a comparison of relative memory strengths. At the time of testing, S2 will be the more recent, and perhaps stronger, memory. The memory representation of S1 will be less recent, and perhaps weaker, than the representation of S2. The bird may use this relative memory strength difference as an order cue as to which stimulus to respond at testing, i.e., in this task "respond to stronger memory first (S2), followed by the weaker memory (S1)". According to this conception, sample duration changes should have a significant effect on accuracy, and on the types of errors pigeons make in the DMTSS task.

On the memory strength view, as S1 duration is increased relative to baseline, more order errors should occur. This is because the relative strength of S1 may be increased by increasing sample duration. If the strength of the memory representation is a cue for test responding, the bird should respond to the comparison corresponding to S1 (the stronger representation) on its first choice more often that on baseline trials, resulting in an increase in order errors. Decreasing the duration of S2 should also result in more order errors. This is because decreasing S2 duration may decrease the strength of the S2 memory representation. The relatively strong S1 representation may result in more first-choice responses to the comparison corresponding to S1, and thus result in an increase in the number of order errors.

Method

Subjects and Apparatus. The five birds that matched at an above-chance level from Experiment 2 (Birds 331, 333, 334, 335 and 337) served as subjects. The apparatus was the same as that used in the previous two experiments.

Procedure. Sessions consisted of 72 trials. Of these, 36 trials were S1 Probe trials. On S1 Probe trials, the duration of S1 was manipulated, with S2 held constant at the baseline duration of 5 s. The remaining 36 trials were S2 Probe trials. On S2 Probe trials, the duration of S2 was manipulated, with S1 held constant at the baseline duration of 5 s. The range of sample durations tested on both Probe trial types was 1, 2, 5 and 8 s. The different probe trial types are shown in Table 1 (p.34). Each of the four durations occurred with each of the probe trial types (S1 or S2), for a total of eight different probe trial types. Each probe trial type was presented for 9 trials during each session. As is evident from the table, a total of 18 Baseline duration (S1=5 s:S2=5 s) trials were presented during each session. In order to equate the number of Baseline and Probe trials, 9 of the 18 trials were randomly selected for comparison with Probe trials. The order of presentation of the baseline and probe trials, and the configuration of the comparison stimuli were randomized within each session. Testing continued for 12 sessions, which provided 108 observations at each Probe type duration.

Results

The mean percentage (collapsed over 12 sessions) of correct first- and second-choices, distractor and order errors at each sample duration is shown in Figure 3 (p. 36). As is evident from the figure, the sample duration manipulation primarily affected first-choice accuracy and the number of order errors. When S1 duration was very long (8 s), or S2 duration was very short (1 or 2 s), many more order errors were made. The increase in order errors was accompanied by a decrease in first-choice accuracy, especially when

Table 1. Probe trials, Experiment 3

S1 Probe trials	S2 Probe trials
S1 (1 s) - S2 (5 s)	S1 (5 s) - S2 (1 s)
S1 (2 s) - S2 (5 s)	S1 (5 s) - S2 (2 s)
S1 (5 s) - S2 (5 s) - Baseline	S1 (5 s) - S2 (5 s) - Baseline
S1 (8 s) - S2 (5 s)	S1 (5 s) - S2 (8 s)

S2 duration was short (1 or 2 s). A secondary finding was an increase in D1 errors when either of the two samples was very short (1 s).

Separate two-factor analyses of variance were performed on the data for first-choice accuracy, second-choice accuracy, order errors and distractor errors with Blocks (of four sessions) and Sample Duration (S1=1; S1=2; Baseline; S1=8; S2=1; S2=2; S2=8) as the factors. The main effect of Blocks and the Blocks by Sample Duration interaction were not significant in any of the analyses, which indicated that the data were highly stable across the 12 testing sessions. The data were collapsed across sessions and analyses of variance were run again on the collapsed data. Each will be described separately.

First-choice Accuracy. The main effect of Sample Duration was highly significant, F (6, 24) = 9.83, p < .001. Planned contrasts showed that first-choice accuracy decreased significantly, in comparison with Baseline accuracy, when S1=8 s (F (1,4) = 9.0, p < .04), when S2=1 s (F (1,4) = 27.5, p < .006) and when S2=2 s (F (1,4) = 35.2, p < .004).

Second-choice Accuracy. The main effect of Sample Duration was not significant, F (6, 24) = .681, p = .66.

Order Errors. The main effect of Sample Duration was highly significant, F (6,24) = 11.17, p < .001. Planned contrasts showed that order errors increased significantly, in comparison with baseline,

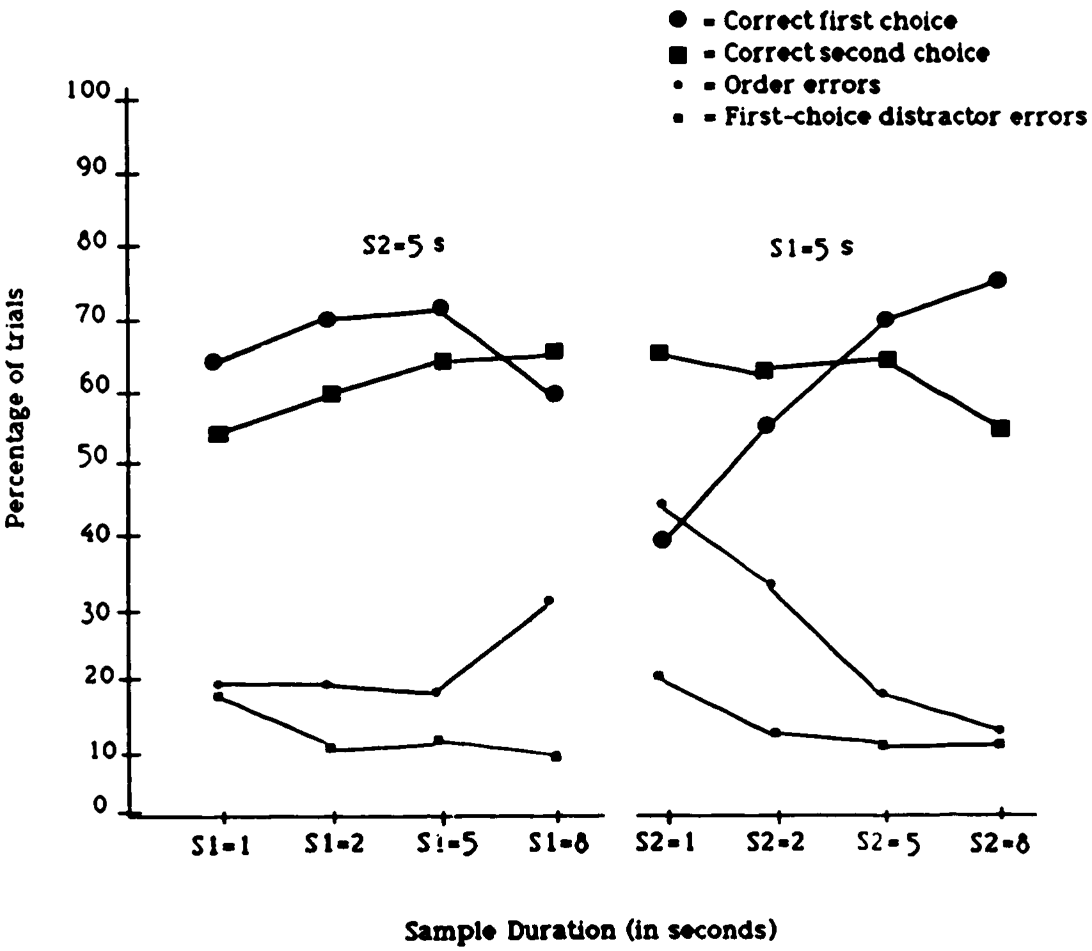

Figure 3. Mean percentage of correct first- and second-choices and errors at each sample duration in Experiment 3.

Note: The data point for S1=5:S2=5 is the baseline level of responding. It is plotted in the S1 function and in the S2 function.

when S1= 8 s (F (1,4) = 36.58, $p < .004$), when S2= 1 s (F (1,4) = 18.47, $p < .01$), and when S2=2 s (F (1,4) = 28.19, $p < .006$).

Distractor 1 (D1) Errors. The main effect of Sample Duration was significant, F (6,24) = 5.51, $p < .01$. Planned contrasts showed that D1 errors increased relative to baseline when S2=1 s (F (1,4) = 15.78, $p < .05$) and when S1=1 s (F (1,4) = 11.07, $P < .03$).

Discussion

The primary finding of Experiment 3 was an increase in order errors when S1 duration was very long or S2 duration was very short, relative to baseline duration. This result strongly supports the strength hypothesis of order representation. According to this view, S1 and S2 establish separate representations in memory. The strength of a representation increases as the duration of sample exposure is increased; representation strength decreases as a function of time, or intervening trial events. In the baseline condition of the current DMTSS task, S1 and S2 were each presented for 5 s. Presumably, the strengths of the individual representations were equal at the time of sample termination. However, because S1 was terminated before the presentation of S2, S1 strength had decreased considerably at the time of testing (as a function of intervening time, or the presence of S2, or both). Under the strength hypothesis, pigeons respond on the basis of the relative strengths of S1 and S2 at the time of test. Specifically, they respond to the comparison corresponding to the stronger S2 representation first, followed by a response to the comparison corresponding to the weaker S1 representation.

In the present experiment, the strengths of S1 and S2 were manipulated by increasing or decreasing sample duration, relative to baseline. Increasing the strength of S1, by increasing S1 duration to 8 s, resulted in a significant rise in the number of order errors. According to the strength hypothesis, this occurred because at the time of test the relative strength difference between the representations of S1 and S2 was reduced from that on baseline trials. Because pigeons use the relative strength difference as a cue to order in the DMTSS task, reducing the strength discrepancy resulted in a decrease in first-choice accuracy, due to an increase in order errors. Similarly, when the strength of S2 was weakened, by decreasing S2 duration to 1 or 2 s, significantly more order errors were observed. Again, this occurred because the difference in relative strength between the sample representations was reduced relative to baseline.

The finding that the number of first-choice distractor errors increased significantly relative to baseline when the duration of either of the two samples was very short (1 s) is more problematic. However, even though pigeons made more D1 errors when S1 or S2 were short, the number of D1 errors on these probe trials was still much less than that expected by chance (S1=1: mean percentage of D1 errors was 18.5; S2=1 s: mean percentage of D1 errors was 19.1;

baseline: mean percentage of D1 errors was 11.0). The increase in D1 errors may be an artifact of testing. The duration of baseline sample sequences was 10 s; the duration of these probe sequences was 6 s. It may be that the pigeons were unprepared for the presentation of the comparison stimuli on these short sequence trials. This may have resulted in either random first-choice responding, or carryover keypecking on some proportion of these trials, which may have artificially increased the number of distractor (and possibly order) errors.

In the present experiment, the representation of order information in the DMTSS task was explored by manipulating sample duration. The following experiment also addressed this issue, and provided a further test of the relational and strength hypotheses of order representation.

V. Experiment 4

This experiment explored further the representation of order information in short-term memory. DMTSS accuracy at several interstimulus interval (ISI) values was tested. The relational and memory strength hypotheses discussed in the previous experiment make differential predictions regarding the outcome of interpolating an interstimulus interval. On the relational view, order information is represented as a link between successive sample items. The items and the order link are maintained as a holistic unit in memory. As ISI increases, then, an increase in second-choice distractor errors should be observed. This is the case because as ISI increases, the representation of S1 must be maintained for a longer time before it can be combined with the representation of S2 to form a single holistic representation. Especially at larger ISI values, S1 should be forgotten. Accordingly, as ISI increases, more D2 errors should be observed. D1 errors should be relatively unaffected by the manipulation, because the encoding of S2 should not be affected by an ISI. In addition to an increase in D2 errors, more order errors may be observed as the interstimulus interval is lengthened. Shiffrin and Cook (1978), using human subjects, found that increasing spacing between items in a list resulted in more order errors when the list was recalled. If the same holds true in pigeons, increasing ISI may result in an increase in D2 and order errors. Results such as these would suggest that ISIs affect both item and order encoding.

Under the strength view, birds retain separate representations of S1 and S2, and use the relative strength of these representations as an order cue. In this case, short ISI values should not affect first- or second-choice accuracy. In fact, short ISI values may slightly increase first- and second-choice accuracy by making the individual representations more distinct. The interpolation of an ISI may affect second-choice accuracy at longer values; if the ISI is long, the representation of S1 may be sufficiently weakened that more D2 errors occur. The number of D1 and order errors, however, should be unaffected by the interpolation of an ISI.

Method

Subjects and Apparatus. The subjects and apparatus were the same as those used in Experiment 3.

Procedure. Test sessions consisted of 72 trials. The trials were identical with the baseline trials of Experiments 2 and 3, except that ISI was manipulated. The ISI values tested were 0.5, 1, 2, and 4 s. Each of these values was presented on 9 trials per session. The remaining 36 trials per session were baseline trials (0 s ISI). Of these, 9 trials were designated as baseline trials for comparison with trials on which an ISI was employed. The remaining 27 baseline trials were included to insure that DMTSS accuracy remained high across sessions. The order of presentation of the trials and the configuration of the comparison stimuli were randomized within a session. Testing continued for 12 sessions, which provided 108 observations at each ISI value.

Results

The mean percentage (collapsed over 12 sessions) of correct first- and second-choices, distractor and order errors at each ISI level is shown in Figure 4 (p. 43). As is evident from the figure, interpolation of an interstimulus interval did not have any systematic effect on DMTSS accuracy, or on the types of errors that the birds made.

Separate two-factor analyses of variance were performed on the data for first-choice accuracy, second-choice accuracy, order errors and distractor errors with Blocks (of four sessions) and ISI value (0 (Baseline), 0.5, 1, 2 and 4 s) as the factors. The main effect of Blocks and the Blocks by ISI interaction were not significant for any of the analyses, which indicated that the data were highly stable across the 12 testing sessions. The data were collapsed across sessions and analyses of variance were run again on the collapsed data. Each will be described separately.

First-choice Accuracy. The main effect of ISI was significant, F (4,16) = 3.96, $p < .02$. Newman-Keuls pairwise comparisons revealed that accuracy at the 2 s ISI condition was lower than accuracy at 0, 1 and 4 s ($p=.05$). No other comparisons were significant. As Figure 4 illustrates, the first-choice accuracy function is "sawtoothed" in form. A test for linear trend was performed on the data for first-choices

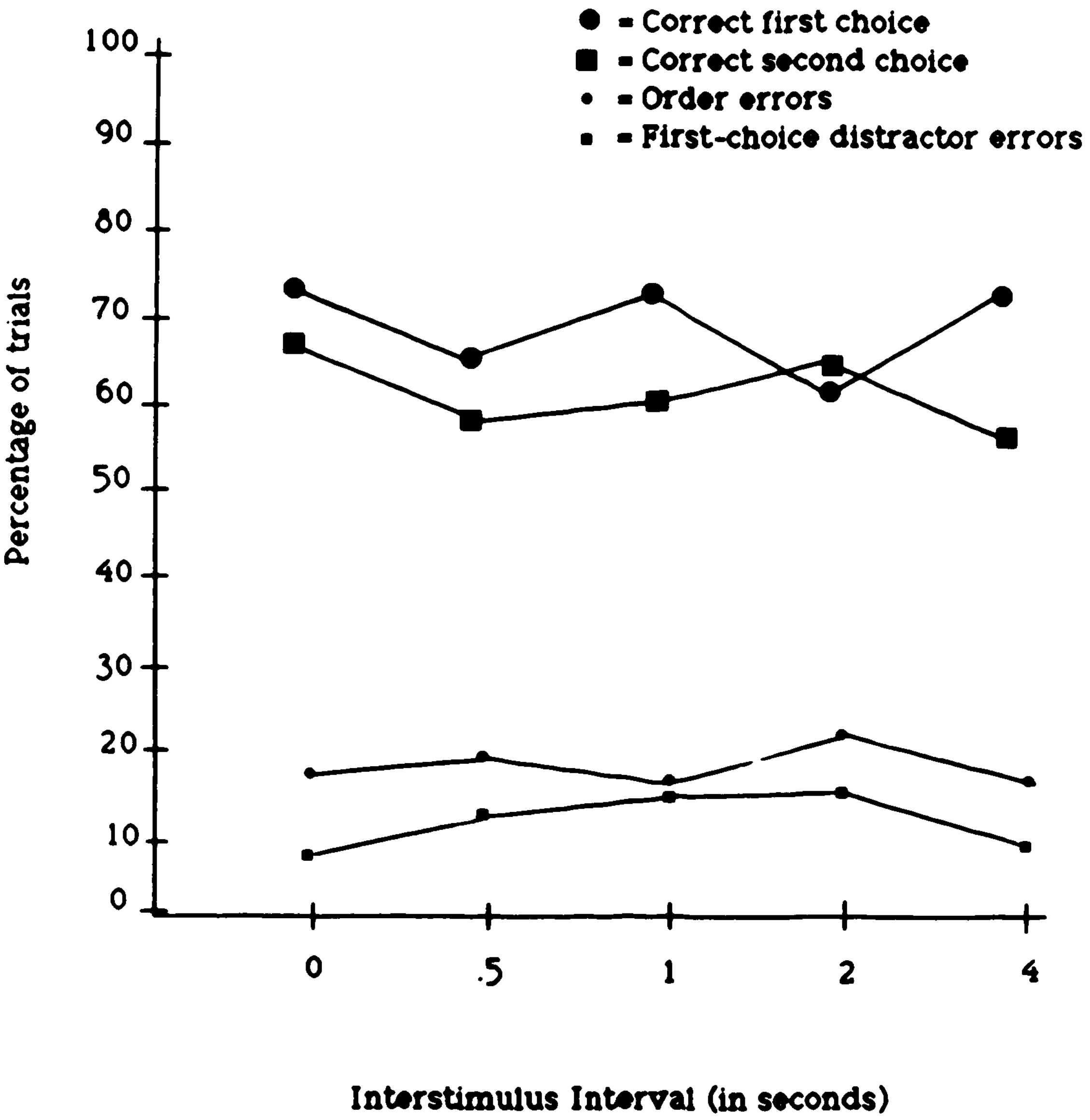

Figure 4. Mean percentage of correct first- and second-choices and errors at each ISI value in Experiment 4.

and was non-significant, F(1,4) = 1.6, p=.27, indicating that ISI did not systematically increase or decrease first-choice accuracy.

Second-choice Accuracy. The main effect of ISI was significant, F (4,26) = 3.3, p = .03. Newman-Keuls pairwise comparisons revealed that Baseline accuracy was significantly higher than accuracy at the 4 s ISI (p=.05). No other comparisons were significant.

Order Errors. The main effect of ISI was not significant, F (4,16) = 1.22, p = .34.

Distractor 1 (D1) Errors. The main effect of ISI was not significant, F (4,16) = 1.29, p = .31.

Overall, first-choice accuracy was not systematically affected by the interpolation of an ISI. Second-choice accuracy was reduced when the ISI was long (4 s). The number of order errors and D1 errors remained relatively constant across the range of ISI values.

.Discussion

The primary finding of Experiment 4 was that first- and second-choice accuracy, and the number of order and D1 errors were not systematically affected by the interpolation of an interstimulus interval. This result provides further support for the strength hypothesis of order representation. According to that hypothesis, birds respond on the basis of relative strengths of the representations of the two sample stimuli. The introduction of a short ISI should not significantly weaken the representation of S1, and should not affect the representation of S2 at all. First- and second-choice accuracy in the present experiment was not affected when ISI duration was short (0.5, 1 or 2 s). When ISI was longer (4 s), second-choice accuracy declined, relative to baseline. Under the strength view, this occurred because the representation of S1 was weakened considerably in the 9.5 seconds between termination of S1 and testing (4 s ISI + 5 s S2 + .5 s delay). The weak S1 representation resulted in an increase in second-choice distractor errors, relative to baseline, on 4-s ISI probe trials. In addition, the ISI manipulation did not affect the number of order or D1 errors, as predicted by the strength hypothesis.

VI. Experiment 5

Results from Experiment 3 and 4 suggest that pigeons respond accurately on the order-relevant DMTSS task by comparing the relative strengths of the memory representations of the two sample items. On this view, order information is derived from item information. The sample items are individually encoded, and information regarding temporal order is derived from a comparison of the relative strengths of the individual memory representations. From this perspective, order information is secondary to item information in short-term memory. This idea is similar to models of human short-term retention which postulate that order and item information are encoded separately. Further, most of these models suggest that delay differentially affects the retention of order and item information. According to these models (e.g., Drewnowski, 1980), order information is lost from memory at a faster rate than item information. This hypothesis was tested in Experiment 5 by manipulating retention interval length. Under this view, the introduction of a retention interval should differentially affect the number of order and first- and second-choice distractor errors. Presumably, order errors result from a loss of sequence order information; distractor errors result from a lost of sequence item information. According to the current view, then, the number of order errors should increase (relative to baseline) as delay is increased and order information becomes unavailable. The number of distractor errors should also increase (relative to baseline) as delay is increased and item information becomes unavailable. However, because order information is lost at a faster rate than item information, the number of order errors observed should "peak" before the number of distractor errors do.

Method

Subjects and Apparatus. The subjects and apparatus were the same as used in Experiment 4.

Procedure. Test sessions consisted of 72 trials. The trials were identical with the baseline trials of the previous experiments, except that retention interval was manipulated. The range of delay values that was tested was 1, 2, and 4 s. Each of these values was presented on 9 trials per session. The remaining 45 trials per session were baseline trials (0.5 s retention interval). Of these, 9 trials were designated as baseline trials for comparison with trials involving longer retention interval values. The remaining 36 baseline trials were included to insure that DMTSS accuracy remained high across sessions. The order of presentation of the trials and the configuration of comparison stimuli were randomized within a session. Testing continued for 12 sessions, which provided 108 observations at each delay value.

Results

The mean percentage (collapsed over 12 sessions) of correct first- and second-choices, distractor and order errors at each delay value is shown in Figure 5 (p. 49). As is evident from the figure, the delay manipulation primarily affected first-choice accuracy. First-choice accuracy decreased considerably as retention interval increased. The decline in first-choice accuracy was accompanied by an increase in both order and D1 errors, although more order than D1 errors were observed at each delay value. Second-choice accuracy was relatively unaffected by increasing delay.

Separate two-factor analyses of variance were performed on the data for first-choice accuracy, second-choice accuracy, order errors and distractor errors with Blocks (of four sessions) and Retention Interval (.5 (Baseline), 1, 2, and 4 s) as the factors. The main effect of Blocks and the Blocks by Retention Interval interaction were not significant for any of the analyses, which indicated that the data were highly stable across the 12 testing sessions. The data were collapsed across sessions and analyses of variance were run again on the collapsed data. Each will be described separately.

<u>First-choice Accuracy</u>. The main effect of Retention Interval was highly significant, F (3,12) = 21.96, p < .001. Newman-Keuls pairwise comparisons revealed that Baseline (.5 s) accuracy was significantly higher than accuracy at 1, 2 and 4 s (p=.05 in all cases). First-choice accuracy at 1 s was significantly higher than accuracy at both 2 and 4 s delays (p=.05 in both cases). Accuracy at 2 and 4 s did not differ from each other. A test for linear trend was highly significant, F (1,4) = 48.31, p< .002, indicating that first-choice

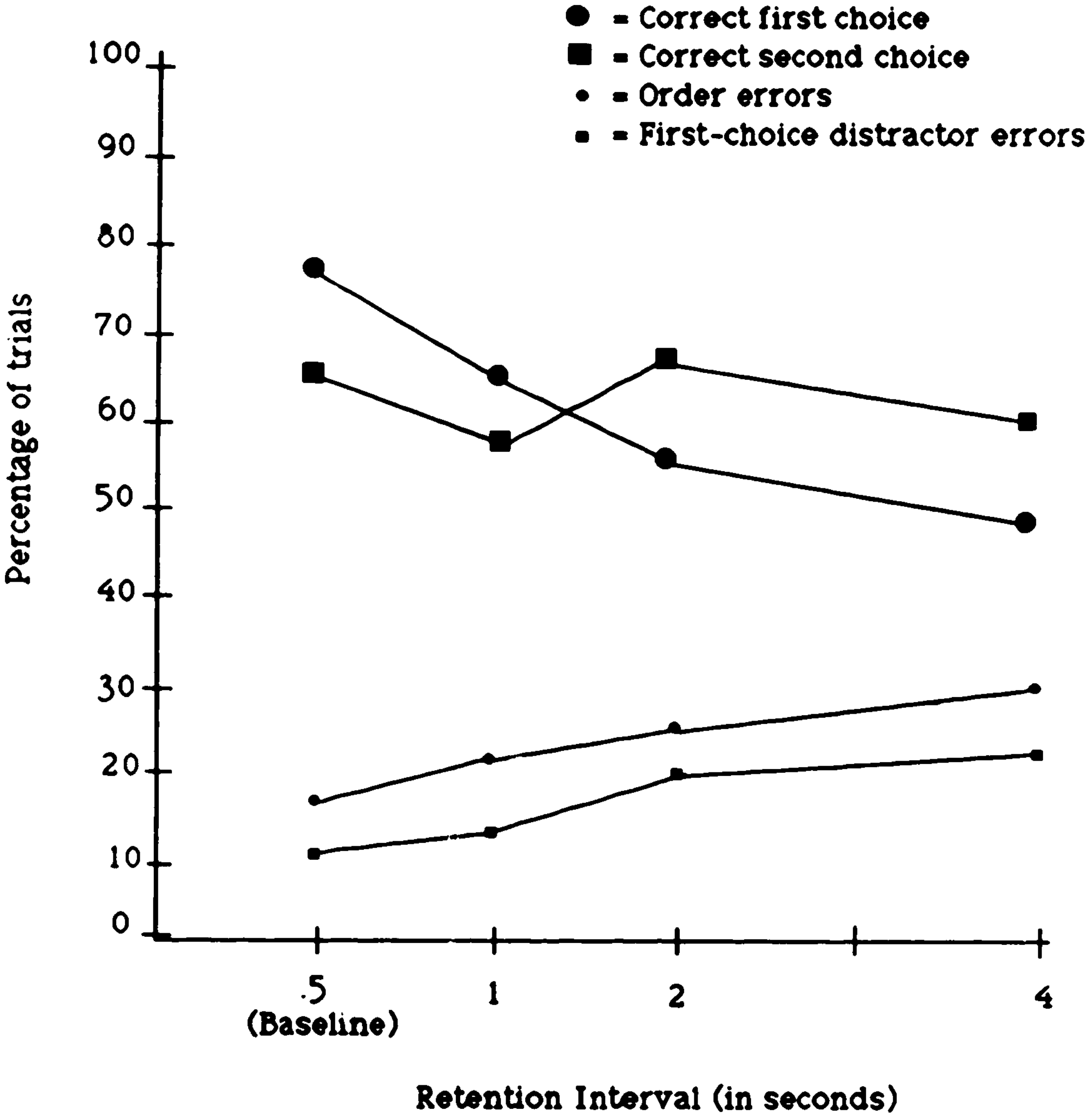

Figure 5. Mean percentage of correct first- and second-choices and errors as a function of delay in Experiment 5.

accuracy decreased in a linear function as delay lengthened.

Second-choice Accuracy. The main effect of Retention Interval was not significant, F (3,12) <1 , p = .48.

Order Errors. The main effect of Retention Interval was significant, F (3,12) = 9.99, p < .01. Newman-Keuls pairwise comparisons revealed that the number of order errors at Baseline and 1 s delay did not differ. The number of order errors at Baseline was significantly less than at 2 and 4 s (both p's =.01). The number of order errors at 2 s was less than that at 4 s (p=.05).

Distractor 1 (D1) Errors. The main effect of Retention Interval was significant, F (3,12) = 13.17, p < .001. Newman-Keuls pairwise comparisons revealed the number of D1 errors did not differ at Baseline and 1 s. There were significantly more D1 errors at 2 and 4 s, compared with Baseline (both p's = .01).

A planned contrast showed that at baseline the number of order and D1 errors did not differ significantly from each other, F (1,4) = 1.04, p = .37. However, an additional planned contrast on the data from the 4 s delay approached significance, F(1,4) = 6.4, p < .06, which indicated that there were more order errors than D1 errors at the longest delay.

Discussion

The primary finding of Experiment 5 was that first-choice accuracy decreased as delay was lengthened, while second-choice accuracy remained constant across delay. This result is somewhat counterintuitive, but can be accounted for within the memory strength perspective. According to this view, S1 and S2 establish separate representations in memory. The strength of these representations decrease over time. Further assume that the function describing the loss of strength (i.e., forgetting) of these representations is negatively accelerated. In this case, the strength of a representation will decline most rapidly immediately after sample termination, and the rate of loss will gradually slow as time since sample termination increases. In a typical DMTSS trial, then, the representation of S1 will lose most of its strength immediately after termination of the first sample, i.e., during the presentation of S2. The representation of S2, however, will remain strong, because the comparison stimuli are presented soon after S2 termination. This relative difference in memory strength for S1 and S2 is assumed to result in accurate DMTSS performance.

In Experiment 5, however, a series of delays were interpolated between S2 termination and comparison onset. According to the current view, the strength of the S2 representation decreased across delay. This was evidenced in reduced first-choice accuracy as retention interval increased. The first-choice accuracy function plotted in Figure 5, then, essentially tracks the decrease in strength of the S2 representation across delay. Further, at the time of testing, the S1 representation had already decreased in strength to a "plateau" level, and so further increases in delay did not significantly affect second-choice accuracy.

The memory strength idea is also consistent with the observed increase in order errors as delay increased. When the retention interval was long (4 s), the representations of S1 and S2 were more equal in strength than when the retention interval was very short. This is because the S2 representation lost most of its strength over the extended delay, whereas, as mentioned above, the S1 representation remained relatively unaffected by the delay. According to the current view, accurate DMTSS performance depends on a difference in strength between the representation of S1 and the representation of S2. Thus, when the strengths of the two representations were approximately equal, they could be easily confused at the time of test. This confusion as to which of the two samples preceded the other resulted in an increase in order errors, especially at the longest delay.

In the DMTSS task, order errors indicate that information regarding the identity of the sample items was retained, but the order of presentation of the items was unavailable. First-choice distractor errors indicate that both order and sample item information was unavailable. At baseline in the present experiment, there were approximately equal numbers of order and D1 errors, but at the longest delay (4 s), more order errors than D1 errors were observed. These results are consistent with previous findings that order information is lost from short-term memory before item information (e.g, Devine, Burke & Rohack, 1979; Maki, Beatty & Clouse, 1984). However, under the strength hypothesis, order information is not "encoded" but instead is obtained from an examination of item information. In this sense, order information is not lost from short-term memory, but the ability to <u>report</u> the order of the two sample items is lost. This ability, according to the strength view, depends upon a difference in memory strengths between the two representations. When delay is increased, the strengths become more equal, and more order errors are observed. Although the ability to distinguish sample order decreases across delay, sample item information continues to be retained for some time. Indeed, item information was surprisingly resistant to forgetting as delay was lengthened in Experiment 5. Pigeons responded on the basis of sample-dependent information on 80.5% of first choices when delay was 4 s; first-choice distractor errors were made on only on 19.5% of trials. If the retention interval was increased further, say, to 8 s, the number of D1 (and possibly D2) errors would probably increase considerably as item information was lost from memory.

General Discussion

The series of experiments reported here addressed the retention of order information in pigeons using a DMTSS task. Experiments 1 and 2 demonstrated that pigeons retained both order and item information from sequences of two successively presented samples that varied from trial to trial. Experiments 3, 4 and 5 explored the representation of order information in the DMTSS task. Experiment 3 involved a manipulation of sample duration. The primary finding from this experiment was that pigeons made more order errors when S1 duration was long or S2 duration was short. Experiment 4 involved the interpolation of a series of interstimulus intervals. Introducing ISIs did not significantly affect DMTSS accuracy. In Experiment 5, retention interval length was manipulated. First-choice accuracy decreased as delay was increased; second-choice accuracy was unaffected by increases in delay. Decreased first-choice accuracy was primarily due to increases in order errors, especially at the longest delay. The combined results of these three experiments supported a memory strength hypothesis of order representation. In the following section, the memory strength hypothesis of order representation is explored further, and a model of pigeons' DMTSS performance is proposed.

Strength Model of DMTSS Performance

The strength model involves two distinct processes: retention and decision. In this respect, the model is very similar to one proposed by Hinrichs (1970) that dealt with judgments of recency by humans. Wickelgren and Norman (1966) also proposed a strength model to account for serial position effects in list recognition memory in humans. Both of these models also distinguished between item retention and response decision. Each of these processes is discussed below.

Retention. Roberts and Grant (1976) proposed a model of pigeons' short-term memory based on numerous studies employing the delayed matching-to-sample paradigm. According to that model, exposure to a sample stimulus establishes a "trace" of the stimulus in memory. The trace is strengthened by increased exposure to the stimulus, and is weakened, or decays, with the passage of time or intervening events. Trace decay follows a negatively accelerated curve. In addition, traces are independent of each other in short-term memory, but "compete" with each other at the time of test. The current model of DMTSS retention is highly similar to the Roberts and Grant (1976) model.

First, rather than referring to stimulus "traces", the strength model assumes that stimuli establish "representations" in memory. Many recent studies of pigeon short-term memory have shown that the notion of a stimulus trace, isomorphic with the sample, may not be appropriate. It appears that pigeons actively encode sample information, (e.g., Grant 1981), and so the term "representation" may be a better descriptor than the more passive "trace". Use of the term, however, does not imply the form that the representation may take in short-term memory. Representations may be coded either retrospectively or prospectively (e.g., Honig & Thompson, 1982; Wasserman, 1986), but the current model does not distinguish between the two. Similarly, increases or decreases in representation "strength" do not imply the mechanism by which this occurs. Increases in strength may be due to increased rehearsal of sample information (e.g., Roberts & Grant, 1978), or to an increased number of stimulus representations available at testing (e.g., Kendrick & Rilling, 1986). Decreases in strength may be due to simple decay of the representation over time (e.g., Roberts & Grant, 1976), or to intervening representations (e.g., Kendrick & Rilling, 1986).

To summarize, the presentation of sample stimuli is assumed to establish separate representations of those stimuli in short-term memory. The strength of a representation increases as exposure to the sample is lengthened; representation strength decreases as a function of time, intervening events, or both. The function describing the decrease in strength is negatively accelerated.

Decision. The decision process is critical to accurate performance on the DMTSS task. The use of the term "decision" does not imply that the process is a conscious one. Rather, the decision process is assumed to be the application of a "rule" or instruction, stored in long-term (or reference) memory. This rule is acquired over training, and is dependent on the reinforcement contingencies present in the particular task. In this sense, the decision process may be viewed as a controlled process similar to the process of maintenance rehearsal (e.g., Grant, 1984; Maki, 1981). The decision process is not an invariant characteristic of the memory system. It is acquired over training trials, and is under the animal's control to the extent that it is flexible and dependent on task demands. In addition, not all birds may acquire the decision rule. In the current case, three of eight birds never performed at above chance levels on the order-relevant DMTSS task. Presumably, these birds did not acquire the decision rule, even after extended training.

According to the strength model, pigeons determine the order of the two successively presented samples by comparing the relative strengths of the sample representations. In this case, the reference decision rule is "respond to the comparison corresponding to the stronger (S2) representation first, followed by a response to the comparison corresponding to the weaker (S1) representation". On this view, order information as such is not encoded, but is derived from item information.

The Strength Model and DMTSS

The strength model accounts nicely for the results of the experiments reported here. According to this model, the manipulations of sample duration (Experiment 3), ISI (Experiment 4) and retention interval (Experiment 5) affected the strengths of the sample representations. The decision process remained constant. In

Experiment 3, sample duration was varied. On the assumptions of the model, increasing sample duration increased the initial strength of the representation. Decreasing sample duration decreased the initial strength of the representation. When S1 duration was increased, relative to baseline, the representation of S1 was stronger at testing than the S2 representation. Application of the decision rule resulted in an increase in order errors on those trials. When S2 duration was decreased, the representation of S1 was (relatively) stronger at testing than the S2 representation. Again, application of the decision rule resulted in an increase in order errors on those trials. The introduction of ISIs in Experiment 4 had little effect on DMTSS accuracy. The representation of S1 at the time of testing was weaker than the S2 representation, and application of the decision rule resulted in above chance DMTSS accuracy, as on baseline trials. Because the decrease in strength across delay is negatively accelerated, the addition of a few extra seconds following S1 termination did not have a significant effect. When the interstimulus interval was very long (4 s), however, the representation of S1 was sufficiently weakened at testing that considerable D2 errors were observed. Experiment 5 involved a manipulation of retention interval length. Introduction of a delay following S2 termination resulted in a weakened S2 representation at the time of test. Evidence for this weakened representation is seen in the reduced first-choice accuracy as delay increased. As delay increased, the strengths of the S1 and S2 representations became more equal. Thus, application of the decision rule resulted in an increase in order errors as retention interval was lengthened.

On the assumptions of the strength model, DMTSS can be affected on two levels: the retention process, or the decision process. Experiments 3, 4 and 5 of the present series primarily involved manipulations of the retention process. All three experiments manipulated the strength of the S1 and S2 representations, either by increasing or decreasing the strength of one of the representations (Experiment 3), or by varying the delay over which memory strength decreased (Experiments 4 and 5). The decision process could also be experimentally manipulated. For example, training with a long duration S1 followed by a short duration S2 would result in much more equal memory strengths at testing. Application of the current decision rule would not result in accurate DMTSS performance. It would be interesting to determine if pigeons could match accurately under these conditions. If so, this would imply the application of another decision rule at testing.

An additional way to manipulate the decision process is to simply allow the birds to respond to the comparison stimuli in any order, as in Experiment 1. Without the order restriction, the current decision rule would not apply. As mentioned above, the three birds that never acquired the order-relevant DMTSS task participated in another series of experiments. These experiments were identical with those described here, but the restriction on order of responding was removed. One of these experiments is detailed in Appendix B. This study was identical with Experiment 3 (sample duration manipulation), except that the birds were not required to respond in any particular order to the comparison stimuli. Interestingly, the pattern of results from this experiment duplicated the results of the order-relevant sample duration experiment, and are shown in Figure B-1. Although there were, of course, no opportunities to make order errors in the order-irrelevant task, the order of responses on correct trials were recorded. At baseline, the birds consistently responded to the comparisons in the order S2-S1. However, as shown in Figure B-2, when the duration of S2 was very short (1 s), the birds reversed the order of responding to the comparison stimuli. When the duration of S1 was increased relative to the duration of S2, all three birds tended to make first-choice responses to the comparison corresponding to S1 at the time of test. This finding suggests that even in the absence of an order restriction pigeons tend to respond to the comparison corresponding to the stronger representation first. It should be noted here that these three birds tended to respond to the comparison corresponding to the stronger representation (S2) on first-choices in the order-irrelevant condition. However, this tendency did not transfer to the order-relevant condition, as evidenced by their failure to acquire the order-relevant task.

Implications

The two-process strength model has important implications for the study of short-term memory. Several researchers have suggested that short-term or working memory is primarily concerned with the recency of events. Staddon (1984) defined working memory as event memory, which is "memory for how long ago something happened, as opposed to its significance in terms of other events" (p. 322). Similarly, D'Amato (e.g., 1973) suggested that the delayed matching-to-single-sample paradigm can be conceptualized as a temporal discrimination task. On this view, accurate DMTS performance depends on the animal's ability to discriminate the most recently presented sample stimulus at the time of test. One method of determining the relative recency of events is to "tag" memories as to their time of presentation (e.g., Yntema & Trask, 1963). On this view, temporal attributes are appended to representations of events. Recency judgments depend on accessing the temporal tags attached to each representation. However, the results of the present series of experiments suggest that judgments of recency may be based on the relative strengths of memory representations, rather than on time tags. Data from Experiment 3 are particularly instructive in this regard. If the representations of S1 and S2 are tagged as to their order of presentation, manipulation of sample duration should not affect DMTSS accuracy. However, increasing S1 duration and decreasing S2 duration produced a reversal in the order of responding in the DMTSS task. It is difficult to explain this result in terms of time tags, but it is easily accomodated within a strength conception.

Order information is delegated to secondary status in the strength model of DMTSS performance. Order information *per se* is not encoded, but is completely derived from item information. This does not imply that order information is never encoded by pigeons. For example, the results of sequence production and discrimination studies strongly suggest that pigeons can and do encode temporal order information. In the DMTSS task, however, it appears that order information is secondary to item information. Pigeons must encode and retain two different sample items on every trial in DMTSS. The addition of order information may overload the cognitive capacities of these animals. It may be that application of a decision rule based on relative memory strengths is the most efficient way to deal with this difficult task.

Memory strength models have received some support from studies using human subjects (Hinrichs, 1970; Wickelgren, 1972; Wickelgren & Norman, 1966). These models have for the most part been replaced by conceptions of temporal coding involving context-sensitive associations (e.g., Toglia & Kimble, 1976; Tzeng, Lee & Wetzel, 1979; Zacks et al., 1984). However, Tzeng et al. (1979) allowed that people may judge the relative recency of items on the basis of memory strengths in some situations. Specifically, humans may rely on memory strength cues when the number of contextual cues available is minimized. Interestingly, most studies which involve an investigation of animal memory explicitly seek to minimize contextual cues. It may be that under similar circumstances both animals and humans rely on the relative strengths of memory representations to judge the temporal order of events. Regardless of the overlap between human and animal order processing, this research highlights the flexibility of the memory system when faced with different task demands.

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Appendix A: Literature Review

Order Memory in Animals: Memory for Sequences of Events

Abstract

Can animals discriminate, retain and utilize temporal order information? To address this question, data from several research areas is reviewed. Experiments on memory for response sequences show that animals can accurately report the temporal order of their recent behavior. The results of sequence production studies indicate that animals may learn something about the relative order of elements in a sequence of events. Sequence discrimination experiments demonstrate that animals can differentiate particular sequences of events. Models of sequence discrimination are discussed, along with possible mechanisms underlying sequence discrimination and production by animals. Theories and important issues in the area of human order memory are reviewed. Results of studies on animal order memory that support and extend findings from human subjects are also discussed.

Order Memory in Animals: Memory for Sequences of Events

Each and every event occurs in the context of a temporal stream of events. Whether or not explicitly acknowledged, the temporal sequence of events is a factor in most, if not all, experiments on animal learning and memory. The principal topic of this paper is an examination of working memory in animals for this ubiquitous information, specifically, memory for temporal order. Humans can and do attach verbal labels (e.g., beginning, middle, end; first, second, third) to sequences of stimuli. The question to be addressed here is: can animals discriminate, retain and utilize information about the temporal order of a sequence of events, and if so, how is this information represented?

Before proceeding, some assumptions regarding memory must be made clear. Typically, a distinction is made between short-term and long-term memory. Short-term or working memory has been conceived of as a limited capacity store of "active" information (e.g., Baddeley, 1986; Honig, 1978; Kendrick & Rilling, 1986; Lewis, 1979). Long- term or reference memory is usually described as a highly structured, inactive or "dormant" store of information, essentially limitless in capacity (e.g., Honig, 1978; Shiffrin & Cook, 1978; Wagner, 1981).

The acquisition, activation and utilization of information in these two hypothesized memory stores has been the subject of much debate in the human and animal literature (see Spear, 1978), but for the present purposes the following distinction will suffice. Working memory will refer to a hypothetical store containing currently active, accessible information that is constantly updated; reference memory will refer to a hypothetical store containing inactive, stable information.

In a typical experimental trial, an animal relies upon both working and reference memory to perform accurately. Working memory is necessary to retain the specific stimuli presented during the trial, while reference memory contains the rules or reinforcement contingencies that govern the response at the time of test. Thus, for maximal effectiveness, the contents of working memory should be cleared or erased after a trial has been completed. Reference memory, on the other hand, is responsible for the "long term maintenance of acquired psychological structures" (Honig, 1978, p. 211).

Early Conceptions

Memory for the temporal order of events is outside the realm of traditional learning theories. Until relatively recently, the complex sequences of behavior exhibited by animals were presumed to be the result of the formation of chains of stimulus-response (S-R) units. This view was shared by most early theorists, including Skinner (1938), Spence (1956) and Hull (1943). The basic idea was that behavior sequences consist of smaller behavioral units, chained together. Consider, for example, a rat trained to perform a sequence of behavior consisting of running down an alleyway, followed by climbing a ladder, and finally ringing a bell. The first response (running) is occasioned by the (experimental) context. The second response (climbing) is elicited by the feedback (presumably internal) generated by the first response. The final response (ringing) is elicited by the feedback generated by the second response. In this way, a chain consisting of S-R links is created (S_1(context) - R_1(running)- S_2(R_1feedback) - R_2 (climbing) - S_3(R_2 feedback) - R_3 (ringing). The entire chain of responses is reinforced by the delivery of food after performance of the terminal response.

Similarly, the recall of serially-presented lists of items by humans was assumed to be the result of sequential associations built up between adjacent list items. On this view, the recall of an item from a list "triggered" recall of the following word (e.g. Postman & Stark, 1967). This idea was called into question by several researchers, who argued that the associations formed in serial list learning in humans were the result of associations between an item and its position in the list, rather than sequential associations between items (e.g., Ebenholtz, 1963; Saufley, 1967; Young, 1962; Young, Hakes & Hicks, 1967).

The move away from an S-R perspective on serially ordered behavior was hastened by an influential paper by Lashley (1951). He argued that complex behavior (e.g., speech, and all skilled movements) could not be adequately explained within an S-R perspective. According to Lashley, skilled movements, such as typing, do not result from the chaining together of motor components, but result from "some organization other than direct associative connections between them" (p. 115). He argued that the speed and fluency with which such movements are performed does not allow sufficient time for feedback within the nervous system, thereby making the S-R conception unlikely. Lashley suggested that complex behavior resulted from an overall organization or schema which in effect was responsible for "overseeing" the performance of the behavior. Individual motor components were important only because they were necessary to the performance of the act. In this sense, Lashley's ideas are somewhat similar to Tolman (1932) who suggested that animals learned more than a chain of responses in the presence of a chain of discriminative stimuli. According to Tolman, "any sequence of behavior-acts involves a sequence of commerces with selected pairs of means-objects and subordinate goal-objects in order to get to, or from, some relatively final goal-object" (p. 450). In Tolman's view, animals had a plan or "cognitive map" of their environment which directed their actions, and which included some information on the spatial and temporal location of objects in that environment.

Under an S-R viewpoint, animals (and humans) had no representation or memory of the temporal order of responses or stimuli. The recent cognitive "revolution" in theorizing (spurred by the ideas of Tolman and Lashley) has been accompanied by a surge of research directed at complex behavior in animals. Order memory in animals is now the subject of extensive experimental investigation.

Order Memory Research

Three main research areas have addressed the issue of order memory in animals. These are 1) experiments on memory for response sequences, 2) sequence production studies, and 3) sequence discrimination experiments. Although it is unlikely that the same processes or representations are employed in these diverse tasks, a common issue is investigated in all three areas. That is, can animals represent order information? "Order information" in this case refers to some representation of the temporal sequence of events. The exact nature of the representation is not a primary issue here; rather, the ability of animals to represent and utilize some [illegible] order information is of interest. The findings of each of the three areas are relevant to the issue of memory for the temporal order of events. Each will be discussed in turn.

Response Sequence Memory

This area of research emerged from the more traditional field of response sequence learning. The generation of complex sequences of responses by animals has been explained in the past (e.g., Skinner, 1938) by the notion of backward chaining. On this view, a sequence of responses can be built up by first reinforcing the terminal response in the sequence and gradually chaining antecedent responses to it. To train an animal on a three-response (1-2-3) sequence, then, the animal is initially required to perform Response 3 to obtain reinforcement. After the animal has mastered this response, it then must perform Response 2 followed by Response 3 to obtain reinforcement. Finally, the entire response sequence (1 - 2 - 3) must be performed in order to obtain reinforcement.

Recently, attention has shifted from response sequence learning *per se* to memory for response sequences. That is, the question of interest has shifted from "Can animals perform complex sequences of responses?"(e.g., Sidman & Rosenberger, 1967) to "Can animals report or reproduce a recently-performed response sequence?".

The results of numerous studies confirm that pigeons, rats and monkeys can accurately "report" the order of spatially presented stimuli, and can report the temporal order of their recent behavior (Grayson & Wasserman, 1979; Jitsumori & Sugimoto, 1982; Kramer, 1982; Mackay & Brown, 1971; Shimp,1976a; 1976b; 1984; Shimp & Moffit, 1974 ; Wasserman, Deich & Cox, 1983; Wasserman, Nelson, & Larew, 1980).

In a representative study, Parker (1984) demonstrated that pigeons could reproduce two-response sequences. The "sample" was two successively illuminated pecking keys. The birds were required to peck the keys as they were illuminated. Four spatial arrangements were possible (e.g., left-left, right-right, left-right and right-left). At the time of test, the birds were required to respond to simultaneously presented stimuli in the same order as they had responded to the successive elements of the sample. The birds in Parker's study were quite accurate at reproducing the orders they had seen and pecked. Further, accuracy remained at levels above chance when a retention interval was interpolated between sample presentation and testing.

Several researchers (e.g., Grayson & Wasserman, 1979; Shimp, 1976a) have suggested that a short-term memory concept is valuable in accounting for the results of these studies. That is, animals retain in short-term or working memory information about the pattern of their recent behavior, and use this memory to guide their performance at the time of testing. Implicit in this assumption is that memory must include information regarding not only response elements but also the relative temporal order of these elements if the animal is to perform accurately.

Sequence production experiments

The production of a simultaneous chain of behavior is not readily explainable by traditional learning theories (e.g., Hull, 1943; Skinner, 1938; Spence, 1952). The assumption underlying traditional learning theories is that sequences of behavior are formed by chaining responses together. According to this view, each response of a chain is elicited or occasioned by a cue produced by the previous response. Fundamental to this view is the necessity of some kind of feedback, either external or internal, for each response in the chain. Recent research consistent with this viewpoint has been conducted by Richardson and his associates (Richardson & Bittner, 1982; Richardson & Kresch, 1983; Richardson & Warzak, 1981). They presented a five-element stimulus array to pigeons, and required the birds to peck the stimuli in a particular order.

Externally-generated feedback (an increase in keylight illumination) was presented after each correct peck. Their experiments, termed "stimulus stringing", showed that birds performed accurately on four-element sequences, and suffered little or no drop in accuracy when tested on novel configurations of stimuli. They interpreted their results in terms of a traditional chaining model in which feedback plays a crucial role. According to this view accurate performance on stimulus strings results from a simple behavior chain. For example, the onset of the stimulus array sets the occasion for a peck to stimulus A. A peck to stimulus A results in an increase in illumination of stimulus A ("bright" A), which sets the occasion for a peck to ("dim") B; a peck to dim B results in bright B, which sets the occasion for a peck to dim C, and so on.

However, several recent studies have shown that pigeons can produce a string of stimuli without the benefit of externally-generated feedback. These experiments are referred to as sequence production studies. One of the first studies of sequence production was conducted by Straub et al. (1979). They presented pigeons with four colors simultaneously displayed on four pecking keys. Pigeons were required to peck the four colors in a particular sequence, designated ABCD. No feedback was provided until all four colors had been pecked. The birds received food reinforcement for pecking the colors in the correct order, and received a brief time-out if they had pecked the colors in any other order. The spatial configuration of the colors was varied randomly from trial to trial, so that on one trial the birds would be presented with, say, a B-A-C-D configuration, and on the next trial a D-C-A-B configuration would be presented. The birds were able to perform quite accurately on this task, at levels far above chance performance. In addition, the birds were able to perform at above chance levels on a generalization test with several novel configurations of the four colors.

Analysis of the error data showed that 90% of the errors that the birds made during training were "forward" to colors later in the sequence, while only 10% were backward. Straub et al. observed the birds during production of the sequences by a video camera, and found that the birds occasionally made "air pecks" to a correct color, but did not actually contact the pecking key. Response latencies also showed that birds were taking time to air peck or skip past the correct color before responding incorrectly. This suggests that at least some of the forward "errors" were simply due to the birds' occasional failure to contact the pecking key. This is even more probable considering that no feedback was given for responses until the entire sequence had been pecked. On the basis of the error data, and the nearly complete generalization of sequence production to novel arrays, Straub et al. (1979) suggested that the birds had abstracted the correct sequence of colors, and that this representation guided their performance through the sequence.

Straub and Terrace (1981) replicated and extended the findings of their earlier work. Pigeons were again trained to produce one particular four-element sequence of colors, regardless of the configuration of the colors on each trial. As in the earlier study (Straub et al., 1979), the birds performed at a high level of accuracy, and exhibited nearly complete generalization to novel configurations of stimuli. In their second experiment, they tested birds on subsequences (e.g., A-D; B-C-D) of the main sequence. Straub and Terrace found that performance on the subsequences was far above chance levels, suggesting again that the birds formed a "representation" of the correct order of sequence stimuli. Accurate performance on subsequences is particularly important because it precludes the possibility that the birds use internally-generated feedback from the just-pecked element to set the occasion for [illegible] the next element in the chain. For example, element D is never preceded by element A during training, and so does not have the opportunity to become "chained" to element A, yet pigeons can perform accurately on an A-D subsequence.

A considerable amount of research on sequence production with "simultaneous" chains has shown that pigeons can learn to produce a sequence of up to 5 elements with no explicit feedback, and can generalize this production to novel stimulus configurations (Straub, Seidenberg, Bever and Terrace, 1979; Straub & Terrace, 1981; Terrace, 1985; Terrace, 1986a; Terrace, 1986b). In addition, pigeons can perform quite accurately on subsequences of the training sequence. Taken together, these results suggest that pigeons do not learn chains of stimulus-response reflexes.

Instead, they may learn something about the relative order of the elements in a sequence of events, and may use a representation of this order to perform accurately on sequence production tasks.

Terrace (1986a) has recently demonstrated that pigeons have some knowledge of the ordinal position of elements of a sequence. In the first phase of his experiments, birds were trained to produce a three-element sequence (e.g., A-B-C). In the second phase, the same birds were trained on new sequences that contained one element from the original (phase 1) sequence. For some of the sequences the original element was maintained in its original position (e.g., X-B-Y), while in other new sequences the original element was not in its original position (e.g., B-X-Y). Of interest was the number of sessions required to master the new sequence. He found that birds took fewer sessions to attain the criterion level of accuracy on sequences in which the original element remained in the same ordinal position; if the position of the original element was shifted, the new sequence was much more difficult to master. This suggests that pigeons retain some information about the ordinal position of each sequence element during production training. This knowledge is reflected in the positive transfer of phase 1 training to the new sequence in phase 2 when the ordinal position of the original element remained the same.

Sequence discrimination experiments

The results of sequence discrimination experiments complement the findings of production studies. Unlike sequence production studies, in which the bird is required to peck a particular sequence of stimuli, sequence discrimination studies require the bird to discriminate a particular sequence of stimuli from several possible alternative sequences. Responding after only one of many possible sequences of stimuli is reinforced. After experience with this task, pigeons presumably acquire a long-term reference representation of the reinforced sequence, and use this representation to guide their behavior at the time of testing.

One of the first sequence discrimination studies was conducted by Weisman, Wasserman, Dodd and Larew (1980). They presented pigeons with successive two-event sequences of colored lights. There were nine possible combinations of elements, including several control combinations. Only one of the sequences (AB) was designated as positive. Responses to the white test stimulus after this sequence had been presented were reinforced. All other sequences were designated as negative, and responses following their presentation were not reinforced. Differentiation was hardest for those sequences ending in B (BB, XB), but discrimination for all other sequences was quite rapid. In their third experiment, color sequences were followed by a line stimulus test. One sequence was designated as positive if the vertical test stimulus was presented; another sequence was designated as positive if the horizontal test stimulus was presented. The birds thus had to remember the order of the stimuli until the test was presented. Weisman et al. (1980) found that pigeons could perform quite accurately on this type of discrimination.

The pattern of responding during training was similar in all three experiments. Early in training, most responding occurred after presentation of sequences terminating in element B. Later in training, most responding occurred after presentation of the complete AB sequence. Initially then, responding at the time of test was under the control of the more recently presented stimulus. After extensive training, responding to the test stimulus was most strongly controlled by the order in which the stimuli were presented. This finding was replicated by Roitblat, Scopatz and Bever (1987). They trained pigeons on a three-item sequence discrimination task, and found that responding was initially controlled by the third sequence element. Eventually, however, responding came under the control of higher order sequence units, which indicated that the birds had formed a representation of the sequence as a whole.

Interestingly, these findings are similar to several early studies investigating the control over responding by successively presented Pavlovian secondary reinforcers (Egger & Miller, 1962). These studies (e.g., Kosiba & Logan, 1978; Seger & Scheuer, 1977; Thomas, Berman, Serednesky & Lyons, 1968) were not designed to assess sequence discrimination *per se* , but their results are relevant to the topic.

The procedure used in these experiments was to present two stimuli in temporal succession, and in the test phase, measure the rate of responding controlled by each stimulus element separately, and by the combination of the two stimuli. Results consistently showed that with only a few pairings of the two stimuli, animals responded most to presentations of the second stimulus. However, with continued pairings, the compound of two successive stimuli controlled the most responding at test. The findings were discussed in terms of stimulus configuring, but can be reinterpreted in terms of gradual control by the sequence of stimuli.

Subsequent studies on sequence discrimination have also showed accurate discrimination of two- and three-element sequences (Weisman & DiFranco, 1981; Weisman, Gibson & Rochford, 1981; Weisman, Duder & Von Konigslow, 1985). Weisman and Von Konigslow (1984) addressed the nature of a possible mechanism underlying pigeons' accurate performance on sequence discrimination tasks. They formulated three models- the perceptual memory trace recognition model, the temporal position recognition model, and the part-sequence order recognition model. According to the perceptual trace recognition model, birds retain perceptual "traces" of all the samples in the sequence. These perceptual traces can be maintained independently (e.g., Weisman & DiFranco, 1981) or holistically (Weisman & Von Konigslow, 1984) . The traces are compared with the reference memory representation of the reinforced sequence at the time of test. The temporal position recognition model asserts that birds compare the perceptual representation of each sample <u>as it is presented</u> with the reference representation of the reinforced sequence and then formulate an outcome decision. This outcome decision (e.g., "peck" or "don't peck" the test stimulus) is maintained in working memory until the time of test. The part-sequence order recognition model states that birds break the sequence into smaller subunits, and then compare these subunits with their reference memory representation of the reinforced sequence. In the two-element sequence case, the subunit is the pair of stimuli, and this subunit is compared with reference memory during presentation of the second sequence element. Again, an outcome decision is formulated, and maintained in working memory until testing.

The three models result in different predictions regarding the time at which an outcome decision is made. According to the perceptual trace model, no response decision is made until the test stimulus is presented. Similarly, although the part-sequence model predicts that birds can generate outcome decisions during sequence presentation, for the two-element sequence case, this decision is not made until the second stimulus is presented. The temporal recognition model, on the other hand, predicts that birds can formulate an outcome decision at any time during sequence presentation.

Weisman, Gibson and Rochford (1984) tested the relative validity of these models using a two-event sequence discrimination task . Again, the sequence AB was designated as the positive sequence and all other possible combinations were negative. Of particular interest , however, was the addition of an "advance key" that the birds could peck to terminate a trial at any time during the presentation of the sequence.

Pecks to this key, therefore, indicated at what point the pigeons had received the critical information as to the nature of the trial. Results showed that the birds pecked the advance key during the first sequence element on 90% of trials beginning with B; they pecked the advance key during the second sequence element on 80% of AA trials; and they pecked the advance key on virtually no AB trials.

These results using the advance key procedure support the temporal position recognition model which suggests that birds can make decisions as to the correctness of the sequence as the sequence is being presented. According to this model, a bird compares the current sequence with a representation of the positive sequence contained in reference memory one position at a time, and makes a prospective outcome decision (i.e., "peck" or "don't peck" the test stimulus) after each sequence element. Successive outcome decisions are combined into a outcome instruction, which is retained in memory until the test stimulus is presented. To illustrate, suppose that the positive sequence is designated AB. If the first sequence element to be presented is, say, A, then according to the model, the bird will make a "peck" decision at the time of presentation. If the second sequence element is B, the bird again will make a "peck" decision. These two decisions would then be combined into a single outcome instruction, in this case to peck the test stimulus. Alternatively, if either or both of the sequence elements presented do not correspond with the reference memory representation of the correct sequence, the bird will make a "don't peck" decision, and the final outcome instruction will be to refrain from pecking the test stimulus. Further support for this view is provided by Terrace (1986b, Experiment 1). In this experiment, pigeons were trained to discriminate ABC sequences from non-ABC sequences. Following presentation of a sequence, two test keys were illuminated. Pecks to one key (left) were reinforced on ABC trials, and pecks to the other key (right) were reinforced on non-ABC trials. Terrace found that the birds responded to the unlit keys before the end of the trial. This strongly suggests that pigeons make outcome decisions before the end of a trial in sequence discrimination tasks.

Combined discrimination/production tasks

Additional research has also been directed at the processing of temporally ordered sequences of stimuli. This research does not fall under the heading of discrimination or production tasks but rather combines aspects of the discrimination and production paradigms. The delayed matching-to-successive samples (MTSS) task introduced by Devine and Jones (1975) is an example of this type of combined task. As the name implies, in the MTSS procedure two or three samples are presented successively to the animal. Following sample sequence presentation, three comparison stimuli are presented. In the two-sample task, the animal must choose the two comparisons that are identical with the previously presented samples, in the same order as the samples were presented. Consider, for example, a sequence consisting of a red sample followed by a green sample. After the second sample stimulus has been extinguished, comparison stimuli are presented simultaneously on three keys. To obtain reinforcement, the animal must initially choose the comparison corresponding to the first sample (in this case, red), and then must choose the comparison corresponding to the second sample (in this case, green). The third comparison stimulus serves as a distractor. Any responses to this distractor stimulus result in trial termination.

Devine, Burke and Rohack (1979) found that their rhesus monkey subjects could perform quite accurately on a DMTSS task, even when relatively long delays were interpolated between sample sequence offset and comparison onset. The MTSS paradigm requires subjects to (a) discriminate the particular sequence presented on each trial and (b) produce or recall the sequence at the time of testing. The monkeys' accurate performance on this task indicates that they were able to retain information about which sample stimuli had been presented, and more important, their accurate performance indicates that they were able to retain information about the order in which the stimuli were presented.

Terrace (1986b) also combined elements of both production and discrimination tasks, in this case to discover the mechanism underlying accurate sequence production/discrimination performance. He assumed that birds use prospective decision processes to perform accurately on both these tasks. According to this prospective processing view, in the sequence discrimination task, pigeons compare each sequence element as it is presented with their reference memory representation of the reinforced sequence. An outcome decision is then formulated on the basis of this comparison. If the current sequence matches the representation of the correct sequence, a "peck" or "match" decision will be made; if the current sequence does not match the reference memory representation, a "don't peck" or "non-match" decision will be made. These outcome decisions are prospective in nature, because they contain information regarding a future action. In contrast with this view is a retrospective account of sequence processing. On this view, pigeons retain a representation of the current sequence in memory until the test stimuli are presented. The current representation is compared with a reference memory representation of the reinforced sequence at the time of testing (for a further discussion of the retrospective/prospective distinction in working memory, see Honig & Thompson, 1982; Wasserman, 1986).

As results from the advance-key procedure employed by Weisman, Gibson, & Rochford (1984) have shown, pigeons can and do make outcome decisions during sequence presentation in discrimination tasks. The results of sequence production studies also implicate prospective processing, because birds must be able to anticipate upcoming elements in a sequence in order to perform accurately (Terrace, 1983). It appears, then, that pigeons may process sample stimuli prospectively in both sequence discrimination and sequence production tasks.

Terrace's (1986b) experiments were designed to test the hypothesis that a similar processing strategy underlies successful sequence discrimination and sequence production performance. As described earlier, in Experiment 1 pigeons were trained to discriminate ABC sequences from non-ABC sequences. Following presentation of a sequence, two test keys were illuminated. Pecks to one key (left) were reinforced on ABC trials, and pecks to the other key (right) were reinforced on non-ABC trials.

Experiment 2 was identical with Experiment 1, except that näive birds received production training on an ABC sequence before transfer to the same discrimination task as the birds in Expt 1. Terrace reasoned that if the same (prospective) process underlies accurate performance in both production and discrimination tasks, birds with prior experience on the ABC production task should acquire the subsequent ABC discrimination in fewer sessions than previously untrained birds. Results showed that the birds that had experienced production training before discrimination training (Experiment 2 birds) attained the criterion level of performance in substantially fewer sessions than did the birds that had experienced no prior training (Experiment 1 birds). A control experiment showed that the production training *per se* was important for establishing positive transfer to the discrimination task; mere exposure to ABC elements was not sufficient to insure positive transfer. This finding suggests that similar processes underlie accurate performance on sequence production and sequence discrimination tasks. Terrace has proposed that the mechanism employed in both sequence production and discrimination by pigeons is a strategy of prospective processing of sample elements in a particular order.

Animal and human processing of order information: A synthesis

There is abundant evidence from the experiments discussed above that animals can discriminate, retain and utilize temporal order information. This conclusion is consistent with the findings of research using human subjects. In the following section, the results of this research will be discussed, together with some of the important theoretical issues in the area of human order memory. The results of studies on animal order memory that support and extend findings from human subjects will also be discussed.

Serial Position Effects

The utilization of order information by humans has been studied extensively. Most research has been concerned with the recall and recognition of serially-presented lists of items, usually words, digits or nonsense syllables. Typically, a list of items is presented in temporal succession, and then in the test phase, the subject is asked to recall or recognize the items. If accuracy is plotted against serial position, a distinctive bowed or U-shaped curve is usually observed (e.g., Murdock, 1968). This curve reflects the higher recall or recognition accuracy of items early (primacy effect) and late (recency effect) in the list as compared with the items from the middle of the list. Although this research has centered on the effect of serial position on recall rather than the recall of temporal order *per se* , a review of this area will help to trace the development of current ideas in order memory research.

Three main theoretical accounts of serial position effects have been advanced. According to the intralist interference model, the primacy effect is due to the lower levels of proactive interference (PI) operating on the initial items in the list, as compared with items later in the list. The recency effect is due to the lower levels of retroactive interference (RI) operating on the terminal list items, as compared with items presented earlier in the list.

Differential accessibility theory (Feigenbaum & Simon, 1962; Murdock, 1960; Tulving, 1968), on the other hand, suggests that primacy and recency effects are due to the distinctiveness of initial and terminal items in the list. On this view, position information (e.g., first or last) acts as an additional retrieval cue at the time of testing. By virtue of their location in the list, initial and terminal list items are more distinctive than are medial items, and thus receive this additional "marking" information which results in differential accessibility at the time of test.

Dual trace theory (e.g., Atkinson & Shiffrin, 1968) suggests that primacy and recency effects result from the interaction of short-term memory and long-term memory processes. On this view, list items are held in a short-term "buffer". The more time an item remains in the buffer, the greater the probability that it will be transferred to the long-term memory store. At the beginning of a list, the buffer is empty. As list items are presented, the buffer fills up. Old items are displaced from the buffer as new items are presented. According to this view, initial list items are held for a longer time in the short-term buffer than medial list items. Because of this, initial list items have a greater probability of being transferred to long-term memory, and thus have a greater probability of recall at the time of test than do medial list items. According to a dual trace conception, the recency effect is observed because terminal list items are still present in short-term memory at the time of test, and so are simply outputted from the short-term buffer.

The theoretical underpinnings of serial position effects continue to be debated. Until recently, research in this area was conducted exclusively with human subjects. Pioneering studies with animals found recency effects, but no primacy effect (e.g., Olton & Samuelson, 1976; Roberts & Smythe, 1979; Thompson & Herman, 1977). The failure to observe a primacy effect in studies with animal subjects suggested that memory processes in humans may not be analogous to those in animals, especially under a dual trace conception of serial position effects. The lack of a primacy effect in animals suggested that a basic function of short-term memory, i.e., rehearsal and transfer of information to long-term memory, may operate only in humans. However, this conclusion proved to be premature. Primacy (and recency) effects have recently been demonstrated in monkeys (Roberts & Kraemer, 1981; Sands & Wright, 1980a; 1980b; Wright, Santiago & Sands, 1984), pigeons (Santiago & Wright, 1984; Shimp, 1976), rats (Kesner & Novak, 1982; Kesner, Measom, Forsman & Holbrook, 1984; DiMattia & Kesner, 1984), and rabbits (Wagner & Pfautz, 1978).

The across-species generality of the primacy effect suggests that there may be more commonalities between animal and human memory processes than previously assumed. Further, research using animal subjects can contribute to the debate regarding the underlying processes responsible for serial position effects. For example, the results of several studies using a serial probe recognition task with monkeys and pigeons have led researchers to suggest that the serial position curve is primarily the result of intralist interference effects (Sands and Wright,1980a; Santiago & Wright, 1984; Wright, Santiago & Sands, 1984).

Item vs. Order Information

The focus of research on order information using human subjects has recently shifted from serial position effects to a direct examination of the retention of order information. Most memory research has traditionally dealt with memory for the items in a list, that is, memory for specific content. Research on order information is directed at memory for the order in which specific items are presented. Obviously, memory for order is usually confounded with memory for items: the items in a list must necessarily be remembered if their order is to be recalled.

The experimental separation of item and order information has generated much interest (e.g., Donaldson & Glathe, 1969; Rohrman & Jahnke, 1965; Zimmerman & Underwood, 1968). Healy (1974; 1982) and Bjork and Healy (1974) studied the recall of order information independent of recall for item information. In the "order only" conditions, item information was irrelevant to performance. The same four stimulus items were presented on every trial, and the subject had to remember only the order of the items. In the "item only" conditions, order information was irrelevant to performance. Subjects were given order information in advance of each trial, so that only item information had to be learned. Serial position curves from the order-only conditions consistently were bowed or U-shaped when accuracy was plotted against serial position. Serial position curves from the item-only conditions, however, were not bowed. This result has also been found by other researchers (Fuchs, 1969; Murdock, 1968), suggesting that the processes underlying the retention of item and order information may be independent.

The item/order information independence issue has been the subject of some controversy, with no clear resolution (e.g. Angiolillo-Bent & Rips, 1982; Conrad, 1965; Crowder, 1979; Drewnowski, 1980; Lee & Estes, 1977). The results of some research indicate that item and order information may be processed independently; other research findings suggest that the two types of information may be interdependent. Regardless of the final outcome of the debate, this research has highlighted the usefulness and the theoretical significance of the item/order information distinction.

Several models of memory now incorporate both item and order information. Drewnowski (1980) has proposed an attribute model in which the abstract or sensory attributes of items are retained in short-term memory. Order information is one of the attributes of items, and functions as an important retrieval cue. This model, and others similar to it, distinguishes between item and order information, but assigns order information to a secondary role in memory. In keeping with this secondary role, most models assume that item and order information are encoded separately, but order information is lost from memory (or becomes unavailable) first, followed by loss of item information (Fozard, Myers & Waugh, 1971; Murdock, 1977; 1983; Murdock & vom Saal, 1967; Sperling & Melchner, 1976).

The hypothesis that order information is lost from memory before item information has received some support from research with animals. Devine, Burke and Rohack (1979) suggested on the basis of error data analyses that their rhesus monkeys remembered the sample stimuli that had been presented on a trial, but that the order of presentation of the samples was forgotten, especially at long delays. Maki, Beatty and Clouse (1984) using a spatial memory task with rats, found that a long post-list delay impaired performance on an order discrimination more than performance on an item discrimination. Regardless of the eventual conceptualization of the significance of item and order information in memory, the item/order distinction has stimulated research which may lead to a better understanding of short-term memory processes in general, and retention of order information in particular.

Concluding Comments

Based on the results of several areas of research, it appears that animals can indeed discriminate, retain and utilize order information. Animals can report the temporal order of their recent behavior, can discriminate ordered sequences of stimuli, and can produce a simultaneous chain of stimuli with no external feedback. Although theorizing is in its preliminary stages, it has been suggested that animals generate memory representations of sequences of stimuli, and that these representations may contain information about the ordinal position of sequence elements (e.g., Terrace, 1986a).

Theories of order memory in animals can draw extensively from theories of order memory in humans. The distinction between item and order information in short-term memory has highlighted the theoretical significance of both types of information. Models of short-term memory include order information as an important member of a complex of abstract or sensory attributes contained in memory. Ideas such as these have generated considerable interest from researchers using animal subjects. In turn, results from animal studies have supported and extended findings from research using human subjects.

Many questions remain to be answered. Are there two distinct processes underlying the retention of order and item information? How is order information retained, and forgotten? How does the retention of temporal order differ from the retention of spatial order information? A particularly interesting research question regards the automaticity of encoding of order information. Several researchers with human subjects have suggested that order information may be encoded automatically (e.g., Hasher & Zacks, 1979), while others have suggested that the encoding of order information is a controlled process (e.g. Tzeng, Lee & Wetzel, 1979; Zacks, Hasher, Alba, Sanft & Rose, 1984). Relevant to this issue is Terrace's (1986b) finding that training on a sequence production task facilitates transfer to a sequence discrimination task. He speculated that the observed positive transfer was due to the gradual establishment of a prospective strategy in the production phase. This suggests that the ability to encode order information develops over the course of training, and so may be a controlled, rather than an automatic process.

Most of these questions can be addressed by researchers using both animal and human subjects. Some areas , however, can be more effectively investigated using animal subjects. Obviously, physiological manipulation is much easier when animal, rather than human, subjects are used. Indeed, research on the physiological bases of memory for order information is a promising field (e.g., Kesner, Crutcher & Measom, 1986, Strominger, Oesterreich & Neff, 1980). Similarly, the use of animal subjects allows memory for order information to be studied independent of verbal labels or strategies that may dominate when human subjects are tested. Research with animal subjects provides a unique forum for testing some aspects of memory for order information.

Similar findings from studies of human and animal memory, such as the across-species demonstration of the primacy effect, point out the commonalities of human and animal processing. Although similar findings do not necessarily indicate that the same processes are operating in humans and animals, there may be basic memory processes shared by both. A continuing interchange of ideas between the two research traditions will lead to a better understanding of the retention of order information and of memory processes in general.

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Appendix B

Order-irrelevant Sample Duration Experiment

Method

Subjects and Apparatus. Three Silver King pigeons (Birds 332, 336 and 338) served as subjects. They had previously participated in Experiment 1 of the series of experiments discussed in the text. The birds were housed under the same conditions as in the earlier experiments. The apparatus was the same used in earlier experiments as well.

Procedure. The procedure for this experiment was identical with the procedure employed in Experiment 3 of the series of experiments discussed in the text. The only exception was that the birds were not required to respond in a predetermined order to the comparison stimuli. Reinforcement was delivered when the birds pecked the two comparison stimuli that corresponded to the two sample stimuli, regardless of the order that the comparisons were pecked. The range of sample durations tested was identical with Experiment 3, and is shown in Table 1. In addition to recording first- and second-choice accuracy, and distractor errors (D1 and D2), the order of responding at each sample duration probe value (S1-S2 or S2-S1) was recorded. Testing continued for 12 sessions.

Results

The mean percentage (collapsed over 12 sessions) of correct first- and second-choices and distractor errors at each sample duration is shown in Figure B-1 (p. 117). As is evident from the figure, the sample duration manipulation did not significantly affect

DMTSS accuracy. However, manipulating sample duration did affect the order in which the birds responded to the comparison stimuli, illustrated in Figure B-2 (p. 118). When S1 duration was short, the birds tended to respond in an S2-S1 order; when S2 duration was short, the birds tended to respond in an S1-S2 order.

Separate two-factor analyses of variance were performed on the data for first-choice accuracy, second-choice accuracy, distractor errors, and order of responding with Blocks (of four sessions) and Sample Duration (S1=1; S1=2; Baseline; S1=8; S2=1; S2=2; S2=8) as the factors. The main effect of Blocks and the Blocks by Sample Duration interaction were not significant for any of the analyses, which indicated that the data were highly stable across the 12 testing sessions. The data were collapsed across sessions and analyses of variance were run again on the collapsed data. Each will be described separately.

First-choice Accuracy. The main effect of Sample Duration was not significant, F (6, 12) = 2.4, p = .09.

Second-choice Accuracy. The main effect of Sample Duration was not significant, F (6,12) = ..306, p = .92.

Distractor 1 (D1) Errors. The main effect of Sample Duration was not significant, F (6,12) = 2.4, p = .09.

Order of Responding. A two-factor analysis of variance was performed on the data for order of responding with Sample Duration (S1=1; S1=2; Baseline;S1=8; S2=1;S2=2;S2=8) and Order (S1-S2 or S2-S1) as the factors. The main effects of Sample Duration and Order were not significant. The Sample Duration by Order interaction was significant, F(6,12) = 3.37, p < .03. Simple effects tests performed on the data showed that birds responded in the order S2-S1 when S1=1, $F(1,2) = 40.2$, $p < .02$, and in the reverse order (S1-S2) when S2=1, $F(1,2) = 15.64$, $p < .05$.

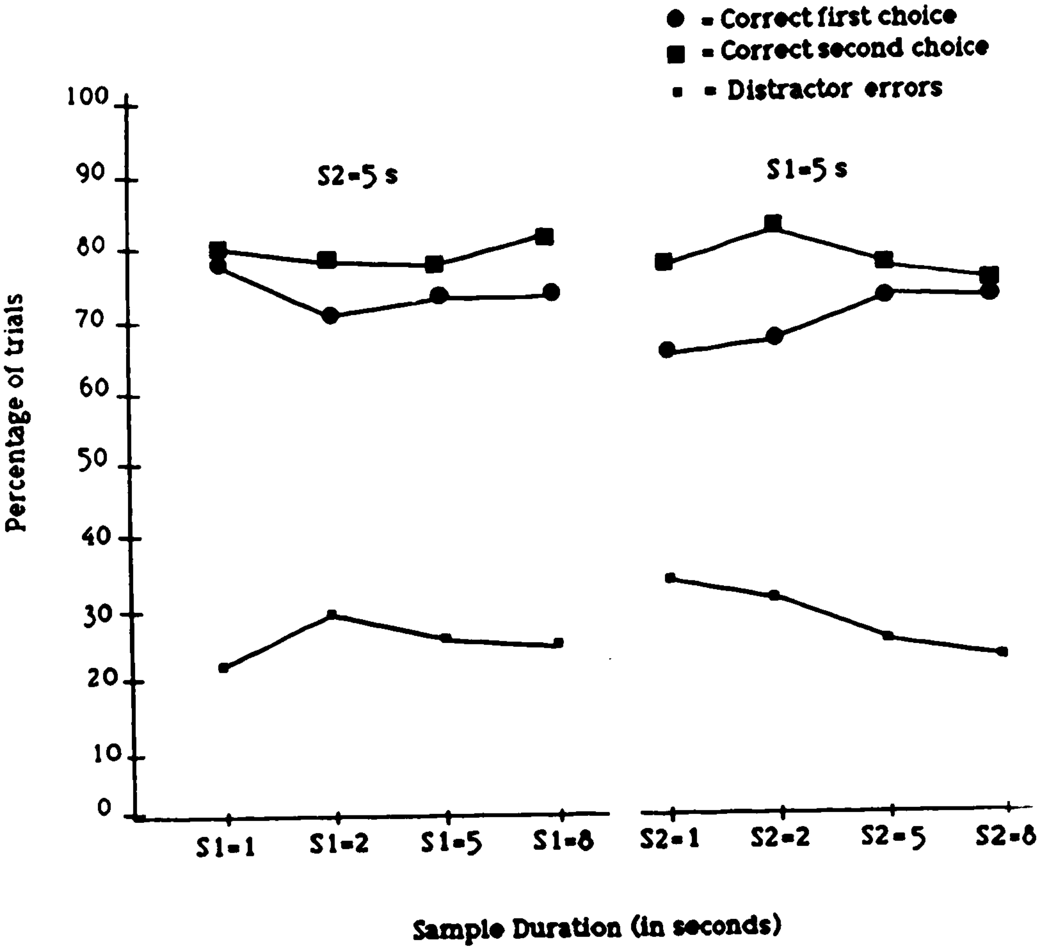

Figure B-1. Data from Order-irrelevant Sample Duration Experiment. Data shown is the mean for three birds, and is collapsed across 12 sessions.

Note: The data point for S1=5:S2=5 is the baseline level of responding. It is plotted in the S1 function and in the S2 function.

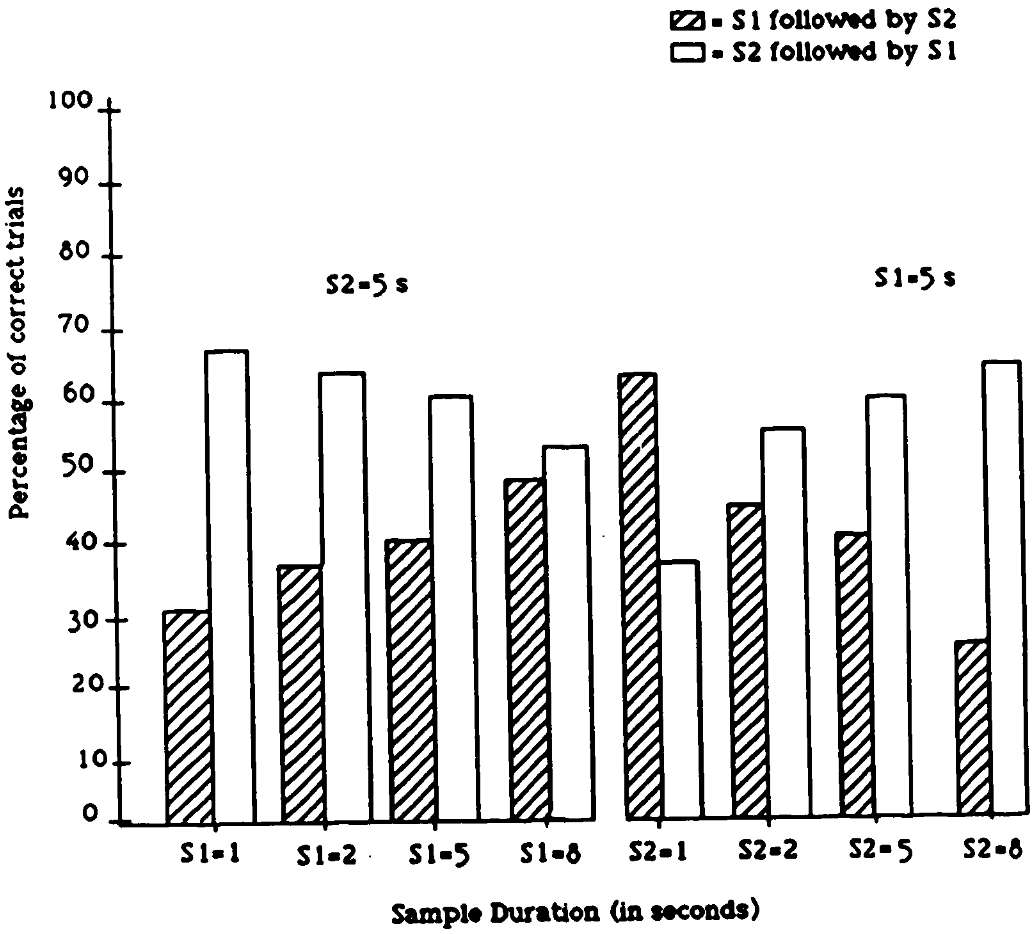

Figure B-2. Mean order of responding on correct trials at each sample duration.