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Short-term item memory in successive same–different discriminations

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Abstract

Pigeons were tested in a successive same–different (S/D) discrimination procedure to examine the short-term memory for individual items in sequences of different or identical pictures. Item-by-item analyses of pecking behavior within single trials revealed this S/D discrimination emerged at the earliest possible point in the sequence — the presentation of the second item. Further, by comparing peck rates at points where different types of sequences diverged (e.g. ABA versus ABC), we determined that the pigeons remembered the first item for at least 4–8 s and across one to two intervening items. These results indicate that this S/D discrimination was controlled by relational comparisons of pictorial content across memories of specific items, rather than the detection of low-level perceptual "transients" between items. A second experiment supported this conclusion by showing increased discrimination with longer first item viewing times, consistent with encoding of details about individual pictures. These findings further support a qualitative similarity among birds and primates in possessing a general capacity to judge certain types of stimulus relations, such as stimulus identity and difference. Implications for the temporal continuity of experience in animals are also considered.

Keywords: Pigeons; Short-term memory; Same–different discrimination; Sequence discrimination; Viewing time; Inter-stimulus interval

1. Introduction

An air traffic controller is regularly faced with the complex problem of serial tracking a number of airplanes on a radar monitor. The memory demands of this task include encoding new planes as they appear on the screen, forgetting old ones as they move out of range, and updating moment-to-moment changes in the position of the current planes. We face similar, if not as demanding, situations almost continually in our ongoing daily experiences. The moment-to-moment continuity of experience requires the constant integration of current perception with memories of the recent past. The farther these memories extend back into time, the greater the complexity in the serial organization of behavior these memories can support. Although a long-standing problem (Lashley, 1951), how sequential events are integrated by animals is still not well understood. A number of intriguing and innovative empirical results (Barnet et al., 1997; Clayton and Dickinson, 1998; Terrace, 2001) and increasingly sophisticated theoretical tools (Killeen, 2001) are bringing such investigations to the forefront of animal cognition. The most frequent approach to studying sequential representations has been to look backward from a terminal behavioral state to make inferences about a previous string of events (Alsop and Honig, 1991; Killeen, 2001; Machado and Cevik, 1997; Wright et al., 1985). In the current experiments we took a fresh approach by asking how pigeons temporally integrate previous experiences to guide behavior in an ongoing stream of stimulus-controlled pecking behavior in a successive same–different (S/D) task. This "on-line" approach has been quite useful in revealing the microstructure of behavior in this task (Cook et al., 2003).

In the S/D task, the subject has to respond "same" when all stimuli on a trial are identical and "different" if one or more of the stimuli are different from the others. Using this task, it has been found that pigeons, parrots, dolphins, rhesus monkeys, baboons, and chimpanzees are capable of learning and applying an S/D concept across a wide variety of simultaneously and successively presented visual elements (Bovet and Vauclair, 2000; Cook et al., 1997; Fagot et al., 2001; Mercado et al., 2000; Pepperberg, 1987; Thompson et al., 1997; Wright et al., 1984; Young and Wasserman, 2001).

The current experiments directly grew out of a set of recent successive S/D experiments (Cook et al., 2003). In their experiments, Cook et al. found that pigeons could learn to discriminate *Same* (AAAA... or BBBB...) from alternating *Different* (ABAB...) sequences of color or gray-scale pictures in a go/no-go task. Pecks to *Same* sequences (S+) were reinforced on a vari-

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able interval schedule, while pecks during *Different* sequences (S−) resulted in a brief time-out. During each 20-s trial, each picture was successively presented for 2 s separated by a brief inter-stimulus interval (ISI). Using this procedure, they showed for the first time that pigeons could perform and transfer such a relational S/D judgment based on differences between only two stimuli (see also Blaisdell and Cook, 2005). The latter was clearly demonstrated by tracking pecking behavior across the successive items in each sequence. They found significant differences in peck rate by the second, and disambiguating, item in the sequence; with peck rates to this item increasing if it were a repetition of the previous item (S+) and decreasing if the second item were different (S−). Further presentations of each item enhanced this difference. It is this capacity to examine the ongoing item-by-item microstructure of when and how such S/D sequences were discriminated by the pigeons that is exploited in the current experiments to reveal further how pigeons temporally integrate S/D information.

Cook et al. (2003) argued that their results were most consistent with the proposition that pigeons have the capacity to form generalized S/D concepts across successive and simultaneous temporal arrangements (Cook et al., 1997; Wasserman et al., 1997). Of course, such important species claims need to be carefully examined and alternative accounts considered to be sure that no simpler account might be responsible for the observed discrimination and transfer (Mackintosh, 2000). One possible alternative account of Cook et al.'s (2003) results is that the pigeons simply detected the presence or absence of low-level visual transients at the change between temporally adjacent pictures. A number of simple and strong visual changes (color, overall brightness, etc.) occur on *different* trials that are not present on *same* trials. Thus, it was possible that the pigeons might have only attended to this coarse perceptual quality of the sequences rather than making true S/D comparisons across time among specific pictures and their details. Arguing against such a simple perceptual transient hypothesis, Cook et al. (2003) found that the pigeons could tolerate ISI separations of over 2 s between the items, consistent with a more complete encoding of a sequence's pictorial content rather than its "flickering" properties. Nevertheless, we wanted to further test this idea by directly examining the specificity of the memories guiding this S/D performance. Any evidence for item memory would help rule out perceptual transients as the direct source in S/D behavior. Thus, the central question posed in the current experiments was whether specific memories for the individual items in the sequence were controlling S/D behavior. Further, if item-specific memories were involved, how were they combined and integrated with other stimuli and memories into the ongoing stream of behavior? The capacity to examine peck rates at different points in the sequence was critical to this determination.

Our approach examined the fate of the initial item in each *same* and *different* sequence. The initial item was selected because its fortunes were most unambiguous to determine early in the sequence. In the typical alternating *different* trial (e.g. ABAB...) used by Cook et al. (2003), each successive transition further decreased peck rate — as information that the trial would not be reinforced accumulated. It is important to note, however, that this alternating ABAB... "different" sequence contains some inherent ambiguities (see Fig. 1). Specifically, consider the third item in the sequence when the A item is repeated for the first time. When compared back to the second B item, it contributes "different" information about the sequence and should thus decrease peck rate. If compared back in time to the first item, however, it would indicate that this is an S+ "same" sequence and should increase peck rate. The observed peck rate to the third item thus may be a combination of these two conflicting tendencies. This experiment attempted to isolate and reveal the presence of exactly this internal competition. This was done by adding a new type of *different* sequence consisting of a series of three different pictures — producing an ABC sequence. By comparing pecking behavior during and after the third item in these two types of sequences (ABA versus ABC), it is possible to assess the effects of repeating the initial item A at the third serial position. If peck rates to the repetition of A in the ABA sequence are higher than to a new third item C in the ABC sequence, it would indicate that a memory for the first presentation of A is still active and results in a partial "same-like" response. This difference would also indicate that the short-term memory for A is sufficiently detailed that it can be recognized upon its re-presentation after several seconds and intervening items. Moreover, the transition from the second B item to the third A item of ABA sequence involves the same degree of perceptual transient as the transition from the second B item to the third C item of the ABC sequence. Thus, any peck rate difference between these sequences to the third item would argue against any such perceptual transients account.

2. Experiment 1

Two different tests were conducted using this general approach in order to decompose the memories controlling the serial organization of the pigeons' S/D behavior. The first tested a number of *different* conditions in which the initial re-presentation of the first item was systematically positioned at progressively later serial positions in the sequence. Specifically, we looked for memories of the initial item during serial positions 3–6 of a sequence. In the second test, we varied the ISI between the items to examine the effects of temporal separation and delay on this item memory.

2.1. Method

2.1.1. Animals

Three male White Carneaux pigeons (*Columba livia*) were tested. They were maintained at 80–85% of their free-feeding weights in a colony room with a 12:12 light–dark cycle and had free access to water and grit in their home cages. Prior to this experiment, they had participated in Cook et al. (2003) and needed no training for the current tests.

2.1.2. Apparatus

Testing was done in a flat-black Plexiglass chamber (38 cm wide × 36 cm deep × 38 cm high). The stimuli were presented on a color computer monitor (NEC MultiSync C500;

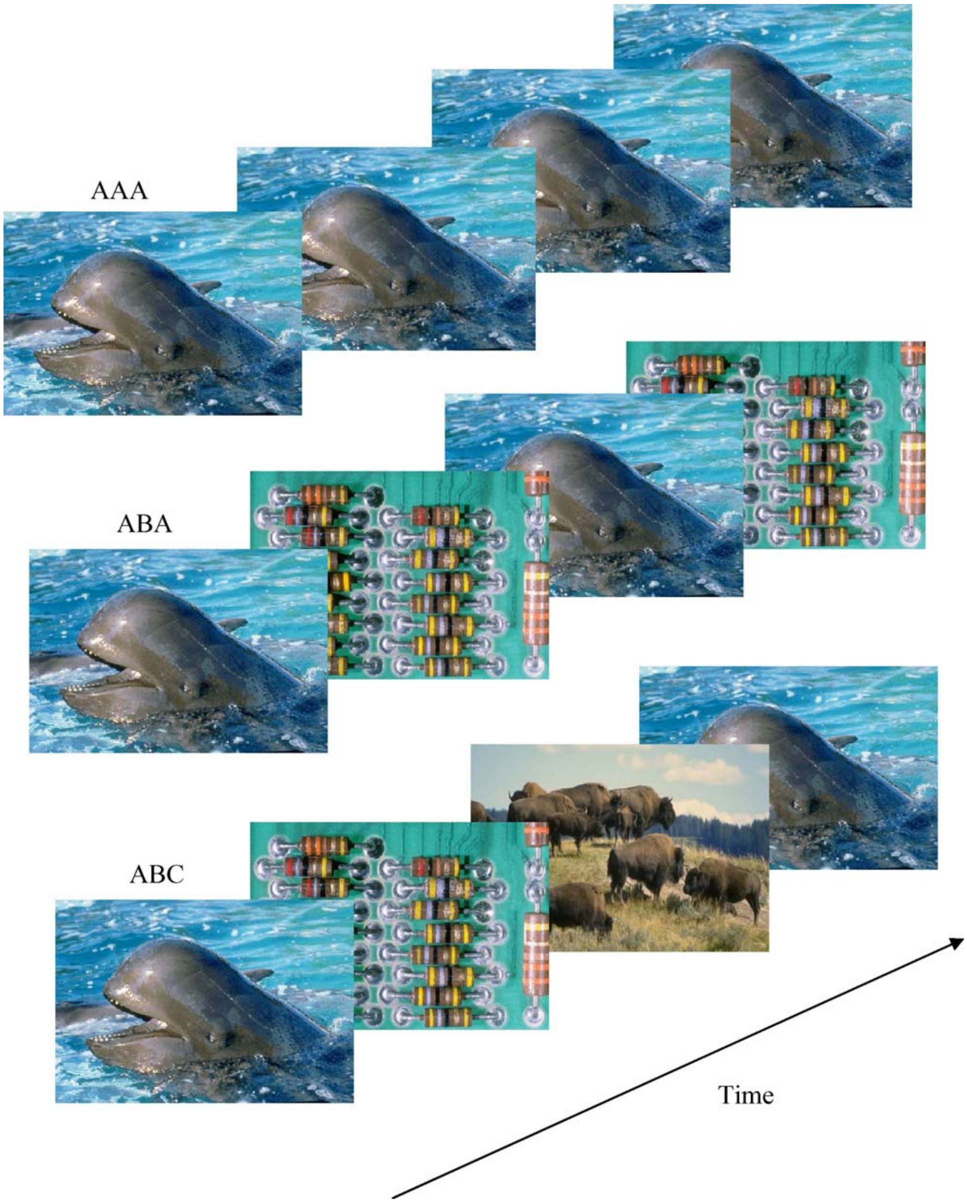

Fig. 1. Schematic representation of the *same* and two of the five *different* sequences tested in Experiment 1. The top sequence shows an AAA *same* trial in which a randomly selected item was repeated over the entire sequence. The middle sequence shows an ABA *different* trial in which randomly selected items were alternated across a sequence. The bottom sequence shows an ABC *different* trial in which randomly selected items were repeated in groups of three across a sequence. Each item appeared for a fixed period of time and was separated by a dark inter-stimulus interval.

McDonough, GA) visible through a 26 cm × 18 cm viewing window in the middle of the front panel of the chamber. The viewing window's bottom edge was 20 cm above the chamber floor. The monitor was protected by a thin piece of glass mounted in this window. Pecks to the monitor were detected by an infrared LED touch screen (resolution of 80 × 48 locations; EMS Systems, Champaign, IL) mounted behind a 40 mm wide Plexiglas ledge that went around the inside edge of the viewing window. A houselight was located in the ceiling of the chamber and was illuminated at all times, except during timeouts. Mixed grain was delivered by a food hopper that was centrally located in the front panel with its access hole flush to the floor of the chamber. All experimental events were controlled and recorded by a computer. A graphics card operated the monitor at an 800 × 600 pixel, 16-bit color resolution. Computer-controlled relays (Metrabyte, Taunton, MA) operated the hopper and house light.

2.1.3. *Testing procedure*

Each trial started with a single peck to the warning signal, followed by a sequence of either identical (AAA. . . = *same* trials) or different (e.g. ABAB. . . = *different* trials) photographic stimuli for 20 s. During each 20-s presentation, each picture was presented for 2000 ms, followed by a 500 ms dark ISI and then the next item in the sequence. Pecks to *different* sequences were never reinforced (S−). Pecks to same trials were reinforced on a VI 10-s schedule (S+). Food hopper presentations were 2.5 s in duration. The picture stimuli used to make each sequence were randomly selected from a total pool 56 color photographs

(480 × 300 pixel). Stimuli consisted of a wide variety of pictures of scenes and objects selected from different picture libraries. An inter-trial interval of 3 s separated each trial.

2.1.4. *Test 1 — Serial Position Test*

Six sequence conditions were tested — five *different* conditions and one *same* condition. In the *same* sequence, all the stimuli were identical across the presentation sequence. In the ABA *different* condition, the successive stimuli alternated between two contrasting stimuli. In the ABC condition, the first three items of a sequence were different and then repeated themselves in this order until the end of the sequence. In the ABCD condition, the first four items of a sequence were different and then repeated themselves for the duration of the sequence. In the ABCDE condition, the first five items of a sequence were different and then repeated themselves. In the ABCDEF condition, the first six items of a sequence were different and then repeated. Within each condition, the specific picture for each *different* component was randomly selected on each trial from the total pool of 56 stimuli available.

Each session consisted of 80 trials. The 40 *different* trials consisted of the five *different* conditions. Because the ABA condition was the baseline condition being tested prior to the experiments it was tested more frequently during this phase. There were 24 ABA trials in total. The remaining *different* conditions (ABC, ABCD, ABCDE, ABCDEF) were tested four times each session. Forty *same* trials (AAA) were also tested in each session. In addition, 15% of the *same* trials were conducted as probe trials in which no reinforcement was delivered to collect uncontaminated measures of peck rates for these trials. All reported S+ data were derived from these probe trials. Because of the small differences in peck rate that we anticipated between *different* condition, 100 test sessions were conducted.

2.1.5. *Test 2 — ISI Test*

Two major changes were made in the second test. First, only three *different* conditions were included (ABA, ABC, ABCD), as the other conditions produced no measurable effects in Test 1 (see Section 2.2 below). Second, we varied the ISI between the successive items of a sequence. The ISIs tested were 500, 1000, and 2000 ms.

Each session consisted of 108 trials. The 54 *different* trials consisted of equal numbers of the three *different* conditions tested at the three ISIs (each combination being tested six times in a session). The 54 *same* trials (AAA) consisted of an equal number of tests with the three ISIs, with 22% of the *same* trials being probe trials. Again, 100 test sessions were conducted with this ISI manipulation, except for bird #2P, who completed 60 sessions.

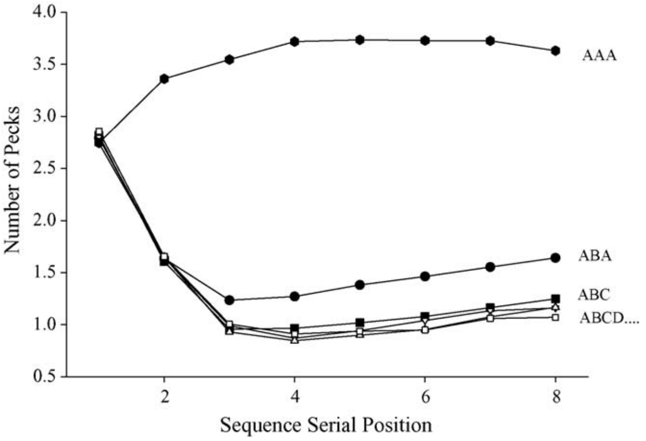

Fig. 2. Mean peck counts across successive items for the *same* and five types of *different* sequences tested in Test 1 of Experiment 1. Because of their great overlap, three conditions are simply labeled ABCD. . . The symbols these conditions are: upward triangle = ABCD; downward triangle = ABCDE; open square = ABCDEF.

2.2. *Results*

2.2.1. *Test 1 — Serial Position Test*

Not surprisingly, the basic discrimination exhibited the same properties as those reported by Cook et al. (2003). *Same* trials produced higher peck rates than *different* trials in all three birds. Turning to the question of central interest, the most important new result is that the pigeons remembered the initial item in the sequences over several seconds and intervening items. To determine this, we counted the combined pecks made during the presentation and subsequent ISI of each item within a trial's sequence of pictures. Fig. 2 shows the results of this analysis for the *same* and separate types of *different* trials tested across the first eight serial positions in each sequence. As can be seen, peck rates during the first item did not differ among the conditions because no disambiguating information had yet been presented. Upon receiving relational S/D information at the onset of second item, substantial peck rate differences between the conditions emerged. Mean peck rates to the second item (3.3) increased relative to the first item (2.7) for the S+ *same* sequence, while mean peck rate to the combined S− *different* sequences decreased (1.6) for the second item relative to the first item (2.7) for all birds. At subsequent serial positions within the sequence, additional differences among the *different* sequences also emerged at different points. A repeated measures ANOVA (condition × serial position) of these S+ and S− data confirmed the presence of significant condition × serial position interaction, F (35, 70) = 12.0 (an alpha level of $p < 0.05$ was used to judge all statistical significance in these experiments).

It is the specific differences among the *different* sequences that are of most interest in the current approach. A repeated measures ANOVA (condition × serial position) of just the five S− *different* conditions further confirmed the presence of a significant condition × serial position interaction among the conditions, F (28, 56) = 6.6. Starting with the simplest comparison, we examined the difference between the ABA and the ABC sequences. At the third serial position in Fig. 2, as these two sequences began to diverge, the pigeons showed a consistently large difference in peck rate from that serial position on for these two conditions. This difference was present in all three pigeons. This is shown in Fig. 3 which displays the individual results for each pigeon for the *different* conditions. Of these types of comparisons, we found the difference between the ABA and ABC conditions supported the largest difference among the birds. The

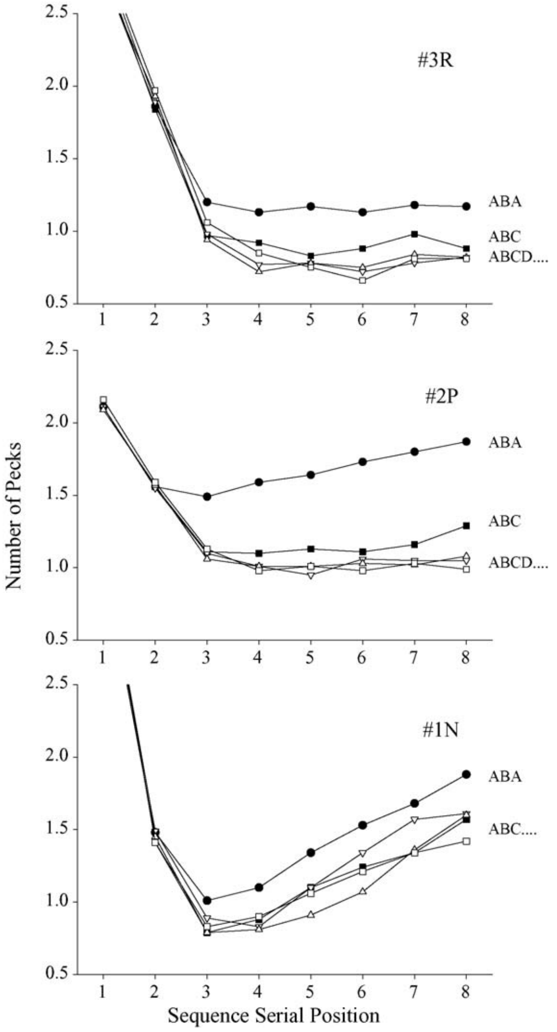

Fig. 3. The individual results for each pigeon in Test 1 of Experiment 1. Displayed are the mean peck counts across successive items for just the five types of *different* sequences tested. The range is adjusted to help see differences in the later serial positions, thus data for the first position is not visible for some pigeons. Because of their great overlap, three conditions are simply labeled ABCD... The symbols these conditions are: upward triangle = ABCD; downward triangle = ABCDE; open square = ABCDEF.

peck rate difference starting at the third serial position indicates that the pigeons must have been recognizing the repeated "same" properties of the first and third items in the ABA condition. Each pigeon showed significant elevation in peck rate during the ABA condition during and after the third serial position in comparison the ABC conditions, Fs $(1, 9) > 12.4$. Nevertheless, the repetition of A in the ABA sequence also produced a decrease in peck rate in comparison to the second B item for all three pigeons (albeit a small one for #2P), suggesting this item also produced "different" properties by virtue of its comparison to the antecedent B item.

Conditions ABC versus ABCD were examined next (the extension (A) has been added to the ABC condition to help clarify the comparisons being made in this section). For these conditions, the point of divergence occurs at the fourth serial position. Because peck rates were typically very low at this point, the differences produced between conditions were small. Pigeon #1N showed no reliable effects of initial item repetition between the ABC(A) and ABCD condition by its equivalent responding at serial position four or later. The other two pigeons did show a consistent and significant difference in peck rate starting at the fourth serial position between the ABC(A) condition and ABCD condition, $F\,(4, 8) = 12.0$, in an ANOVA of their combined data. This difference indicates that these two birds were also recognizing the repeated "same" properties among the first and fourth items of sequence in the ABC(A) condition. Comparisons of the other *different* conditions (ABCDE; ABCDEF) where the initial item repetition occurred much later in the sequence revealed no measurable differences of significance.

2.2.2. *Test 2 — ISI Test*

The most important result from the second test was not only further evidence that pigeons remembered the initial sequence item over several seconds and items, but that this item memory was influenced by the ISI or temporal gap between the items. Shown in Fig. 4 are peck rates for the separate *different* conditions (ABA, ABC, ABCD) as a function of the three ISIs tested. Because certain serial positions were not possible for some ISIs, as the total sequence was limited to 20 s, a repeated measures ANOVA (condition × serial position × ISI) was conducted only on the data from the first five serial positions. This ANOVA confirmed the presence of significant differences between conditions as a function of serial position and ISI, $F\,(24, 48) = 4.1$.

While the general pattern of results is similar across the three panels, several differences are noticeable. First, the number of pecks emitted during the first item varied as the longer ISI provided more time for slightly more pecks to occur. During the second item, all three ISI conditions show similar levels of discrimination in terms of peck rate. Of more current interest is the size of the difference between ABA and ABC condition from the third serial position onwards. Again, all three birds showed higher peck rates to the ABA relative to the ABC condition like in Test 1. This difference progressively decreased for each bird with increasing ISI. The mean peck difference between these conditions was 0.42, 0.32, and 0.25, respectively, for the 500, 1000, 2000 ISI conditions after serial position 3.

The same pattern holds true for the ABC and ABCD comparison, but is much smaller and the individual pigeons differed in the sustained influence of the initial item in the ABCD sequence. But like the ABA/ABC comparison, the differences between these conditions were largest at the shorter ISI (500 ms = 0.1; 1000 ms = 0.07; 2000 ms = 0.07). However, only #3R showed a consistent difference between ABC(A) and ABCD conditions in this test. Bird #1N showed a difference between these conditions at the 500 ms ISI, but no differences at the two longer ISIs. Bird #2P showed no consistent difference between these more demanding conditions at any ISI.

2.3. *Discussion*

Overall the results for the first experiment indicate that the pigeons were influenced by their memory of the first item for at least several seconds into the sequence. All three birds showed a consistent and large peck rate difference at the critical juncture

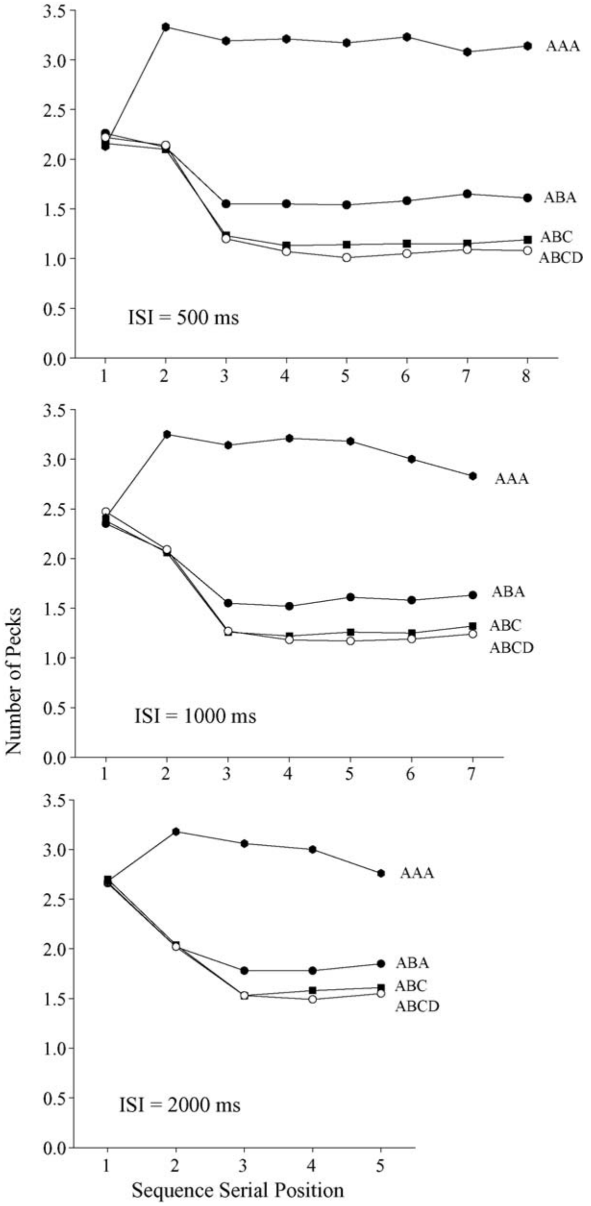

Fig. 4. Mean peck counts across successive items for the *same* and three *different* sequences tested in Test 2 of Experiment 1. The top, middle and bottom panels show the results of each condition for the three ISI (500, 1000, 2000 ms) tested. The increasingly truncated abscissa across the panels was because later serial positions did not occur with longer ISIs.

between the ABA and ABC conditions. In all three birds, peck rates were higher with the repetition of the A item in the third position. This increased peck rate is exactly what one would expect if this repetition was seen as having "same" properties because of its similarity to the first item. This suggests that all three birds were remembering the first item through at least 3–5 s (intervening item presentation times and ISIs) and one intervening item. Once it occurred, this influence was sustained over later serial positions and the difference between conditions did not appear to diminish.

Beyond the influence of item repetition, it should be noticed that this third item was also simultaneously seen as being "different" from the second item. This is reflected in the decrease in peck rate in comparison to the second item in the ABA sequence. Thus, the repeated third item (A) was likely being compared in memory to both the first (A) and second (B) items, but producing conflicting "same" and "different" response tendencies, respectively. To help evaluate whether this conflict occurred within a trial (both items in memory) or between trials (one or the other item in memory, but on separate trials), we looked at the distribution of peck rates during the repeated and non-repeated third items. If the birds were comparing only one item in memory on any given trial, then the peck rates on ABA trials should be a bimodal distribution, reflecting either the "same" and "different" decision determined on each trial (but averaged by their combination during analysis). If the birds were comparing the third item with both previous items in memory, then the distribution might consist of intermediate peck rates more reflective of such a simultaneous conflict. Examinations of the frequency histograms from all individual trials were most consistent with the latter notion, showing a shift in a unimodal distribution of pecks on ABA trials relative to ABC sequences. This suggests the pigeons were sometimes faced with conflicting tendencies in short-term memory about what to do with the third item, with comparisons to the first item increasing peck rate and to the second item conversely driving it down.

It was harder to obtain evidence for item memory into the fourth serial position because of the progressively smaller differences available on the well-discriminated *different* sequences. Nevertheless, one bird (#3R) was consistently able in both tests to remember the first item through 10 s and two intervening items. The other birds were able to remember through two intervening items to a more limited degree during either the first or second phase of the experiment (but not both). For these two birds, this difference only occurred when the ISI was brief (500 ms) and the total time between the first and fourth items was around 5 s. No evidence of first item memory could be obtained for any later serial positions. Whether this reflects a failure of short-term memory or procedural limitation due to a floor effect related to the low rates of responding on these *different* trials can not be determined at this time.

3. Experiment 2

The purpose of Experiment 2 was to examine the effects of initial item duration on the formation of the S/D discrimination. If the pigeons were encoding pictorial information from the stimuli as indicated by the repetition effect detected in Experiment 1, it should be possible to manipulate how much first item information is encoded by varying how long they get to observe this specific item. For example, control by sample item duration is known to have large effects in pigeon matching-to-sample procedures (Maki and Leith, 1973; Roberts and Grant, 1974). On the other hand, if the pigeons were only detecting perceptual transients in the sequence, then viewing time should have little effect, since such low-level features are detected quickly (Cook et al., 1997), and the detail and specific content of the pictures is irrelevant to this account of the discrimination.

For this study, we varied the presentation time of only the initial item in a sequence. Again, the first item was selected because its effects could be most effectively and precisely examined within the sequence. The viewing time of the first item was varied between 500 and 3000 ms across sequences within a session. The effects of this manipulation were then examined by looking at how this duration affected S/D responding to just the second item in the sequence, as this serial position specifically isolated the effects of first item viewing time. As a result, only *same* (AAA) and alternating *different* (ABA) sequences were tested in this experiment.

3.1. Methods

3.1.1. Animals and apparatus

The same pigeons and apparatus were used as in Experiment 1, with the addition of a fourth pigeon who also had received similar training in this successive S/D task (Cook et al., 2003).

3.1.2. Procedure

Each session consisted of 192 (96 same/96 different) trials. Only two trial sequences were tested: AAA same trials and ABA different trials. Trials were conducted similarly to Experiment 1, except that the viewing time of the first A item was manipulated for both *same* and *different* sequences. Four first item viewing time durations were tested (500, 1000, 2000, and 3000 ms). The viewing or presentation time for all subsequent items in a sequence was held constant at 2000 ms. An ISI of 500 ms separated each item. Each viewing time was tested 48 (24 S+/24 D−) times in a session. In addition, 25% of the *same* trials were conducted as probe trials each session. All reported S+ data were derived from these probe trials. An inter-trial interval of 3 s separated each trial. The picture stimuli used to make each sequence were randomly selected from the pool of 56 color photographs. Twenty sessions were conducted.

3.2. Results

The duration of the first item had a significant effect on the subsequent S/D behavior of all four pigeons tested, especially as measured during the critical second item. The 2nd position is most critical because it exclusively isolates just the effects of first item duration, whereas any subsequent serial positions represent the combined effects of several presentations and repetitions. This first item duration effect is shown in Fig. 5, which displays mean discrimination ratio (DR = S+ pecks/[S+ pecks + S− pecks] × 100) across the serial positions for the four first item viewing times tested. Since the different durations of the first item permitted more pecks to be emitted during the longer presentations (mean pecks to first item; 500 ms = 0.76; 1000 ms = 1.46; 2000 ms = 3.1; 3000 ms = 4.7), we used DR to compare performance.

The most critical comparison is among the conditions at the second position, where longer first item durations significantly increased DR during the presentation of the second item. A repeated measure ANOVA (duration × trial type × sessions) confirmed this pattern as a comparison among S+ and S− pecks to just the second item revealed a significant duration × trial type interaction, F (3, 9) = 16.1. This interaction reflects a faster decline in pecking during the second item on *different* trials following long first item presentations (mean pecks to second item; 500 ms = 2.35; 1000 ms = 2.16; 2000 ms = 1.8; 3000 ms = 1.6) in comparison to the *same* trials (mean pecks to second item; 500 ms = 3.3; 1000 ms = 3.3; 2000 ms = 3.4; 3000 ms = 3.3). This significant interaction in peck rate is directly reflected in the DRs displayed in Fig. 5. Comparisons of second item DR performance revealed that all durations supported above chance discriminations by the second item, (mean second item DR; 500 ms = 59, $t(3) = 4.2$; 1000 ms = 61.4, $t(3) = 4.4$; 2000 ms = 65.8, $t(3) = 4.4$; 3000 ms = 68.1, $t(3) = 6.2$). One further possibility that was considered was whether the effect of viewing time might also affect responding to the repetition of the third item. For instance, the poorer encoding reflected at short viewing times might allow a greater gain at the third position because the amount of "same" information generated by this comparison would be reduced relative to longer durations. This seemed to occur in the 1000 ms condition, but not in 500 ms condition. After the second item, it took several additional items to overcome the effects of the initial short presentation of the first item, but eventually all of the conditions converged towards similar high levels of discrimination, although this occurred more slowly for the 500 ms condition.

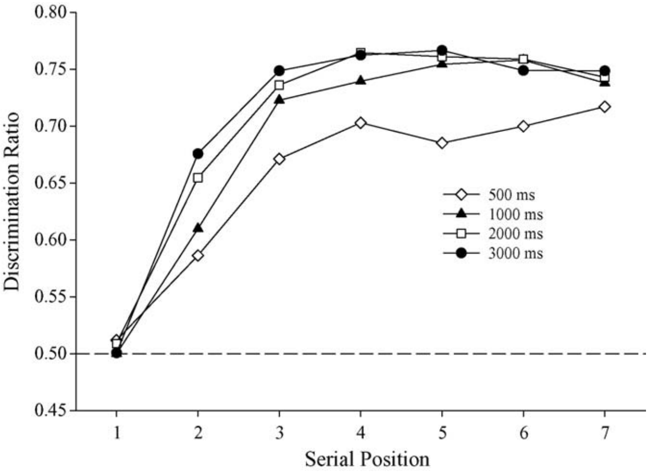

Fig. 5. Mean discrimination ratio as a function of serial position and first item presentation time in Experiment 2. The dotted line shows chance performance.

3.3. Discussion

This experiment revealed that the duration of the first item significantly influences the quality of the S/D discrimination by the pigeons as expressed during the disambiguating second item. The longer the first item is exposed, the better this subsequent S/D discrimination. These results further confirm the results of Cook et al. (2003) and Blaisdell and Cook (2005) that pigeons can perform S/D discriminations based on just two items. Further, as in Experiment 1, these results are inconsistent with the perceptual transient account of this task. Instead, the finding that increasing viewing time for the first item helps discrimination is more consistent with the memory effects seen in Experiment 1. On the one hand, increased viewing time should enable the pigeons to encode more information about the content of the pictures and permit a better comparison of its specific similarity to any subsequently presented item. On the other hand, increased viewing time should, if anything, reduce perceptual transients and flicker.

These viewing time results are generally consistent with those of Wasserman et al. (2002). They found that with 16-item simultaneous arrays of *same* and *different* icons, pigeons increased S/D discrimination performance with increasing numbers of pecks (and time) to the array and could make reliable discriminations with stimulus exposures as little as two seconds. Our results suggest a somewhat faster encoding of S/D properties might be possible. This is mitigated, however, by the fact that our pigeons only had to encode a single item at a time, while Wasserman et al.'s had many more items to process simultaneously. Both of these S/D duration results are consistent with the well-established benefits of increased exposure time on pigeon discriminative performance in general (Guttenberger and Wasserman, 1985; Maki and Leith, 1973; Nelson and Wasserman, 1978; Roberts and Grant, 1974; Sacks et al., 1972). Clearly longer stimulus viewing times engage processes in pigeons that almost universally result in stronger memories and greater discriminative control.

4. General discussion

These S/D experiments document that pigeons can remember and be influenced by the initial item in a pictorial S/D sequence for about 3–10 s after its presentation. This information can be used to determine simultaneously its difference from and similarity to at least two antecedent and intervening memories. All three birds in Experiment 1 were able to remember the first item through at least 8 s (Test 2 — one intervening item presentation time and two 3 s ISIs) and one intervening item. One bird was consistently capable of remembering the first item up to 10 s and two intervening items. The second and third birds were able to remember through two intervening items to a more limited degree, but only when the ISI was brief (500 ms) and the total time between the first and fourth items was around 5 s. Increases in the temporal gaps or ISIs between items reduced the impact, and likely the retention, of the first item in later serial positions. Increases in the viewing time of the first item in Experiment 2 monotonically influenced the strength of first item memory, with longer durations always supporting better discrimination of the subsequent S/D items.

Together, these repetitions, viewing time, and ISI effects strongly indicate that the pigeons were storing information about the specific details of these pictures and using this information across time to generate and guide their S/D behavior. This specificity rules out the alternative account that the birds were simply detecting low-level perceptual changes between temporally adjacent items to perform the discrimination. The beneficial effects of viewing time and the specificity of the content stored across temporal intervals and intervening items are all inconsistent with this account. The memory comparisons identified in these experiments indicate the birds were doing more than responding to the moment-to-moment flux in stimulation. Thus, the current results contribute to the growing evidence that pigeons are indeed able to make generalized relational judgments concerning the similarity and difference of successively and simultaneously presented items (Cook, 2002; Cook et al., 1995, 1997, 2003; Cook and Wasserman, 2006).

The absolute duration of the first item memories detected in these experiments is generally in keeping with the brevity of pigeon short-term memory as previously revealed in matching-to-sample settings, where delays of several seconds are typically enough to substantially reduce matching behavior (Blough, 1959; Farthing et al., 1977; Grant and Roberts, 1973; Kraemer and Roberts, 1984; Maki et al., 1977; Wright et al., 1985). Although active processes may possibly be involved (Maki and Hegvik, 1980), the vast majority of the current evidence suggests that information retention in the pigeon begins to decline with the immediate termination of the item (this may also be true of rhesus monkeys; Cook et al., 1991). Certainly, nothing in the current data would suggest anything more than that. We found no evidence of *specific* first item memories after the fourth item, although the cumulative effect of these earlier experiences may still be operative in some sense in the trajectory of the pigeons' ongoing same and different behavior.

Several recent theoretical papers have also featured this simple trace degradation notion (Killeen, 2001; Wixted, 2004). For example, Killeen suggests in sequential situations similar to the current one, that new information is written into short-term memory during the presence of a particular stimulus and overwrites any previous short-term memories in a probabilistic manner. Additional successive items progressively degrade this and other previous memories, producing a geometric/exponential decrease for each item across time. Attempts to use this overwriting model with the current results provided satisfactory fits to the general patterns of the current data using memory parameter q values similar to those published in Killeen (2001).

One important factor in our experiments was that it was only possible to get uncontaminated measures of the first item's fate given our item-by-item procedure. It has been proposed many times that the first item of a sequence may be special because of its salience or unique position in memory. Although not nearly as ubiquitous as recency effects, some primacy effects have been reported in pigeons and other animals (Machado and Cevik, 1997; Wright, 1998; Wright et al., 1985). How might this impact the current results? Perhaps the first item was processed more deeply because it did provide the initial route, along with the second item, to obtaining the most critical information to determine a trial's reinforcement status. Thus, the first and second items may have been remembered longer than any of the subsequent items that came along later, after the nature of any particular sequence had been firmly established. That the discrimination of each sequence continued to improve over the first 3–5 items, however, suggests that the birds were continuing to integrate information for some time in each sequence.

Although not possible to verify directly in the current setting, our preference would be for an independent trace model, in which each item sets up an identical independent trace that declines similarly with interference (or time) and that this process likely continues for the entire sequence (Grant and Roberts, 1973; Killeen, 2001; Peterson and Peterson, 1959). The current results further suggest that simultaneous S/D comparisons among all of these independent traces can occur during their continued presence in memory. Like in humans, these comparisons within and between items may generate interference that eventually reduces item memory (e.g. Keppel and Underwood, 1962). One potentially interesting way to explore these types of ideas would be to insert at different points in the sequence varying length strings of the alternative condition (a run of *same* items amidst a *different* sequence and vice versa). This would allow one to measure the amount of conflicting information needed to change the direction of behavior after various types of short and long-term experiences, a measurement idea very similar to the notions used to test behavioral momentum (Nevin, 2002).

Finally, much attention has recently been given over to the degree to which animals process episodic events both forward and backward in time (Clayton and Dickinson, 1998; Roberts, 2002). The current results certainly suggest that pigeons at least experience a string of events that continues back in time for several seconds and that are continually "updated" to evaluate whether the current situation is the same as or different from their memory of the recent past. James (1910) suggested that this type of recognition and integration and "sense of sameness is the very keel and backbone of consciousness" (p. 240). Laying the keel, however, is far from completing the ship. Thus, while pigeons likely have a limited sense of sequential continuity to their cognitive "window" on the world, its temporal extent, scope, and flexibility may be dramatically reduced in comparison to primates, for example. The present results suggest that for pigeons this may be on the order of seconds. Thus, the capacity to integrate information over extended periods of time may be critical to understanding differences in animal intelligence and their experience of phenomenological continuity.

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