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Change Detection by Rhesus Monkeys (*Macaca mulatta*) and Pigeons (*Columba livia*)

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Abstract

Two monkeys learned a color change-detection task where two colored circles (selected from a 4-color set) were presented on a 4×4 invisible matrix. Following a delay, the correct response was to touch the changed colored circle. The monkeys' learning, color transfer, and delay transfer were compared to a similar experiment with pigeons. Monkeys, like pigeons, showed full transfer to four novel colors, and to delays as long as 6.4 s, suggesting they remembered the colors as opposed to perceptual based attentional capture process that may work at very short delays. The monkeys and pigeons were further tested to compare transfer to other dimensions. Monkeys transferred to shape and location changes, unlike the pigeons, but neither species transferred to size changes. Thus, monkeys were less restricted in their domain to detect change than pigeons, but both species learned the basic task and appear suitable for comparative studies of visual short-term memory.

Keywords

change detection; visual short-term memory; visual working memory; monkey; pigeon

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Introduction

Essential to all memory is the ability to store and process information in short term memory (STM). One of the most popular procedures to study human visual short-term memory (VSTM) has recently been change detection. In change detection, several objects (e.g., colored squares) are presented as an array (sample array) followed by a retention delay and then a test array. Participants identify the changed object (or indicate whether or not an object has changed). Change detection is well suited to investigating VSTM because many memory objects can be presented simultaneously within the time period of VSTM, and because the task can be used to estimate the capacity of VSTM. For example, considerable research has shown humans to have a fixed capacity of 4 ± 1 items (Cowan, 2001, 2005).

Nonhuman animals should be eminently capable of learning the change-detection memory task. The task can be made simple (e.g., 2 items), the stimulus change can be made bold (e.g., 50-ms delay) and the contingencies for reinforcement can be made clear (e.g., touch the changed object). Moreover, it has been shown that the task can be performed in the absence of verbal rehearsal without severely impacting performance (e.g., Alvarez & Cavanagh, 2004; Luck & Vogel, 1997).

Animals would provide opportunities over and above what can be accomplished by investigating human VSTM. Animals would provide definitive controls for the role of verbal memory. Animals have neural architectures that differ across species (including humans) and would provide an opportunity to manipulate and study the role of different brain areas in VSTM. Understanding memory of different animal species is important in its own right. Identifying similarities and differences may ultimately lead to better understanding of the roles of different brain structures in VSTM. Change detection presents a rare opportunity to test a variety of animal species in the same memory task with same items for direct comparisons of VSTM memory, perhaps shedding light on the notion of fixed-capacity VSTM as opposed to alternative conceptual frameworks (Elmore et al., 2011; Wilken & Ma, 2004; Bays & Husain, 2008).

Change detection differs from other tasks (e.g., matching-to-sample, same/different) that are typically used to test animal memory. Human visual search (a matching-to-sample task) shows dramatic changes over time compared to stable measures of change detection (e.g., Eng, Chen, & Jiang, 2005). Change detection involves a change across time, whereas same/different (and list memory) involves “no notion of transformation” (Rensink, 2002, p. 250). In change detection, multiple objects to remember are presented simultaneously, while in same/different or matching-to-sample tasks, stimuli are presented one per trial or in a serial list. Additionally, change detection depends upon recognizing that the two object arrays (i.e., sample and test arrays) are related. Perhaps critical to this concept of transformation is that test objects are the same as the sample objects, presented in the same locations—except for the one object that changes. These similar locations and objects provide a “no-change” conditioning context possibly making it easier to relate the two object arrays and learn the concept of transformation.

Rhesus monkeys are an ideal species to train and test in change detection. They have a well-developed visual system comparable to humans and they perform well in other visual memory tasks like list memory (e.g., Wright, 2007). An additional advantage is that the rhesus' brain architecture is more similar to humans than other animal species, for example the pigeon, which has been shown to be capable of learning change detection (Wright et al., 2010). To this end, rhesus monkeys were trained in change detection in order to make direct comparisons to pigeons learning this same memory task with the same training items (colored circles), same transfer tests with longer delays (100ms-6.4s) and same novel-item transfer tests (color, shape, size, location).

The first experiment describes training monkeys in a task similar to the one used to train pigeons (see Procedure Note for differences). Acquisition, as well as color and delay transfer are presented for individual monkeys in the results section, and then mean performances are compared to pigeons from a prior study (Wright et al., 2010) in the Discussion section of Experiment 1. Experiment 2 presents results from further transfer tests with monkeys and results from similar tests with pigeons conducted following the Wright et al. (2010) study.

Experiment 1

We trained monkeys in a change-detection task which required them to view a sample array with 2 different colored circles. Following a 50-ms delay, one circle changed color and the monkeys were required to touch the changed circle in order to receive a pellet or juice reward. After the monkeys learned this task, they were tested with novel color stimuli. They were also tested with longer delays to determine whether their performance was based on memory for the sample stimuli or an attentional capture-like process. Attentional capture can result from the abrupt onset or offset of a stimulus along with an internal mechanism that guides attention to the locus of change (Yantis, 1993). Since the rapid changes (50-ms delay) used in training were within the time range of human attentional capture we extended testing delays well beyond the limits of human attentional capture (e.g., > 1s) so that the monkeys would have to remember the sample stimuli to perform accurately (Cusack et al., 2009; Pashler, 1988).

Method

Subjects—Two male rhesus monkeys (*Macaca mulatta*), Cisco and Captain, were the subjects. Both monkeys had approximately 3 years prior experience in same/different and list-memory tasks. This prior experience occurred in a different chamber with different stimuli (travel slide images), different display configurations, different response templates, delayed vs. simultaneous test presentations and variable vs. fixed stimulus locations. It is our experience that such radically different contexts and task requirements do not result in carryover effects from the prior task or savings in learning the subsequent task.

At the start of this experiment, Cisco was 8 years old and Captain was 12 years old. The animals were tested 5 days per week. On testing days, the monkeys were not fed or watered prior to their individual testing sessions. Immediately following the sessions, the monkeys received their daily requirement of primate chow and water in their home cages. On non-testing days, the monkeys had free access to chow and water as well as fruit and vegetable

supplements. All animal procedures conformed to National Institutes of Health guidelines and were approved by the Institutional Animal Care and Use Committee at the University of Texas Health Science Center at Houston.

Apparatus

Chambers: The monkeys were trained and tested in a (47.5 cm wide $\times$ 53.13 cm deep $\times$ 66.25 cm high) custom-made aluminum test chamber. The monkeys were unrestrained and free to move about the confines of the chamber. A white noise sound generator was located outside of the chamber to mask extraneous noise. An infrared touch-screen (17-inch Unitouch; ELO, Round Rock, TX) detected responses to the computer monitor. Reinforcement was dispensed in 2 ways. Banana pellets (Bio-Serv, 300-mg, Frenchtown, NJ) were delivered into a pellet cup (5.6 cm in diameter and 2.5 cm deep) located below the touch-screen on the left side of the chamber. Cherry Kool-aid was dispensed through a sipper tube located below the touch-screen on the right side of the chamber.

Stimuli: Training stimuli consisted of 4 colored circles that were 4 cm in diameter. RGB 24-bit values for the training stimuli were: Red - 255, 0, 0; Aqua - 0, 255, 255; Yellow - 255, 255, 0; and Purple - 180, 0, 255, respectively. Four additional colored circles were used as transfer test stimuli, and RGB 24-bit values for these stimuli were: Blue - 0, 0, 255; Green - 0, 255, 0; Magenta - 255, 0, 255; and Orange - 255, 128, 0. The circles were presented on an invisible rectangular 4 $\times$ 4 matrix (26 $\times$ 22 cm) which was aligned with the response template. The response template was made of clear Plexiglas and had 16 circular 4-cm cutouts matching the 4 $\times$ 4 matrix.

Experimental Control: Experimental sessions were created, controlled, and recorded using custom software written in Microsoft Visual Basic 6.0. A video card (ATI graphics adaptor) controlled the monitor. A computer-controlled relay interface (Model PIO-12; Metrabyte, Taunton, MA) was used to operate the green light, pellet dispenser, and the juice system.

Pretraining Procedure—Pretraining sessions contained 96 trials. Trials began with the presentation of an achromatic circular stimulus for 3 seconds in one of the 16 positions on the invisible 4 $\times$ 4 grid. After a 50-ms delay, the circle would change from white to grey or from grey to white. The monkeys received Cherry Kool-aid or Banana Pellets for touching the circle (FR 1) after it changed. Trials continued until the monkey responded. Later pretraining sessions were similar but the 4 colored training stimulus circles were used. Trials were separated by a 15-second intertrial interval (ITI), during which the chamber was illuminated with green (25 watt) light bulbs located outside of the chamber. Green light illuminated the chamber through a small (0.5 cm) gap between the touchscreen and the monitor.

Cisco required 10 shaping/pretraining sessions to respond reliably in the new chamber. For one 96-trial session, Cisco was presented with a white circle randomly placed in 1 of 16 possible locations (varied from trial to trial) which he was required to touch (FR 1) in order to receive reinforcers. He failed to touch the circles despite extensive response shaping. The template was then removed and Cisco completed 3 sessions of his familiar same/different

task in order to encourage responding in the new chamber. Next, he was returned to the white circle procedure for 2 sessions, with the template reintroduced on the second session. He responded more readily during these 2 sessions and then completed 4 sessions of pretraining with the training stimuli (4 colored circles). During this phase of pretraining, a single randomly selected colored circle was presented for 3 seconds on each trial, and then it changed to one of 3 other colors. The first response after the color change was reinforced. Captain responded more readily than Cisco and began change-detection training after 2 sessions of pretraining.

Change-Detection Training—Figure 1 shows two examples of change-detection trials. Trials began with a 5-s presentation of two circles (sample array) of different colors in 2 positions on an invisible 4×4 matrix. Next, there was a 50-ms delay during which the screen was blank. The test array then appeared, consisting of two circles in the same positions as the circles in the sample array, but one circle had changed color. Banana pellet and Cherry Kool-aid reinforcers were allocated pseudorandomly, following correct choice responses. Cisco received juice on 70% of correct trials and pellets on the remaining 30%, whereas Captain received 50% juice and 50% pellets on correct-response trials. Pellet and juice ratios were calibrated to the individual monkey's preferences. Other experimental details were identical to pretraining.

Training sessions were 96 trials. Each monkey had 2 hours to complete one session per day. If the session was not completed in one day, it was continued the next day (this rarely occurred). Trials were counterbalanced such that the four training colors appeared as sample stimuli and as the changed-to color with equal frequency.

Several procedural manipulations were made to enhance acquisition for the monkeys including: a correction procedure of repeating incorrect trials, a short 5-s ITI, and a 0-s delay between the sample and test arrays to enhance perception of the sample-test array transition. The 0-s delay was in effect for a maximum of 14 days and Captain had the shorter ITI for the first 48 sessions of training. Training continued until the monkeys achieved 80% correct on a session. The correction procedure was then removed and training continued until the monkeys achieved one session with performance 80%.

Color Transfer—Immediately following acquisition, the monkeys were tested in 6 consecutive color-transfer test sessions. In each test session, 12 test trials composed of novel color stimuli replaced 12 training trials within the 96-trial session. The 4 novel colors were blue, green, magenta, and orange. Each novel color appeared in the sample array on 6 trials and served as the change-to stimulus in 3 of the 6 trials where it was not in the sample array. Correct responses on test trials were reinforced, as in training trials.

Variable Delay Testing—Following the color transfer test, the novel colors used in that test were incorporated into baseline training. Both monkeys were trained with all 8 colors until they achieved a criterion of 1 session 80% correct with correction procedure followed by one session 80% correct without the correction procedure (Captain: 16 sessions; Cisco: 18 sessions). They were then tested with variable delays for 24 consecutive sessions. Within each session, delays of 100, 200, 400, 800, 1600, 3200, and 6400ms were

randomly intermixed with the original 50ms training delay (total of 12 trials per delay per session). All correct responses were reinforced.

Results

Acquisition—Figure 2 shows learning functions for individual monkeys trained in this task. Captain and Cisco both showed an early increase in performance to 81%, but these performances were not counted towards acquisition criterion because they likely resulted from the special 0-s delay training. Following the 0-s delay training, both monkeys' performance gradually rose to 80% with Captain and Cisco meeting criterion on sessions 51 and 53 respectively.

The last 3 sessions of acquisition were analyzed to determine whether touching a particular object in the sample array would influence the monkey's later choice response. Monkeys made touch responses during the sample array a mean of 2.49 ± 0.32 (S.E.M.) times per trial. Captain's accuracy was not influenced by the object that he touched prior to the change ($M = 81.7\%$ for last-touch changed item vs. $M = 83\%$ for last-touch unchanged item, paired sample t -test, $t(2) = 0.227$, $p = 0.841$). Cisco's accuracy, however, was influenced by the last object he touched prior to the change ($M = 88.04\%$ for last-touch unchanged item and $M = 74.2\%$ for last-touch changed item, $t(2) = 7.407$, $p = 0.02$, $d = 2.63$).

Color Transfer—Figure 3 shows novel color transfer results. Cisco and Captain both transferred well to the novel colors, averaging 72.2% and 83.3% correct respectively while performing 78.8% and 80.7% correct on baseline trials, respectively. Neither monkey's color-transfer performance was significantly different from their respective baseline as determined by paired sample t -tests (Cisco: $t(5) = 1.09$, $p = 0.33$; Captain: $t(5) = 0.48$, $p = 0.65$). Session 1 transfer performance for Captain and Cisco was 92.0% and 83.0% correct respectively, and both were significantly above chance (binomial tests, $p_s = 0.01$).

Variable Delay Testing—Delay performance is presented in Figure 4. Separate one-way repeated measures ANOVAs for delay repeated over sessions were conducted on each monkey's performance revealing a significant effect of delay for both [Cisco: $F(7,23) = 8.02$, $p < 0.001$, $\eta_p^2 = 0.26$; Captain: $F(7,23) = 9.20$, $p < 0.001$, $\eta_p^2 = 0.29$]. As shown in Figure 4, performance decreased as delay increased from 50 to 6400 ms. Mean performance, however, was not significantly correlated (Pearson product-moment correlation) with session for either monkey (Cisco: $r = -0.31$, $p = 0.14$; Captain: $r = 0.18$, $p = 0.39$). Because performance was stable across session but differed across delays, we compared mean performance at each delay across test sessions using single-mean t -tests against chance (50%). Mean performance at each delay was significantly above chance (all $t_s(23) > 2.46$, all $p_s < 0.02$, all $d_s > 0.51$). The stable performance on these delay tests coupled with no prior longer-delay training suggests mnemonic processing of the sample stimuli at all delays (including the 50-ms training delay) and immediate transfer of this memory to longer delays.

Figure 5 compares the mean monkey acquisition with mean pigeon acquisition in a nearly identical task (Wright et al., 2010). (Results from individual pigeons are shown in Wright et al., 2010). These six pigeons were trained with the same stimulus colors (presented at the same visual angle as the monkeys) and their task was identical in terms of timing and

response requirements. Time to acquisition was similar for the two species, with pigeons averaging 42 sessions (range 2784 – 5760 trials) and monkeys averaging 52 sessions (range 4896 – 5088 trials) to meet criterion. As shown in Figure 5, the monkeys showed an early rise in performance during the time in which they were trained with a 0-s delay. The procedures for the monkeys were then changed to match those for the pigeons; unfortunately their performance suffered upon this change to the 50-ms delay was instituted (see Figure 2: Session 12 for Captain, Session 32 for Cisco). Because Captain's 0-s delay training occurred at the start of training, his performance fell to chance (50% correct) at session 12, resulting in a large difference in performance between the pigeon and monkey groups from session 12 to 42, after which the monkeys appear to catch up to the pigeons. Although the 0-s delay training was intended to speed acquisition for the monkeys, the change to 50-ms delay appears to have been detrimental (particularly for Captain) and may have actually slowed acquisition. In any case, both monkeys and pigeons achieved criterion for acquisition in a similar amount of time.

Comparing accuracy and sample responding following acquisition, Captain was equally accurate regardless of whether he touched the object that would or would not change, while Cisco was more accurate when he touched the item that would not change. Interestingly, pigeons were more accurate if they had been pecking the object that would change (85.0%) versus the object that would not change (69.6%). This difference in performance was statistically significant (paired samples *t*-test, $t(5) = 3.73$, $p = 0.01$, $d = 1.52$).

Both species performed well when tested with 4 novel colors as shown in Figure 6. Like monkeys, the pigeon color transfer was not significantly different from their baseline performance (Wright et al., 2010). In addition, monkeys and pigeons did not differ in their color transfer as shown by a three-way repeated measures ANOVA of Trial Type $\times$ Session $\times$ Species (Pigeon, Monkey), $F(1, 5) = 3.50$, $p = 0.11$, which did not reveal any significant interactions.

The mean variable delay transfer performance for monkeys and pigeons is shown in Figure 7. A three-way repeated measures ANOVA of Session (1–24) $\times$ Delay (50–6400ms) $\times$ Species (Pigeon, Monkey) revealed a significant effect of species, $F(1, 5) = 7.45$, $p = 0.04$, $\eta_p^2 = 0.60$. Interestingly, pigeons were more accurate than monkeys in this test. There was also a significant interaction of Delay $\times$ Species, $F(7,35) = 2.33$, $p = 0.05$, $\eta_p^2 = 0.32$. This interaction was due to the more rapidly declining monkey performance at delays longer than 400 ms. The ANOVA also revealed a significant effect of Delay [$F(7,35) = 21.69$, $p < 0.001$, $\eta_p^2 = 0.81$], demonstrating that performance declined as delay increased for both pigeons and monkeys.

Discussion

The results of Experiment 1 demonstrate that the monkeys learned the change-detection task. Learning was not restricted to the training colors, as both monkeys showed full transfer (transfer equivalent to baseline) to novel color stimuli. In addition, both monkeys performed above chance at all delays in the variable delay test, with no obvious abrupt drop in accuracy, suggesting that performance was unlikely to depend solely on an attentional-capture mechanism. It is important to emphasize that delay performance was not extensively

trained before the results in Figure 4 were collected. The monkeys were abruptly tested on the new delays out to 6.4 seconds. Stimulus-driven attentional capture is a bottom-up process which can result from abrupt stimulus changes and from the onset or offset of stimuli (Yantis, 1993). Attentional capture results from these abrupt changes through an internal mechanism that guides attention to the locus of change. Although the 50-ms initial color-change delay may have been within a human attentional-capture window, longer test delays (800–6400) were well beyond the limits of human attentional capture (Cusack et al., 2009; Pashler, 1988). If attentional capture were critical to these change detection results, then performance should have fallen abruptly to chance once the delay was beyond the limits of attentional capture (likely in about 1 second). However, considering that the monkeys were above chance performance at all delays, that they transferred quickly to longer delays, and that their performance gradually (not abruptly) fell as delays increased, it is highly unlikely that the monkeys' change detection was mediated by attentional capture.

In summary, both pigeons and monkeys learned the change-detection task to a high criterion of 80% correct. They transferred to novel colors at a level equivalent to their baseline performance confirming that pigeons and monkeys learned to detect color changes generally as opposed to learning something specific to their 4 training stimuli. Both species were able to perform the task at delays exceeding the limits of attentional capture, without extensive training. Lastly, pigeons performed better than monkeys with increasing delays.

Experiment 2

The results of the novel color transfer test in Experiment 1 showed that both species learned to detect color changes including changes with novel colors not used in training. In order to test whether color-change learning was restricted to circular stimuli, pigeons and monkeys were tested with color changes of novel shapes. In order to test whether color-change detection would transfer to other dimensions, both species were tested with shape changes, location changes and size changes.

Method

Subjects—The subjects were the same two monkeys that participated in Experiment 1, plus 5 of the White Carneaux pigeons whose performance was previously compared to that of the monkeys in Experiment 1. The pigeons ranged in age from 2 to 7 years old, and were acquired from the Palmetto Pigeon Plant (Sumter, SC). Pigeons were tested 5 days per week. Two pigeons were tested at the University of Texas Health Science Center at Houston, and 3 pigeons were tested at Auburn University (a collaboration using identical testing chambers). The pigeons at Auburn, similar to the monkeys, had prior experience in a same/different task in a different chamber. They were maintained at 85% of their free-feeding weights, and had free access to grit and water in their cages. The tests reported here were conducted immediately following those of Wright et al. (2010). All animal procedures conformed to National Institutes of Health guidelines and were approved by the Institutional Animal Care and Use Committees at the University of Texas Health Science Center at Houston and at Auburn University.

Apparatus

Chambers: The monkeys were tested in the chambers described in Experiment 1. Pigeons were tested in two, nearly identical, custom-built wooden test chambers. The pigeons' monitors and touchscreens were the same as previously described for the monkeys. The pigeons' touchscreens were 16.5 cm from the floor of the chamber, a height that allowed pigeons to easily reach to peck. A grain hopper was centered below the touchscreen and delivered mixed grain for reinforcement.

Stimuli: The 8 different colored circles from Experiment 1 were used as baseline stimuli for the tests in Experiment 2 and as test stimuli for the location change test. Test stimuli included 7 shapes (butterfly, club, heart, pentagon, rectangle, star, triangle) in 8 colors (aqua, blue, green, magenta, orange, purple, red, yellow). The size of the matrix (9 cm horizontal, 7 cm vertical) and stimuli (1.5 cm diameter) for pigeons was equated to the visual angle of the monkeys' matrix and stimuli.

Procedure

Color-change detection with novel shapes: Monkeys and pigeons were tested with the 7 novel shapes for 18 sessions with one sample object changing color. The 18 sessions were divided into 3 blocks of 6 sessions with each session having 14 test trials intermixed with 82 baseline training trials. In the first block of 6 sessions (Shape Test 1) there was one novel shape per trial displayed in 2 different colors in the sample array; one object changed to a third color in the test array. For example, if a red heart and a blue heart were displayed in the sample array, then following the delay, the blue heart might change to a green heart in the test array. In the second block of 6 sessions (Shape Test 2), there were 2 different shapes (and colors) in the sample array and one object changed color for the test array. For example, if a purple club and a yellow triangle appeared in the sample array, then the yellow triangle might change to a magenta triangle in the test array. In the third block of six sessions (Shape Test 3), there were 2 shapes and 2 colors in the sample array, and then one object changed in both color and shape. For example, if the sample array consisted of an orange rectangle and an aqua star, then the aqua star might change to blue pentagon in the test array. All correct responses were reinforced.

Shape-change detection: Monkeys and pigeons were tested for their ability to detect changes in shape over the course of 12 test sessions following the test for color changes with novel shapes. As before, there were 14 test trials per session. In the first test block of 6 sessions (Shape Test 4), there were 2 shapes and 2 colors in the sample array, and then one changed in shape (i.e., no color changes). For example, if there was a purple triangle and a magenta star in the sample array, then the magenta star might change to a magenta rectangle for the test array. The last block of six sessions contained 2 kinds of test trials (7 of each per session). One (Shape Test 5A) had 1 shape in 1 color in the sample array, and one object would change shape. For example, if there were two green clubs in the sample array, then one of the clubs might change to a green triangle. The other (Shape Test 5B) had 2 shapes in 1 color in the sample array and 1 item would change in shape for the test array. For example, if there was a red pentagon and a red heart in the sample array, then the red heart might change to a red butterfly. All correct responses were reinforced.

Location-change detection: Over 7 sessions (12 test trials per session), monkeys and pigeons were tested with changes in location. Location-change trials started with 2 colored circles in the sample array, as in the original training. After the delay, both circles remained the same colors, but one circle moved to a new location. Responses to the circle that had changed location were reinforced.

Size-change detection: Using the 7 shapes described previously, monkeys and pigeons were tested for their ability to detect changes in size. Fourteen test trials were tested in each of six 96-trial sessions. A typical test trial was composed of 2 shapes displayed in the same color in the sample array (e.g., orange star and orange triangle). Following the delay, one of the shapes either increased or decreased in size by 25%. Responses to the item that had changed size were reinforced.

Results

Color-change detection with novel shapes—Figure 8 shows mean baseline and test performance by the monkey and pigeon groups. A four-way repeated measures ANOVA of Block (Shape Test 1–3) $\times$ Session (1–6) $\times$ Trial Type (Baseline, Transfer) $\times$ Species revealed a main effect of Trial Type, $F(1,5) = 91.74$, $p = 0.002$, $\eta_p^2 = 0.95$. The ANOVA also revealed a significant interaction of Block, Trial Type, and Species, $F(2,10) = 6.59$, $p = 0.02$, $\eta_p^2 = 0.57$. This interaction was due to lower performance by monkeys on test trials (average of 60.0% correct) than on baseline trials (average of 73.0% correct) during the first two test blocks, whereas pigeon performance was stable throughout. The monkeys' performance was not significantly greater than chance in Shape Test 1 [separate single mean t -tests, all $t_s(1) < 0.6$, $p_s > 0.2$]. However, their performance was significantly greater than chance in Shape Tests 2 and 3 as indicated by separate single mean t -tests [Test 2: Cisco $t(1) = 4.59$, $p = 0.003$, $d = 1.87$; Captain: $t(1) = 2.49$, $p = 0.02$, $d = 1.01$; Test 3: Cisco: $t(1) = 6.38$, $p < 0.001$, $d = 2.60$; Captain: $t(1) = 4.39$, $p = 0.003$, $d = 1.79$]. Pigeons performed significantly better than chance in all tests as determined by single mean t -test [Test 1: $t(4) = 8.45$, $p = 0.001$, $d = 3.78$; Test 2: $t(4) = 7.92$, $p = 0.001$, $d = 3.55$; Test 3: $t(4) = 15.73$, $p < 0.0001$, $d = 7.04$]. Interestingly, pigeons performed more accurately (72.4%) than monkeys (52.8%) in Shape Test 1. In addition the pigeons' good transfer on the test was not due to rapid learning, as their mean first session performance was 70%.

Shape-change detection—Figure 9 shows shape-change detection by monkeys and pigeons. A four-way repeated measures ANOVA of Block (Shape Test 4, 5A, 5B) $\times$ Session (1–6) $\times$ Trial Type (Baseline, Transfer) $\times$ Species revealed a significant interaction of Trial Type and Species, $F(1,5) = 7.24$, $p = 0.04$, $\eta_p^2 = 0.59$. This interaction is due to the fact that monkeys performed better than pigeons on these shape tests where shape change had to be detected. There were no significant interactions with session, nor was there a main effect of session confirming that performance was relatively stable throughout the test for both species. The monkeys performed well in Shape Tests 4 and 5A. Their test performance was not significantly different than baseline, as demonstrated by paired samples t -tests [Cisco: Test 4: $t(5) = 0.89$, $p = 0.40$, Test 5A: $t(5) = 2.29$, $p = 0.07$; Captain: Test 4: $t(5) = 0.49$, $p = 0.60$, Test 5A: $t(5) = 0.44$, $p = 0.68$]. However, in Shape Test 5A, both monkeys performed significantly worse on test trials as confirmed by paired samples t -tests [Cisco: $t(5) = 3.73$, p

= 0.01, $d = 1.85$; Captain: $t(5) = 6.45$, $p = 0.001$, $d = 2.27$]. By contrast, the pigeons' performance was not significantly different than chance throughout these tests (single mean t -tests, $t(4) < 1.71$, $p > 0.16$). Thus, monkeys transferred to shape changes, whereas pigeons did not.

Location-change detection—Figure 10 shows transfer of location-change detection by monkeys and pigeons. A three-way repeated measures ANOVA of Session (1–7) $\times$ Trial Type (Baseline, Transfer) $\times$ Species (Monkey, Pigeon) revealed a significant interaction of Trial Type and Species $F(1,5) = 96.58$, $p < 0.001$, $\eta_p^2 = 0.95$. This interaction resulted from the difference in performance on location change trials between the two species; namely the monkeys outperformed the pigeons in this test. The pigeons mean performance of 45% correct was not significantly different from chance (single mean t -test, $t(4) = 4.71$, $p = 0.18$, $d = 1.21$). For monkeys, however, their location-test performance was as accurate (i.e., not significantly different from) as their baseline performance (average of 82% correct) as shown by paired samples t -tests (Cisco: $t(6) = 1.28$, $p = 0.25$; Captain: $t(6) = 0.65$, $p = 0.54$). Day 1 performance for Cisco and Captain was 75 and 67% correct respectively, which increased to 100 and 91.7% correct respectively by the final day of testing.

Size-change detection—Neither species performed well in the size change test, as shown in Figure 11. A three-way repeated measures ANOVA of Session (1–6) $\times$ Trial Type (Baseline, Transfer) $\times$ Species (Monkey, Pigeon) revealed no significant interactions, but a main effect of Trial Type [$F(1,5) = 52.21$, $p = 0.001$, $\eta_p^2 = 0.91$] demonstrating that both species performed significantly worse on size change trials than on baseline trials. Only one of the monkeys (Captain, 62% correct, single mean t -test, $t(5) = 3.94$, $p = 0.01$, $d = 1.61$) performed significantly better than chance across testing, whereas Cisco and all of the pigeons performed at chance.

Discussion

Monkeys and pigeons showed partial transfer to color changes with novel shapes; their performance was somewhat less than baseline but significantly better than chance. Interestingly, the pigeons outperformed the monkeys during Shape Test 1, which was their first exposure to the novel shapes. This test only required that the subjects detect a change in color. Hence, it is possible that the pigeons did not attend to the irrelevant shape dimension as their performance was not disrupted by these new shapes. The monkeys, however, performed at chance (52.8%) in this test, suggesting that they were disrupted by these new shapes. The monkeys may have been adverse to the novelty of the new shapes or encoded both shape and color of the stimuli which may have led to confusion on presentation of the test array. Indeed, the monkeys' accurate performance in shape tests 4 and 5 suggests that they did attend to shape.

In Shape Tests 4 and 5 monkeys showed good transfer, whereas pigeons did not transfer above chance performance. Both species had experience with the novel shapes during prior color-change tests with novel shapes. However, unlike the monkeys, pigeons did not transfer accurately to shape changes. To determine whether pigeons were capable of detecting shape changes they were trained extensively (up to 32 96-trial sessions) with these shape changes.

These shape-change training sessions were composed entirely of trials consisting of 2 shapes presented in one color, with one changing shape after delay (like the Shape Test trials of 5B). None showed any learning of the shape-change task, as shown in Figure 12. This lack of learning suggests that pigeons either had difficulty learning shape changes, or their prior color-change learning may have blocked shape-change learning.

It is interesting that neither species performed well when tested with size changes. Indeed, only 1 subject (Captain, a monkey) performed significantly better than chance (62% correct). The size-change test was interesting in that it was the only test in which identical (in shape and color) items were presented in identical locations following the delay. Perhaps the 25% size change was less obvious than other types of changes.

In order to determine whether or not changes other than to the items themselves could be detected by monkeys and pigeons, they were tested with location changes. The monkeys again demonstrated full transfer to location changes, whereas the pigeons performed at chance. Here too, the pigeons' prior color-change learning may have blocked location-change learning. Another possibility might be related to the tendency for pigeons to peck one of the sample stimuli multiple times during the sample display presentation. If pigeons were pecking the item not-to-change, then they may not have noticed the location change of the other sample stimuli. Furthermore, such pecking may have carried over to the test display resulting in an incorrect choice response. Monkeys, by contrast, tended to distribute responses to both sample stimuli, thereby increasing the chance that changes in either sample stimulus would be noticed.

General Discussion

The results of Experiment 1 demonstrate that monkeys learned to perform the change-detection task, and transferred their performance to novel colors and delays. These results were compared to previous results from pigeons (Wright et al., 2010), showing that both species learned the change-detection task at similar rates, transferred to novel colors, and transferred to longer delays. Transfer to delays of several seconds suggested that both species encoded the sample array into short-term memory and later were able to identify the changed item. Interestingly, the pigeons maintained a higher level of performance than the monkeys when tested with these extended delays.

The results of Experiment 2 provided some contrasts between these two species. While monkeys transferred well to shape and location changes, pigeons did not. Successful transfer performance in change detection requires learning an abstract relation, a rule that transcends the identity of individual stimuli, and requires understanding the relationship between stimuli. In the case of change detection, this relationship must be judged across time from the beginning of learning. The test display must be compared to the subject's memory of the sample display in order to decide which stimulus had changed. Interestingly, other animal memory tasks (matching to sample, same/different) typically begin training with simultaneous presentations of the stimuli to be related. This is not possible with change detection. Nevertheless, these animals learned the change-detection task at about the same rate that they sometimes learn those other tasks.

The pigeons' lack of change-detection transfer to shapes, size, or location is evidence for restricted-domain relational learning like that shown in same/different tasks (e.g., Elmore et al., 2010; Katz et al., 2010; Wright & Katz, 2009). While pigeons in the present experiments learned to detect changes in color, and were unimpaired by novel colors or novel shapes which changed in color, their inability to detect shape, location and size changes, indicates that their change-detection learning was restricted to the color domain. Indeed, the pigeons' somewhat better delay transfer than monkeys may reflect the dominant and overshadowing role of colored stimuli for pigeons.

Monkeys too evidenced restricted-domain relational learning, but their domain was clearly broader, as shown by their transfer to both shape and location changes in addition to full transfer to novel colors and fairly good transfer to color changes with novel shapes. However, their failure to transfer to size changes suggests some restriction of the change-detection domain.

Comparisons can be made to results from same/different tasks with these species. Monkeys and pigeons learn the abstract concept of same and different, but monkeys learn more quickly and require fewer exemplars of the rule than pigeons to demonstrate full concept learning (Wright & Katz, 2006). While neither species demonstrated learning of the full abstract relation of change in this study, the monkeys were less restricted than pigeons in their domain of accurately detecting change, as demonstrated by their immediate transfer to shape and location changes. Although the monkeys had prior experience in the same/different task and learning the same/different concept, the same can be said about 3 of the 5 pigeons (Auburn pigeons). Nevertheless, the pigeons with same/different experience learned and transferred at similar rates to the two naïve pigeons, suggesting that prior same/different experience had little or no effect on the change-detection results.

Both monkeys and pigeons appear to be good candidates for exploring VSTM, but monkeys perhaps have a slight advantage given their good performance with at least 3 types of change (color, shape, and location). Human change-detection studies often employ a variety of stimulus types (e.g., colored squares, random polygons, Snodgrass drawings, and shaded cubes). The multiple stimulus types with which monkeys can readily detect change encourage direct comparisons to human change detection (Alvarez & Cavanagh, 2004; Eng, Chen, & Jiang, 2005). Humans can be instructed to look for change generally, but because the rules of the task must be communicated to non-human animals through the contingencies of reinforcement, species, like monkeys, which readily learn multiple types of change, may have advantages for comparative analyses of VSTM. Nevertheless, pigeons with further training may reveal learning of these other types of change, thereby also permitting direct comparisons of VSTM. In addition to the comparative analysis of short-term memory, a number of studies can be conducted in pigeons and monkeys that are impossible to conduct in humans, including lesions, neurophysiological recordings, and neurotransmitter manipulations, which are likely to be essential in any complete understanding of the neurophysiological underpinnings of VSTM.

Procedure Note

The pigeons were trained and tested identically to the monkeys except for a few minor differences. The six pigeons ranged in age from 2–7 years, three of which were experimentally naïve, and the other 3 had prior experience in the same/different task, much like the monkeys. Pigeons were reinforced with mixed grain and had free access to grit and water in their home cages. Supplemental feedings were provided as needed to maintain their weight at 85% of maximum. The pigeons' 4×4 matrix was smaller (9×7 cm) and the stimuli measured 1.5 cm in diameter; however the visual angle of the matrix and stimuli were equivalent to that used with the monkeys. The pigeon chambers differed from the monkey chambers and are described in detail in Wright et al., (2010). Pigeons made pecking responses to the stimuli. The experimentally naïve pigeons were hopper trained and autoshaped, and all pigeons received pretraining consisting of pecking achromatic circles following a change from white to grey and vice versa. Finally, the pigeons were only trained with delays of 50-ms and a 15-s ITI.

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References

- Alvarez GA, Cavanagh P. The Capacity of Visual Short-Term Memory is Set Both by Visual Information Load and by Number of Objects. *Psychological Science*. 2004; 15:106–111. [PubMed: 14738517]
- Bays PM, Husain M. Dynamic shifts of limited working memory resources in human vision. *Science*. 2008; 321(5890):851–4. [PubMed: 18687968]
- Cowan N. The magical number 4 in short-term memory: a reconsideration of mental storage capacity. *Behavioral and Brain Sciences*. 2001; 24:87–114. [PubMed: 11515286]
- Cowan, N. *Working Memory Capacity*. Psychology Press; New York: 2005.
- Cusack R, Lehmann M, Veldsman M, Mitchell DJ. Encoding strategy and not visual working memory capacity correlates with intelligence. *Psychonomic Bulletin & Review*. 2009; 12:1127–1133.
- Elmore LC, Wright AA, Rivera JJ, Katz JS. Individual differences: either relational or item-specific learning in a *same/different* task. *Learning & Behavior*. 2009; 37:204–213. [PubMed: 19380897]
- Elmore LC, Ma WJ, Magnotti JS, Leising KJ, Passaro A, Wright AA. Visual short-term memory compared in Rhesus Monkeys and Humans. *Current Biology*. 2011; 21:975–979. [PubMed: 21596568]
- Eng HY, Chen D, Jiang Y. Visual working memory for simple and complex visual stimuli. *Psychonomic Bulletin & Review*. 2005; 12:1127–1133. [PubMed: 16615339]
- Katz JS, Sturz BR, Wright AA. Domain is a moving target for relational learning. *Behavioral Processes*. 2010; 83:172–175.
- Luck SJ, Vogel EK. The capacity of visual working memory for features and conjunctions. *Nature*. 1997; 390:279–281. [PubMed: 9384378]
- Pashler H. Familiarity and visual change detection. *Perception & Psychophysics*. 1988; 44:369–378. [PubMed: 3226885]
- Rensink RA. Change detection. *Annual Review of Psychology*. 2002; 53:245–277.
- Wilken P, Ma WJ. A detection theory account of change detection. *Journal of Vision*. 2004; 4:1120–1135. [PubMed: 15669916]
- Wright AA. An experimental analysis of memory processing. *Journal of the Experimental Analysis of Behavior*. 2007; 88:405–433. [PubMed: 18047230]

- Wright AA, Katz JS. Mechanisms of *same/different* concept learning in primates and avians. *Behavioural Processes*. 2006; 72:234–254. [PubMed: 16621333]
- Wright AA, Katz JS. A case for restricted-domain relational learning. *Psychonomic Bulletin & Review*. 2009; 16:907–913. [PubMed: 19815797]
- Wright AA, Katz JS, Magnotti J, Elmore LC, Babb S, Alwin S. Testing pigeon memory in change detection. *Psychonomic Bulletin & Review*. 2010; 17:243–249. [PubMed: 20382927]
- Yantis S. Stimulus-driven attentional capture. *Current Directions in Psychological Science*. 1993; 2:156–161.

Figure 1.

Change-detection task progression. Two trials are depicted. Colors (aqua, blue, green, magenta, orange, purple, red, yellow) were used in the actual task, but grey scale fills are used to represent colors here.

Figure 2.
Acquisition by two monkeys, Cisco and Captain, in change detection.

Figure 3. Novel color transfer test showing baseline and transfer performance for Cisco and Captain. Error bars represent 95% confidence intervals.

Figure 4. Variable delay test showing performance for Cisco and Captain. Error bars represent 95% confidence intervals.

Figure 5.
Mean acquisition functions by monkeys and pigeons of change detection.

Figure 6.

Mean color transfer performance by monkeys and pigeons in the change-detection task. The pigeon's transfer and baseline were the means of the individual performances shown in Figure 5 of Wright et al., 2010. Error bars represent 95% confidence intervals.

Figure 7.
Mean variable delay test performance by pigeons and monkeys in the change-detection task.
Error bars represent 95% confidence intervals.

Figure 8.

Baseline and transfer performance for monkeys and pigeons with the color changes of novel shapes in the change-detection task. Example trials are depicted below each set of histograms. Shape Test 1 refers to trials containing one shape displayed in two different colors in the sample array, followed by a change in color of one object. Shape Test 2 refers to trials containing two different shapes in two different colors in the sample array, followed by a change in color of one object. Shape Test 3 refers to trials containing two different shapes in two different colors in the sample array followed by a change in shape and color of one object. Error bars represent 95% confidence intervals.

Figure 9.

Baseline and transfer performance for monkeys and pigeons in tests requiring detection of shape changes (i.e., no color changes). Example trials are depicted below each set of histograms. Shape Test 4 refers to trials containing two shapes of two different colors in the sample array, followed by a change in shape of one object. Shape Test 5A refers to trials containing two of the same shape presented in the same color in the sample array, followed by a change in shape of one object. Shape Test 5B refers to trials containing two different shapes in the same color in the sample array, followed by a change in shape of one object. Error bars represent 95% confidence intervals.

Figure 10. Baseline and transfer performance for monkeys and pigeons in the location change detection test. Error bars represent 95% confidence intervals.

Figure 11.

Baseline and transfer performance for monkeys and pigeons in the size change detection test. Error bars represent 95% confidence intervals.

Figure 12.
Shape training performance by pigeons.