

Rapid Visual Processing of Picture Stimuli by Pigeons in an RSVP (Rapid Serial Visual Presentation) Task

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Three experiments that were carried out in series with 5 pigeons used novel training methods to investigate the rapid visual processing of picture stimuli by pigeons. On each trial, a sequence containing 1 of 2 bird pictures (the target) and nontarget bird pictures (the distractors) was presented. After the termination of the last item in the sequence, the pigeons were required to choose 1 of 2 colored squares corresponding to the target presented in the preceding sequence. The pigeons learned the task with 2-item lists (1 target and 1 distractor) in Experiment 1 and with 3-item lists (1 target and 2 distractors) in Experiment 2. The pigeons showed better performance when the target appeared last in the sequence (a recency effect) and poorer performance the shorter the item duration. In Experiment 3, the pigeons were tested with 3-item lists, but on half the trials 2 distractors were replaced with blanks; for example, a target-distractor-distractor trial became a target-blank-blank trial and performances on these trials were compared. When the item duration was 80 ms or greater, omission of the distractors did not have an effect of increasing performance, suggesting that the recency effect was determined by simple passage of time. With the item durations less than 80 ms, the distractors interfered with memory of the target. When the distractors were omitted, performance remained slightly above chance even at the shortest, 17-ms, item duration. These findings indicate that pigeons are equipped with visual mechanisms that enable them to process visual stimuli rapidly.

Keywords: rapid serial visual presentation, picture perception, serial position effect, pigeons, comparative cognition

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For some visual species to survive in their natural environments, rapid visual processing is of great biological importance. Wild-living spider monkeys, for example, individually recognize their partners and a large number of other conspecifics quickly and adequately and also discriminate them from other species (J. Delius, personal observation; Jitsumori & Delius, 2001). Nonhuman animals, like humans, must cope with numerous moment-to-moment changes in visual inputs. How fast do they identify objects embedded within a complex background scene? This question is

particularly interesting in relation to species of bird such as pigeons. When they are flying, taking off, or landing, visual inputs may change rapidly from moment to moment. We presume that pigeons identify objects as fast as, or even faster than, humans do. However, only a few studies have examined how fast pigeons can identify objects embedded within a complex background scene.

Ohkita, Obayashi, and Jitsumori (2014) used human faces in a visual search task for pigeons (see also Ohkita & Jitsumori, 2012). Pigeons were required to respond to a target face embedded within distractor faces. The pigeons showed fast search of about 1200 ms in the best case (Experiment 3) of a series of experiments, regardless of the number of identical distractors in a display (i.e., the target popped out of the display). This duration included times to guide attention to the target, to approach and fixate it, and finally to emit a motor response to it. Given that it takes about 250 ms to approach the detected target and 400–500 ms for a motor response (see Cook, Katz, & Blaisdell, 2012), the pigeons likely localized and identified the target within approximately 500 ms after the onset of the search display.

Cook, Cavoto, Katz, and Cavoto (1997) used rapidly changing texture stimuli and examined the time course of pigeons' search for an odd target array of elements that differed in color or shape from those of the distractor surround. Rapidly changing the color of the target facilitated its localization, even when it changed as fast as 100 ms, suggesting that target detection can occur within this temporal range (≤ 100 ms). However, based on previous findings suggesting that 100 ms or less are presumably too brief

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for pigeons to identify specific individual colors (e.g., Cook, Riley, & Brown, 1992), Cook et al. (1997) argued that pigeons responded by relying on relational properties (target-distractor contrasts) rather than on the absolute individual values of the colors presented on a trial (see also Cook et al., 2012; Cook & Wixted, 1997). This argument is related to the distinction between processing of “where” and “what” information in humans (e.g., Atkinson & Braddick, 1989; Zeki, 1993).

The rapid localization of the odd target region in pigeons was confirmed by Cook et al. (2012), using a flanking secondary target. A flanker presented for as little as 100 ms disrupted search for the primary target on some trials. Although the flanker effect was very small, this finding suggested that, at least on some of these trials, the flanker was identified at this duration, and its sudden onset interfered with attentional processing of the primary target. However, the authors acknowledged that the time required to identify the target may have been longer than 100 ms, because longer flankers (500 ms) were more effective than 100-ms ones.

It has been recently demonstrated that nonhuman animals, such as monkeys and pigeons, are capable of learning change-detection memory tasks (Elmore, Magnotti, Katz, & Wright, 2012; Hagmann & Cook, 2011, 2013; Wright et al., 2010). For example, Wright et al. (2010) showed pigeons a 5 s display involving two colored circles. After a 50-ms delay, a test display was presented, in which the color of one of the two circles was changed, and the pigeons were required to peck the changed one. The pigeons learned to detect color changes and showed successful transfer to novel colors. When the pigeons were tested with longer delays of up to 6.4 s between the displays, they maintained accurate performance without prior delay training. These findings indicated that the pigeons detected the color changes by relying on memory for the colors in the first display, instead of a perceptual-based, attentional capture process that may work at very short delays. Hagmann and Cook (2011) used displays that varied in their rate of continuous brightness change and found that pigeons could integrate past experiences over approximately 20 to 30 s. These studies have revealed that people, monkeys, and pigeons share similar visual short-term memory (VSTM) mechanisms (see also Gibson, Wasserman, & Luck, 2011).

In the present study, a series of experiments investigated the rapid visual processing of picture stimuli by pigeons, using novel training methods that allowed us to require pigeons to make a single two-choice response at the end of a single sequence of perceptual events. In the early stage of training, a stimulus sequence included one of two bird pictures (the target) and one nontarget bird picture (the distractor) drawn from a set of distractors on each trial, yielding a two-item list. Then, a second distractor was added, so the sequence consisted of one target and two distractors, yielding a three-item list with the target in Serial Position 1, 2, or 3. The major questions of interest were how fast pigeons would identify the target bird appearing in a rapid sequence of the distractor birds and to what extent the distractors would interfere with visual processing of the target. Category BIRD is a typical natural category and pigeons successfully categorize bird pictures at different levels of abstraction (see Roberts & Mazmanian, 1988).

A trial with a three-item list is illustrated in Figure 1, with the target in Serial Position 2. A blank interval intervened between termination of one item and onset of the next, so that the items in

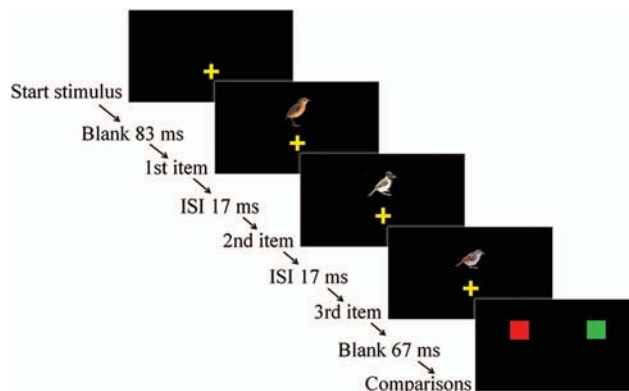


Figure 1. Illustration of a trial, with the target in Serial Position 2 and the distractors in Serial Positions 1 and 3. Each trial began with the display of a cross. A peck to the cross was followed after 83 ms by the first item. The items in the sequence were separated by an interstimulus interval (ISI) of 17 ms; a blank interval intervened between termination of one item and onset of the next. Comparison stimuli (red and green squares) appeared 67 ms after the last item. The left and right positions of the colored squares varied in the actual task. See the online article for the color version of this figure.

the sequence were separated by an interstimulus interval (ISI) of 17 ms. After a 67-ms blank interval inserted at the offset of the last item, the final array that consisted of two colored squares (green and red) appeared. Pigeons were required to choose one of the comparison stimuli that corresponded to the target of the preceding sequence.

The online supplemental material is a video clip of a bird engaging in the task, with each item presented for 133 ms. The task is a modification of the rapid serial visual presentation (RSVP) procedure typically used in human research on visual processing. An advantage of this procedure is that it allows us to directly assess the speed of identifying the target by simply looking at decreases in correct responses as viewing time decreases. The durations of target and distractor were equalized, except the early stage of training in which the target appeared longer than the distractor, so as to eliminate the possibility that pigeons make use of durations to selectively remember the target.

The target and distractor pictures (see Figure 2) depicted birds from a suborder (*Furnarii*) of *Passeriformes*. The task required rapid discrimination of target birds that were substantially similar to, but still discriminably different from, one another and the other birds that served as distractors. Minute discrimination was therefore required, on the basis of visual features that were specific to the individual targets. Thus, the task examined visual processing of concrete objects at an exemplar level rather than of more abstract properties at a category level (e.g., identification of *bird* in general). The rapid visual processing required to identify and discriminate individual objects and, on the other hand, to categorize a variety of objects are both vital in nature. Our first pigeon RSVP study focused on the former.

Three experiments were carried out in series with five pigeons. The assignment of red and green squares with the two different targets were varied across pigeons, but the assignments were consistent for each pigeon throughout the experiments. The goal for Experiment 1 was practical. We simply wanted to develop an

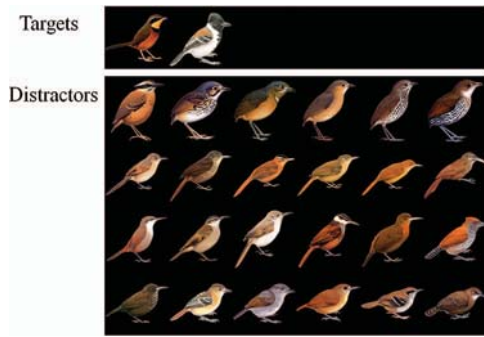


Figure 2. Stimuli that served as targets (two images in the top panel) and distractors (24 images in the bottom panel). The stimuli were reproduced by scanning a set of photographs from *Handbook of the Birds of the World vol. 8* (Barcelona: Lynx) and edited using Adobe Photoshop CS2. The images were presented in color at a refresh rate of 60 Hz, with one frame corresponding to a presentation time of about 17 ms. See the online article for the color version of this figure.

RSVP procedure for pigeons that was comparable to those used for humans, and we succeeded in training pigeons in a task in which a target appeared preceding or following a distractor (a 2-item list consisting of one target and one distractor), with each item presented for 483 ms. In Experiment 2, we extended the method to 3-item lists consisting of one target and two distractors. We gradually decreased the item duration to assess the minimum viewing time needed for identification of the target in Serial Position 1, 2, or 3. In Experiment 3, we tested the pigeons in a new condition in which distractors were replaced with blank intervals. Comparisons between the performances on these and regular RSVP trials allowed us to examine the effects of the distractors on visual processing of the briefly presented picture stimuli. We also assessed the minimum viewing time needed for identification of the target presented alone in the absence of distractors. In humans, a picture as brief as 20 ms is easy to recognize if it is followed by a blank visual field (e.g., Thorpe & Fabre-Thorpe, 2001; Thorpe, Fize, & Marlot, 1996; see Fabre-Thorpe, 2011, for a review). We tested our pigeons by gradually decreasing the viewing time until it reached 17 ms (1 frame).

To measure durations of picture stimulus presentation independent of pecks at these stimuli and to test pigeons with the duration that is too short to make observing response, the comparison stimuli appeared automatically after the offset of picture stimuli to which no observing response was required.

Experiment 1: 2-Item List

The main concern of Experiment 1 was to develop a variant of the human RSVP procedure for pigeons. A key question was whether pigeons are capable of discriminating briefly presented targets to which no observing response is required. This approach is new and challenging. Previous pigeon studies have used long stimulus durations and often required observing responses to produce the appearance of comparison stimuli. It is well known that the pigeon is more likely to observe the discriminative stimulus if a peck to it is required (e.g., Kelleher, Riddle, & Cook, 1962). However, in the present study, we had to avoid having our pigeons

(accidentally) learned to peck picture stimuli to produce the comparison stimuli. To overcome this difficulty, we first trained our pigeons to repeatedly peck at a yellow cross presented alone in the display. The target was then introduced. It appeared near the yellow cross, so that the pigeons could see the target as they were responding to the cross. In addition, we used a changeover-delay procedure to train the pigeons to refrain from pecking at the target.

Method

Animals. We used five homing pigeons (*Columba livia*) that were housed individually. Their weight was maintained at approximately 85% of their free-feeding weight. They had free access to grit and water in their home cage. Four of the five pigeons (Birds 1–4) had experienced several behavioral experiments, but they had never been exposed to the stimuli used in the present study. The remaining pigeon (Bird 5) was naïve to any experimental tasks.

Apparatus. We used four identical handmade operant chambers, sized 29 (W) × 35 (D) × 35 (H) cm, with two birds (Birds 2 and 5) tested individually in the same chamber. The front panel of each chamber had an 16 (W) × 9 (H) cm opening through which the pigeons could access the 15-in color liquid crystal display (LCD) monitor (Touch Panel Systems, Yokohama, Japan, ET1529L-8CJA-1-BG-G), which was equipped with an acoustic pulse recognition (APR) touch sensor (Tyco Electronics, Menlo Park, California, ET1529L-AUJA-1-BG-F). The bottom edge of the viewing window was 20 cm above the chamber floor. A 3W house light located on the transparent ceiling panel illuminated the chamber during intertrial intervals (ITIs). A 6 (W) × 7 (H) cm food aperture located below the viewing window enabled the pigeons to access a solenoid-operated food tray (Sanso Ltd., Tokyo, Japan, CJ-1) containing mixed grains when the birds were rewarded. When the food tray was presented, a small light bulb (a 2W feeder light) immediately below the aperture turned on. Each box was controlled by a computer (Dell, Texas, Vostro 220; OS: Windows XP). The control program was written in Microsoft Visual Basic 6.0.

Microsoft DirectX 7 for Visual Basic allowed frame-by-frame control of the stimulus presentation. The refresh rate of the monitor was 60 Hz so that the theoretical duration of one frame was about 17 ms. To examine the temporal properties of the monitor, we measured the time course of its luminance transition. The measurement revealed that the luminance transition from 10% to 60% with respect to the maximum luminance (100%) took 4.2 ms. The luminance then increased slowly and took another 12.8 ms to reach 90%. The measurement also revealed that the stimulus-offset transition from 90% to 10% took 1.8 ms, ensuring that the images on the monitor went off immediately when the specified duration had elapsed.

Stimuli. Figure 2 displays the bird images used in the present study, each showing its right-side profile. The stimuli were reproduced by scanning a set of photographs from *Handbook of the Birds of the World*, 17 volumes (del Hoyo, Elliott, Sargatal, & Christie, 1992–2013; Barcelona: Lynx). The images were resized so that the maximum length of height or width was 30 mm (100 pixels, where one pixel corresponded to 0.30 mm on the monitor).

The spatial arrangement of the stimulus elements are shown in Figure 3. The bird image located right above the starting stimulus (a yellow cross sized 15 × 15 mm), separated by 30 mm vertically

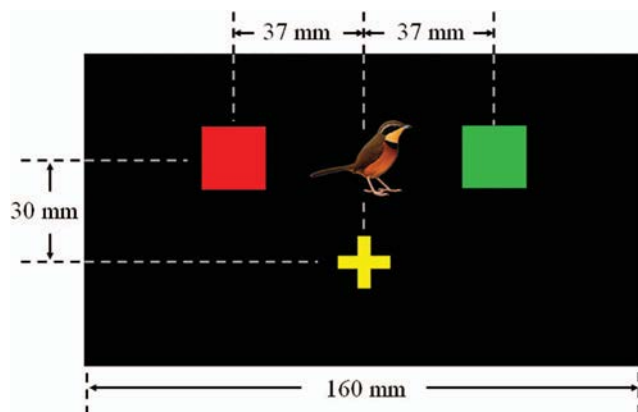


Figure 3. Spatial arrangement of the stimulus elements. In the actual task, the final array on each trial did not include a bird picture but simply consisted of the red and green squares. See the online article for the color version of this figure.

from the center to the center. The comparison stimuli (the red and green squares sized 18×18 mm) appeared either to the left or the right of the bird image, separated by 37 mm from the center of the bird image to the center of each of the squares. The left and right positions of the colored squares varied in the actual task. Note also that, although a picture of a bird is shown between the red and green squares in the figure, the final array on each trial did not actually include a bird picture but simply consisted of the red and green squares.

Procedure. The pigeons received step-by-step training in a series of prior training, target discrimination training, one-item list training, and two-item list training.

Prior training. The pigeons were given one or two sessions with a conventional hand-shaping procedure to establish reliable pecking to the cross. They were then trained under a fixed-interval (FI) 3-s schedule of food presentation; pecks at the end of the interval removed the cross, and this was immediately followed by a food reward. Magazine time was adjusted for each bird so as to maintain it at 80%–85% free-feeding weight. There were 72 trials per session, with successive trials separated by a 5 s intertrial interval (intertrial interval; ITI) during which the houselight was turned on. The pigeons received six sessions.

Target discrimination training. The pigeons were then trained to discriminate the pictures that served as targets. Each trial began with the onset of the cross, the starting stimulus. A peck to it was followed by an 83-ms blank interval during which the pigeon's head resumed its position before pecking. After the blank interval, the target was presented. The target and cross both remained on the screen for 3 s and until the pigeon pecked at the cross at the end of this interval. If the pigeon accidentally pecked at the target, responses at the cross became ineffective for 1 s. The stimulus display was thus not extinguished until a changeover delay of 1 s had passed and a response occurred to the cross.

The comparison stimuli appeared on the screen 67 ms after the offset of the stimulus display and remained on the screen until the pigeon pecked at one of the comparison stimuli (the 67-ms delay was introduced to create a break between the displays for stimulus presentation and recognition test). The association of the red and

green squares with the two different targets varied across pigeons. A correct response blackened the screen and immediately delivered food. An incorrect response produced a 3 s blackout. Following an incorrect response, the same trial was repeated until the pigeon responded correctly. Correction trials were not scored for data analysis.

There were four different types of trials: 2 targets $\times$ 2 positions (left and right) of the correct comparison stimulus. A session consisted of six randomized blocks of 12 trials, with each of the four different trial types appearing three times in a block. Over a session of 72 trials, the same target appeared on no more than three trials in succession. The training continued until performance was at least 80% correct in each of two consecutive sessions.

The fixed-interval value was then gradually decreased across sessions, so that the target duration decreased in steps of 0.5 s until it reached 1 s. Training with a given interval continued until the pigeon again met the 80% correct criterion described above.

One-item list training. After the completion of training with a fixed interval of 1 s, the requirement of pecking the cross at the end of the interval was removed, and the target and the cross turned off automatically at the end of this interval (accordingly, the change-over delay became unnecessary). Consequently, a peck to the cross started trials and produced a target for 1 s, which was followed by the recognition test. This training procedure is referred to as one-item list training. The pigeons were given 12 sessions. Procedural details that were the same as those in the previous training phase have been omitted.

Two-item list training. A pecking response to the cross produced a 2-item list consisting of one target and one distractor with an interstimulus interval (ISI) of 17 ms. The target appeared for 1,000 ms, as before, and the distractor was presented for 483 ms. There were two different types of list sequence. In the T-D sequence, the target (T) occupied Serial Position 1, and the distractor (D) occupied Serial Position 2. In the D-T sequence, the distractor occupied Serial Position 1 and the target occupied Serial Position 2. There were eight types of trials: 2 targets $\times$ 2 sequences $\times$ 2 positions of the correct comparison stimulus. A session consisted of 9 randomized blocks of 8 trials, with each of the 8 trial types appearing once in a block. The distractor was pseudorandomly selected from the pool of 24 bird pictures on each trial, with the restriction that each picture appeared equally often (3 times) in a session of 72 trials. Responses to the list items had no scheduled consequences. The training continued until performance was at least 80% correct in each of two consecutive sessions, and until accuracy of 70% or greater was obtained respectively on T-D and D-T trials (a twofold criterion).

The durations of target and distractor were then gradually equalized until both were presented for 483 ms, by decreasing the target duration (starting from 1,000 ms) to 883 ms, 750 ms, 617 ms, and finally 483 ms. Training with a given duration continued until the pigeons again achieved the performance criterion described above.

Results

Target discrimination training. With the target duration of 3 s, the pigeons required an average of 35 sessions (range = 20–56 sessions) to meet the performance criterion. When the target duration was gradually decreased until it reached 1 s, the pigeons

continued to perform accurately, and they generally required 2 sessions to meet the criterion at a new duration.

One-item list training. When the pigeons proceeded to the one-item list training, they again did not show signs of performance decrement, and the training terminated after 12 sessions. Mean accuracy in the last two sessions for the five pigeons was 90% (range = 88%–93%).

Two-item list training. Mean accuracy in the first two sessions was 89% (range = 88%–93%) on D-T trials and 66% (range = 61%–72%) on T-D trials. The pigeons performed accurately on D-T trials from the beginning of the two-item list training, while performances on T-D trials decreased dramatically. Birds 1, 2, 3, 4, and 5 required 76, 53, 37, 19, and 49 sessions, respectively, to achieve the twofold criterion described above. In the last two sessions, they performed an average of 90% correct on D-T trials and 85% correct on T-D trials. Thus the pigeons successfully learned to improve their performance on T-D trials by practice.

When the target duration gradually decreased, the birds took, on average, 3 sessions at 883 ms, 4 sessions at 750 ms, 5 sessions at 617 ms, and 17 sessions at 483 ms, to achieve the twofold criterion. Figure 4 compares performances on T-D and D-T trials in the last two sessions, with accuracy plotted as a function of target duration (1,000 to 483 ms). Over the whole range of target durations, the pigeons consistently performed more accurately on D-T trials than on T-D trials.

A two-way repeated measures analysis of variance (ANOVA), with sequence (T-D vs. D-T) and target duration (1,000 ms vs. 883 ms vs. 750 ms vs. 617 ms vs. 483 ms) as within-subject variables, was performed. In this and all other tests, an alpha level of .05 was used. Only the effect of sequence, $F(1, 4) = 45.32$, $p = .003$, partial $\eta^2 = 0.919$, was significant. The effect of target duration, $F(4, 16) = 1.73$, $p = .192$, partial $\eta^2 = 0.302$, and the interaction, $F(4, 16) = 0.73$, $p = .584$, partial $\eta^2 = 0.154$, were not significant.

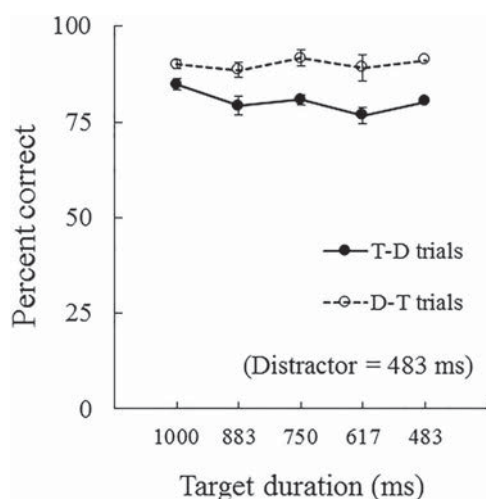


Figure 4. Mean accuracy of target recognition on T-D trials (target in Serial Position 1) and D-T trials (target in Serial Position 2) in the last two sessions of Experiment 1, as a function of the descending sequence of target durations. Error bars are standard errors of the means.

Discussion

It was surprisingly easy for pigeons to discriminate the briefly presented targets to which no observing response was required. A remarkable finding at the beginning of two-item list training was that the pigeons initially showed a strong serial position effect, specifically, a “recency” effect: Target discrimination remained high on D-T trials but was severely disrupted on T-D trials. Previous pigeon studies that used longer stimulus durations have repeatedly demonstrated that this species is strongly inclined to weigh events in the most recent past (e.g., Jitsumori & Sugimoto, 1982; Shimp, 1976; Shimp & Moffitt, 1974).

Nevertheless, the pigeons eventually learned to perform accurately on T-D trials. This performance improvement suggests that the pigeons learned to selectively process a particular picture, that is, the target, and discriminate it from the distractors, a finding similar to voluntary attentional encoding in humans (e.g., Intraub, 1984). However, the recency effect did not disappear completely; the pigeons performed significantly more accurately on D-T trials than on T-D trials over the extensive training with the target duration gradually decreasing from 1,000 ms to 483 ms (see Figure 4). Thus the well-trained pigeons continued to exhibit a recency effect that was not capable of being overcome by practice.

Experiment 2: 3-Item List

Experiment 2 used the pigeons tested in Experiment 1 and extended the method to 3-item lists consisting of one target and two distractors. A major concern was to investigate serial position effects. There were at least three possible outcomes.

1. **U-shaped serial position curve.** A U-shaped serial position curve would result if the magnitudes of recognition accuracy were Serial Position 1 > Serial Position 2 (primacy effect) and Serial Position 2 < Serial Position 3 (recency effect). Distractors both preceding and following the target would cause interference effects. Wright, Santiago, Sands, Kendrick, and Cook (1985) obtained U-shaped curves in people, monkeys, and pigeons by using relatively long item durations and retention intervals in a serial probe-recognition task.
2. **Recency effect characterized by benefit for the last item.** In a recency effect for only the last item, the magnitudes of accuracy would be Serial Position 1 = Serial Position 2 < Serial Position 3. According to the proposal of Potter (1976), based on human studies, all pictures briefly presented in a sequence are momentarily understood. However, when the time available for consolidation of a picture is very short, the immediately following picture causes interference, and all pictures in the sequence are forgotten except the last one. In other words, one immediately following picture is enough to halt visual processing of a preceding picture that is not fully consolidated (see also Potter, 1975; Potter & Levy, 1969; Potter, Staub, Rado, & O'Connor, 2002; Raymond, Shapiro, & Arnell, 1992).
3. **Recency effect characterized by increasing benefit toward the end of the sequence.** If the recency effect

takes the form of increasing recall for items toward the end of the sequence, the magnitudes of accuracy would be Serial Position 1 < Serial Position 2 < Serial Position 3. Memory for a briefly presented target is fragile and lost rapidly with the passage of time. Thus the simple passage of time predicts that recognition accuracy would increase to the end of the sequence. Another possible source of this recency benefit is interference from subsequent pictures in the sequence, not merely the picture immediately following but also those that occur later. Accordingly, there should be less interference when fewer pictures follow a given picture.

An additional question addressed in this experiment is how fast pigeons identify the target in each serial position. The item duration was decreased below 483 ms to discover the minimum duration required for the pigeons to identify the target.

Method

Animals, apparatus, and stimulus materials. The five pigeons that served as subjects in Experiment 1 were used. Housing, maintenance, apparatus, and stimulus materials were the same as in Experiment 1.

Procedure.

Training. The pigeons were placed in three-item list training immediately after Experiment 1 and then received testing in which item duration was gradually decreased. A three-item list consisted of one target and two different distractors, each of which appeared for 483 ms with an ISI of 17 ms. The target occupied Serial Position 1 (T-D-D), Serial Position 2 (D-T-D), or Serial Position 3 (D-D-T). There were 12 different types of trials (2 targets $\times$ 3 sequences $\times$ 2 positions of the correct comparison stimulus). A session consisted of six randomized blocks, with each of the 12 trial types appearing once in a block. Two different distractors in a list were pseudorandomly selected from the pool of 24 bird pictures, under the restriction that each picture appeared once in a block of 12 trials.

The training continued until performance was at least 80% correct in each of two consecutive sessions, and until an accuracy of 70% or better was obtained respectively on T-D-D, D-T-D, and D-D-T trials. If a bird showed no performance improvement to meet this twofold criterion, training for the bird was terminated after 12 sessions. Other procedural details were the same as in the previous experiment.

Testing. Item duration was gradually decreased across sessions. At each duration, three test sessions were conducted, and mean accuracy over the sessions was computed for each pigeon. The test duration decreased (starting from 433 ms) in steps of 50 ms until it reached 133 ms, and then it decreased in steps of 17 ms. The descending testing sequence continued until the pigeon's accuracy for each of the two consecutive test durations fell below 62.5% correct (the lowest limit of accuracy significantly above chance in a binomial test; $p = .05$, $N = 72$).

Before testing with a new duration, baseline session(s) were conducted until performance was at least 80% correct in a session of 483-ms item duration. However, the predetermined criterion had to be mitigated for the birds that performed poorly on T-D-D

and D-T-D trials; the baseline training was terminated after 80% or better accuracy was regained on D-D-T trials.

Results

Training (item duration 483 ms). Discrimination of the targets during the first two days averaged 68% correct (range = 63%–73%) on T-D-D trials, 73% correct (range = 67%–77%) on D-T-D trials, and 85% correct (range = 71%–98%) on D-D-T trials. Two pigeons (Birds 2 and 4) attained the twofold criterion quickly, requiring only 3 and 9 sessions, respectively. The remaining three pigeons (Birds 1, 3, and 5) received 12 sessions, during which they performed 80% or more accurately on D-D-T trials but failed to improve on T-D-D and D-T-D trials. Discrimination of targets during the last two days for all pigeons averaged 64% (range = 54%–81%), 76% correct (range = 65%–83%), and 91% correct (range = 86%–98%) on T-D-D, D-T-D and D-D-T trials, respectively. A recency effect characterized by an increasing benefit toward the end of the sequence was obtained.

Testing (item duration <483 ms). Figure 5 shows performance accuracy on T-D-D, D-T-D, and D-D-T trials as a function of item duration for each of the five pigeons. For one bird (Bird 1), the testing ended at 133 ms. The mean accuracy averaged among the five pigeons was therefore obtained over the range from 433 to 133 ms, as shown in the bottom-right panel. Only one bird (Bird 5) continued to show a recency effect similar to that found in the preceding training phase. In the remaining four birds, performance difference between D-T-D and T-D-D trials was not apparent, with the recency effect characterized by a benefit for the last item.

A two-way repeated measures ANOVA, with sequence (T-D-D vs. D-T-D vs. D-D-T) and duration (433 ms vs. 383 ms vs. 333 ms vs. 283 ms vs. 233 ms vs. 183 ms vs. 133 ms) as within-subject variables, was performed. The main effects were both significant; for sequence, $F(2, 8) = 15.90$, $p = .002$, partial $\eta^2 = 0.799$; for duration, $F(6, 24) = 3.97$, $p = .007$, partial $\eta^2 = 0.498$. Multiple comparison with Shaffer's method revealed that the pigeons performed significantly more accurately with the targets in Serial Position 3 than with those in Serial Position 1, $t(4) = 3.75$, $p = .020$, $r = .88$, and Serial Position 2, $t(4) = 8.16$, $p = .004$, $r = .97$. No significant difference in accuracy was found for the targets in Serial Positions 1 and 2, $t(4) = 0.44$, $p = .681$, $r = .22$. The interaction, $F(12, 48) = 1.79$, $p = .077$, partial $\eta^2 = 0.309$, fell short of significance. These results reflected a recency effect characterized by benefit for the last item, unlike the recency effect found in the preceding training, which was characterized by increasing benefit toward the end of the sequence. The following discussion focuses on this inconsistency.

Discussion

We obtained no evidence of a primacy effect. When item duration remained constant at 483 ms during training, recognition accuracy increased as the target appeared later in the list. In contrast, when item duration decreased in the descending testing series, the pigeons generally performed accurately only with the target in Serial Position 3, with similarly poor performance for the targets in Serial Positions 1 and 2.

The item duration of 483 ms may have been long enough to allow the pigeons to fully process the to-be-remembered target

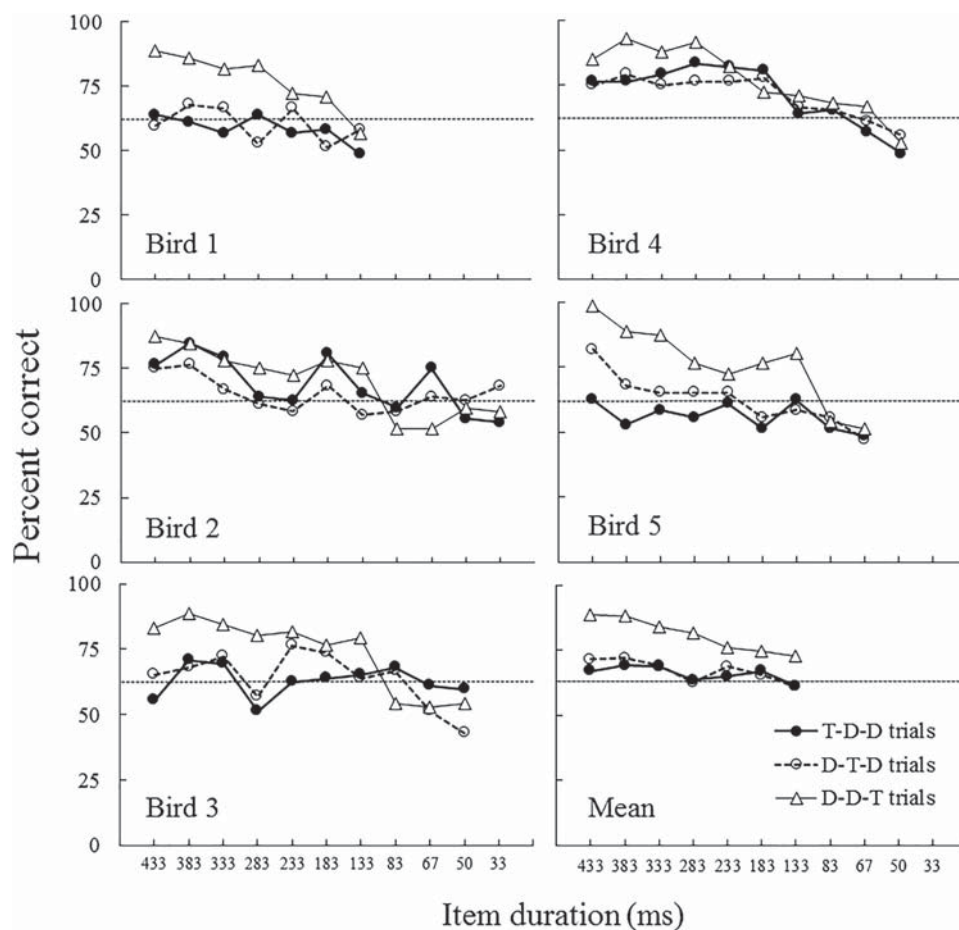


Figure 5. Mean accuracy of target recognition on T-D-D trials (target in Serial Position 1), D-T-D trials (target in Serial Position 2), and D-D-T trials (target in Serial Position 3) in Experiment 2, as a function of the descending sequence of item durations. Dotted lines show the lowest limit of accuracy significantly above chance (binomial test, $p = .05$).

picture while it was in view, so that there was no interference from subsequent pictures. In addition, the pigeons had been long trained with the item duration constant at 483 ms, which may have possibly enhanced encoding of the target. If so, the recency effect can be explained by the simple passage of time; there is no need to postulate any interference between the items. When the item duration decreased during testing, on the other hand, the target pictures may not have been fully processed and they were therefore subjected to interference from the immediately following picture. One distractor may have been enough to halt visual processing of the target. An alternative possibility is that, regardless of item duration, recognition accuracy decreased with the passage of time. The difference in accuracy between T-D-D and D-T-D trials decreased or virtually disappeared when the difference in retention interval became small as item duration decreased during testing. Experiment 3 examined these possibilities.

Experiment 3: Effects of Distractors and Blank Intervals

The pigeons that served as subjects in Experiments 1 and 2 were tested in a new condition in which distractors were replaced with

blank intervals. Performance was compared to that in the RSVP condition, with the delay interval equalized between the conditions. If memory loss of earlier items in a list is due to mere passage of time, performance accuracy should remain unchanged from RSVP trials. If, on the other hand, the distractors interfere with visual processing of the targets, the absence of distractors should improve performance. In addition, Experiment 3 assessed the minimum viewing time needed for identification of the target presented alone in the absence of distractors. We carried out a descending testing sequence, with the targets presented for as brief an interval as 17 ms.

Method

Animals, apparatus, and stimulus materials. The same five pigeons that served as subjects in Experiments 1 and 2 were used. Housing, maintenance, apparatus, and stimulus materials were the same as in the previous experiments.

Procedure. The pigeons received training sessions consisting of two different types of trials with and without distractors.

Training. A session consisted of 96 trials. One half of the trials were RSVP trials, with the three different sequences

(T-D-D, D-T-D, and D-D-T) appearing equally often (16 trials each). In the other half of the trials, the distractors were replaced by a uniform field (blank interval, or B). These trials (T-B-B, B-T-B, and B-B-T) are referred to as TO (Target-Only) trials.

As the pigeons were naïve for TO trials, they were first trained in sessions consisting of RSVP and TO trials. There were 24 different trial types: 2 targets $\times$ 3 sequences $\times$ 2 conditions (RSVP vs. TO) $\times$ 2 positions of the correct comparison stimulus. A session consisted of four randomized blocks of 24 trials, with each trial type appearing once in a block. On six trials per block (three RSVP trials and the same number of TO trials), correct responses raised the food hopper for only 0.5 s in order to prevent the birds from overeating. The probability of food rewards (75%) was equated among targets, serial positions, and left-right correct comparison stimuli. The item duration was set at 483 ms, and the pigeons were trained until 80% or more correct responses were obtained on both RSVP and TO trials in each of two consecutive sessions.

Training continued by gradually decreasing the item duration in steps of 50 ms, until it reached 233 ms, the minimum duration at which the pigeons on average performed 70% correct on RSVP trials in Experiment 2. This training phase was introduced for the birds to become familiar with the targets briefly presented on TO trials. Training at a given duration continued until performance on targets in Serial Position 3 for both RSVP (D-D-T) and TO (B-B-T) trials was at least 80% correct in each of two consecutive sessions. Bird 2 was the exception; this bird met the criterion quickly, and training continued until performance was 80% correct or better on both RSVP and TO trials.

Testing. We performed a descending sequence of tests, with item duration gradually decreasing from 233 ms to 17 ms. These decreases were in steps of 50 ms until the duration reached 83 ms, and then were in steps of 17 ms. Before testing with a new duration, the pigeons received baseline sessions of 233 ms until they achieved the performance criterion applied in the preceding training phase. Four sessions were conducted at each duration.

Results

Training. Figure 6 compares accuracies on RSVP and TO trials in the first two training sessions at each duration. Data points are averages among the five pigeons and are plotted in each figure as a function of the serial position of the target. The percentage in each panel is the overall accuracy.

The pigeons' performance was generally not influenced by the presence or absence of the distractors and showed the same pattern of results on RSVP and TO trials. The blank intervals on TO trials did not appear to improve recognition performance and resulted in a recency effect virtually the same as that occurred on RSVP trials.

A three-way repeated measures ANOVA, with duration (483 ms vs. 433 ms vs. 383 ms vs. 333 ms vs. 283 ms vs. 233 ms), condition (RSVP vs. TO), and serial position (SP1 vs. SP2 vs. SP3) as within-subject variables, was performed. The effect of serial position, $F(2, 8) = 47.75$, $p < .001$, partial $\eta^2 = 0.923$, was significant. Multiple comparison with Shaffer's method revealed that the pigeons performed significantly more accurately with the targets in Serial Position 3, relative to those in Serial Position 1, $t(4) = 10.00$, $p = .002$, $r = .98$, and Serial Position 2, $t(4) = 6.47$, $p = .003$, $r = .96$. Accuracy was significantly greater for targets

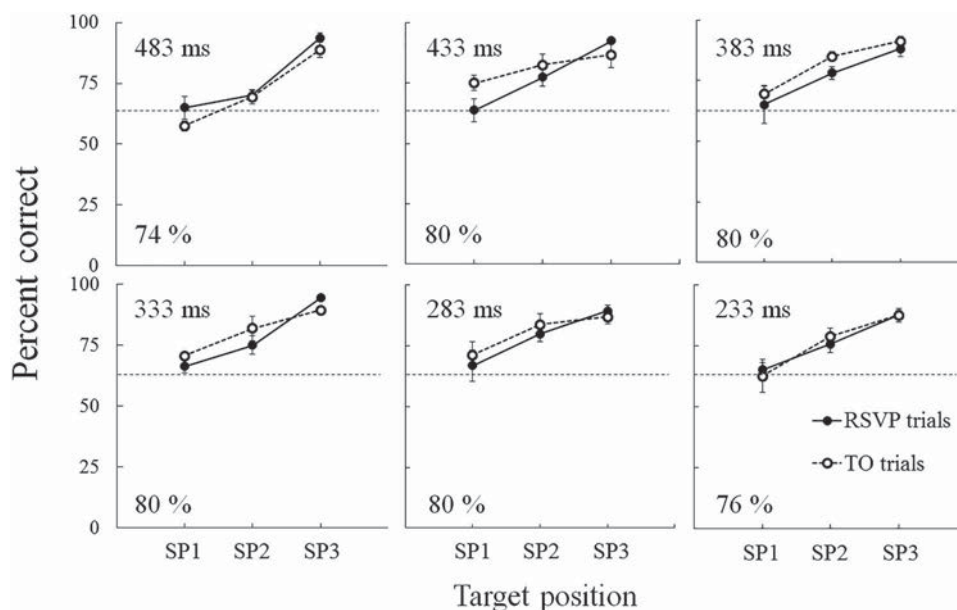


Figure 6. Mean accuracy on RSVP trials and TO trials in the first two sessions of Experiment 3 at each of the gradually decreasing item durations of 483–233 ms, as a function of target position (SP1 = Serial Position 1, SP2 = Serial Position 2, SP3 = Serial Position 3). Dotted lines show the lowest limit of accuracy significantly above chance (binomial test, $p = .05$). Percentages in each panel represent overall accuracy averaged over pigeons and conditions. Error bars are standard errors of means.

in Serial Position 2 than for those in Serial Position 1, $t(4) = 4.03$, $p = .016$, $r = .90$. Thus, a recency effect characterized by increasing benefit toward the end of the sequence was obtained. The effect of duration was marginally significant, $F(5, 20) = 2.67$, $p = .052$, partial $\eta^2 = 0.401$, suggesting that the pigeons tended to perform less accurately when TO trials were first introduced in the 483-ms sessions (a novelty effect). The effect of condition was not significant, $F(1, 4) = 0.50$, $p = .517$, partial $\eta^2 = 0.112$; there was no evidence of impairment of target recognition on RSVP trials. The interactions were not significant. These findings confirmed that the simple passage of time was responsible for the recency effect shown by the pigeons during training.

Testing. Figure 7 compares the mean accuracies on RSVP and TO trials during the descending sequence of testing. Overall accuracy decreased as target duration decreased from the top-left panel (233 ms) to the bottom-right panel (17 ms).

The pattern of results at 233, 183, and 133 ms was highly similar to that observed during the preceding training phase (see Figure 6). When the duration decreased further, the recency effect became weak or even disappeared. Instead, a difference in accuracy between RSVP and TO trials became apparent; the pigeons performed less accurately on RSVP than on TO trials.

Again, a three-way repeated measures ANOVA was performed. The effect of duration, $F(7, 28) = 6.08$, $p < .001$, partial $\eta^2 = 0.603$, was significant, reflecting the finding that the relatively long targets (233, 183, or 133 ms) were generally better recognized than the shorter ones (83, 67, 50, 33, and 17 ms). The ANOVA also showed a significant effect of condition, $F(1, 4) = 45.78$, $p = .002$, partial $\eta^2 = 0.920$; the pigeons performed significantly better on TO trials (average 74% correct) than on RSVP trials (average 68% correct). The interaction, $F(7, 28) = 2.56$, $p = .036$, partial $\eta^2 = 0.391$, of these two variables was significant. The simple main effect of condition revealed significant benefit of the TO

condition at 67 ms, $F(1, 32) = 12.11$, $p = .001$, partial $\eta^2 = 0.177$; 50 ms, $F(1, 32) = 27.47$, $p < .001$, partial $\eta^2 = 0.402$; 33 ms, $F(1, 32) = 14.24$, $p = .001$, partial $\eta^2 = 0.20$; and 17 ms, $F(1, 32) = 8.13$, $p = .008$, partial $\eta^2 = 0.119$. No significant effect was found at 233, 183, 133, or 83 ms. The main effect of serial position was also significant, $F(2, 8) = 17.29$, $p = .001$, partial $\eta^2 = 0.812$. Multiple comparison with Shaffer's method revealed that the pigeons performed less accurately at Serial Position 1 (66% correct) than at Serial Position 2, 72% correct; $t(4) = 5.54$, $p = .005$, $r = .94$, and Serial Position 3, 76% correct; $t(4) = 4.32$, $p = .012$, $r = .91$. The performance difference between Serial Positions 2 and 3 fell short of significance, $t(4) = 2.62$, $p = .059$, $r = .80$. The interaction between serial position and duration was significant, $F(14, 56) = 2.26$, $p = .016$, partial $\eta^2 = 0.361$. The simple main effect of serial position was significant at 233 ms, $F(2, 56) = 17.77$, $p < .001$, partial $\eta^2 = 0.37$; 183 ms, $F(2, 56) = 11.52$, $p < .001$, partial $\eta^2 = 0.241$; and 133 ms, $F(2, 56) = 8.07$, $p = .001$, partial $\eta^2 = 0.169$. When the duration decreased to 83 ms or shorter, the recency effect became less obvious, though the effect was significant at 50 and 33 ms ($ps < .05$). The interaction between condition and serial position was significant, $F(2, 8) = 5.95$, $p = .026$, partial $\eta^2 = 0.598$. The simple main effect of condition revealed that the benefit of TO condition was significant at Serial Position 1, $F(1, 12) = 27.05$, $p < .001$, partial $\eta^2 = 0.404$, and at Serial Position 2, $F(1, 12) = 36.82$, $p < .001$, partial $\eta^2 = 0.551$. No significant effect was found at Serial Position 3, $F(1, 12) = 3.01$, $p = .109$, partial $\eta^2 = 0.045$, where the target was not followed by the distractor on both RSVP and TO trials. The interaction of the three variables was not significant, $F(14, 56) = 0.83$, $p = .631$, partial $\eta^2 = 0.172$.

It is surprising that the pigeons continued to perform significantly above chance on TO trials, even when the target duration decreased to 83, 67, 50, 33, and 17 ms (binomial test, $ps < .05$).

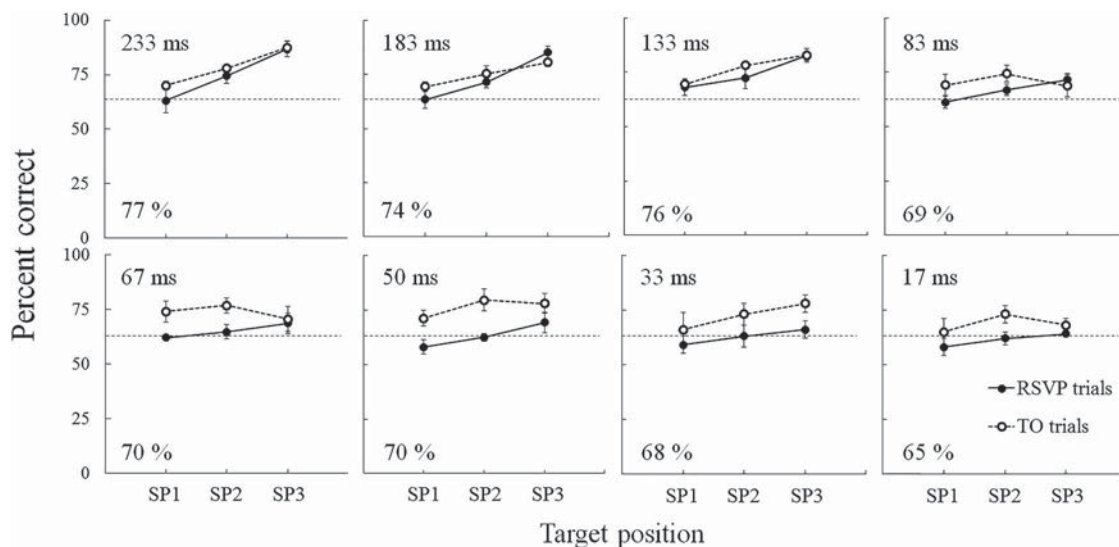


Figure 7. Mean accuracy on RSVP trials and TO trials in the four test sessions of Experiment 3 at each of the gradually decreasing item durations of 233–17 ms, as a function of target position (SP1 = Serial Position 1, SP2 = Serial Position 2, SP3 = Serial Position 3). Dotted lines show the lowest limit of accuracy significantly above chance (binomial test, $p = .05$). Percentages in each panel represent overall accuracy averaged over pigeons and conditions. Error bars are standard errors of means.

Over the range of these durations, the pigeons showed overall accuracy of 70, 76, and 74% correct on T-B-B, B-T-B, and B-B-T trials, respectively. Even at 17 ms (the shortest duration available in this study), recognition performance was slightly, but still significantly, better than chance: 63, 73, and 68% correct on T-B-B, B-T-B, and B-B-T trials, respectively. Our conclusion is that, at least on some TO trials, the pigeons could identify the target when it was presented as briefly as 17 ms.

Discussion

We observed a clear discontinuity in the pattern of results as the target duration decreased. With durations of 133 ms or longer, the distractors did not disrupt performance on RSVP trials, and accuracy increased as the target appeared later in a list (a recency effect). That is, the target and distractors were processed independently of one another (i.e., there was no interference), and visual memory of the target decreased with the simple passage of time similarly on RSVP and TO trials. On the other hand, with durations of 67 ms or shorter, the distractors substantially disrupted performance on RSVP trials, compared with performance on TO trials, and serial position had only a modest effect. It is interesting to note that the sharp discontinuity seems to be consistent with the temporal characteristics of so-called *iconic memory* (e.g., Neisser, 1967) and the following *visual STM* (VSTM; e.g., Posner & Keele, 1968), which constitute a hierarchical visual process proposed in human studies. The first component (iconic memory) has high capacity, is lost rapidly (storage time of about 500–1,000 ms), and is highly sensitive to masking of subsequent stimulation. The second component (VSTM) has limited capacity, is lost slowly, and is not necessarily masked by subsequent stimulation (Avons & Phillips, 1980; Oyama, Kikuchi, & Ichihara, 1981; Kikuchi, 1987; Phillips, 1974).

We suggest that visual processing of the target is completed on most trials in approximately 80 ms. Presumably, pigeons require a minimum viewing time of 80 ms to identify the target. If the distractor appears after the target processing has been completed, visual memory of the (identified) target is not impaired by the distractors, and performance accuracy decreases merely with the passage of time. Thus a recency effect occurred similarly on RSVP and TO trials. If the target terminates before its processing is completed, on the other hand, further processing is disrupted by the distractor immediately following the target.

It has often been shown in human RSVP studies that viewers can continue to process the final picture beyond its actual time in view (*visual persistence*: Potter & Levy 1969; Potter, Wyble, Hagmann, & McCourt, 2014; see also Eriksen & Collins, 1967, 1968; Di Lollo, 1977, 1980). In the present pigeon experiment, the pigeons performed above chance with a target as brief as 17 ms on TO trials (and on D-D-T of RSVP trials, as well). This result may suggest that visual information about the target that is temporarily stored as iconic memory receives further processing necessary for later identification of the picture. However, the present experiment was not designed to examine visual persistence in pigeons. Further research is needed to examine whether nonhuman animals, such as pigeons, continue to process a picture stimulus beyond its actual time in view.

General Discussion

In the present study, we established for the first time that an RSVP task can be used to investigate the pigeon's rapid visual processing of serially presented picture stimuli. The results of Experiment 1 demonstrated that pigeons learned to perform an RSVP task in which one target (T) and one distractor (D) were presented in a T-D or D-T sequence at 483 ms per picture, with an ISI of 17 ms. Recognition performance was accurate when the target appeared as the last item, whereas performance was uniformly less accurate when the target appeared as the first item, thus showing clear evidence of a recency effect.

Experiment 2 extended the method to 3-item lists, with one target and two distractors appearing in a T-D-D, D-T-D, or D-D-T sequence. During training with item durations of 483 ms, the pigeons showed a recency effect characterized by increasing benefit toward the end of the sequence. However, when they were tested by gradually decreasing item durations until their performance dropped almost to chance, a recency effect characterized by benefit for the last item occurred. The limitation of the recency benefit to the last picture in the sequence implied that one distractor immediately following the target was enough to halt visual processing of the target. This finding is consistent with those of human studies that used complex pictures as stimuli (e.g., Potter, 1976; see also Intraub, 1980, 1981, 1984). Potter (1976) suggested that all pictures in the sequences are identified but immediately forgotten. She referred to this interference as *conceptual masking*, as distinct from *perceptual masking*, and she argued that conceptual masking disrupts the consolidation necessary for retention. Although the present study did not allow us to examine whether our pigeons were able to *momentarily* identify the soon-to-be-forgotten target, the test results suggest that pigeons have evolved an encoding process for picture stimuli similar to that of humans. Although the bird's brain is not equipped with a cortex similar to that of mammals, the ability to integrate information over a time period is requisite for monitoring of the coherent environment. We speculate that this common necessity of humans and pigeons may have led to the convergent development of early visual processing in these species (see also Hagmann & Cook, 2013).

Experiment 3 was designed to examine whether the recency effect shown by the pigeons was attributable to simple passage of time or to interference from the following picture in a sequence. We compared memory loss on the regular RSVP condition and the Target-Only (TO) condition. The pigeons received training until they achieved the predetermined performance criterion in sessions consisting of RSVP and TO trials, with durations decreasing from 483 ms to 233 ms. A descending testing sequence, with durations of 233–17 ms, then revealed a sharp discontinuity in the pattern of results, with a boundary at about 80 ms. When the duration was longer than this value, memory loss likely occurred merely with the passage of time. In contrast, when the duration decreased further, the distractors led to forgetting of the target. As already discussed, this finding suggests that visual processing of the target is completed on most trials in approximately 80 ms. That is, pigeons required a minimum viewing time of 80 ms to identify the target picture in the present experimental situation.

Another implication of this finding is that forgetting of the target because of interference from the distractors is not gradual (see Potter et al., 2002, for the time course of forgetting in humans over

a longer range of retention intervals), while picture memory is retained for a while once it is consolidated and gradually lost with passage of time. We speculate that the visual inputs occurring at moments of about 80 ms in duration are integrated to form a coherent visual experience necessary to navigate, search for objects, and execute other motion activities. In the natural environment, visual information may overlap considerably from moment to moment. This was, of course, not the case in the present experiment. It is highly possible that pigeons are able to integrate visual information in the natural environment more rapidly than considered in the present study. We leave answers to this question for future research.

An unexpected finding was that the pigeons continued to perform significantly above chance on trials where no distractor followed the target, even when the target duration was as brief as 17 ms. Thorpe, Fabre-Thorpe, and colleagues (e.g., Fabre-Thorpe, Delorme, Marlot, & Thorpe, 2001; Rousselet, Fabre-Thorpe, & Thorpe, 2002; Thorpe et al., 1996) used a go/no-go task with human participants and found that viewers could decide in under 400 ms whether a picture presented for 20 ms on a given trial contained an animal (see also VanRullen & Thorpe, 2001, for rapid categorization of artificial objects, such as “means of transport”). The event-related potential (ERP) analysis of Thorpe et al. (1996) revealed that the human visual system requires 150 ms to achieve categorization of rapidly presented stimuli. Using the same task, Fabre-Thorpe, Richard, and Thorpe (1998) trained rhesus monkeys to categorize briefly presented natural pictures accurately and very rapidly, with even faster responses than human participants. More recently, Potter et al. (2014) found that human participants in an RSVP task were able to detect and recall a named target or scene (e.g., *boat* or *picnic*) in a sequence of six or 12 novel pictures presented as briefly as 13 ms per picture, even in a viewing condition with no ISI where there was masking. These studies typically used a categorization task, whereas the present pigeon study used a discrimination task with only two bird pictures as the targets. Although we are unable to compare the results from different visual tasks used for different species, we conclude that pigeons, as well as humans and nonhuman primates, are equipped with visual mechanisms that enable them to process picture stimuli very rapidly.

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