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No evidence for feature binding by pigeons in a change detection task

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Abstract

We trained pigeons to respond to one key when two consecutive displays were the same as one another (*no-change* trial) and to respond to another key when the two displays were different from one another (*change trial*; change detection task). Change-trial displays were distinguished by a change in all three features (color, orientation, and location) of all four items presented in the display. Pigeons learned this change-no change discrimination to high levels of accuracy. In Experiments 1 and 2, we compared Replace trials in which one or two features were replaced by novel features to Switch trials in which the features were exchanged among the objects. Pigeons reported both Replace and Switch trials as “no-change” trials. In contrast, adult humans in Experiment 3 reported both types of trials as “change” trials and showed robust evidence for feature binding. In Experiment 4, we manipulated the total number of objects in the display and the number of objects that underwent change. Unlike people, pigeons showed strong control by the number of feature changes in the second display; pigeons’ failure to exhibit feature binding may therefore be attributed to their failure to attend to items in the displays as integral objects.

Keywords

change detection; binding; visual short-term memory; variability

1. Introduction

Recent research suggests that human visual short-term memory (VSTM) often stores bound representations of objects instead of individual object features. In one representative experiment, human participants were shown two consecutive displays containing from one to four colored bars and asked to report whether the two displays were the same or different (Vogel, Woodman, and Luck 2001). On some trials, the participants were asked to remember only the color (or the orientation) of the bars, whereas on other trials they were asked to retain both color and orientation information. If color and orientation were stored

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independently, then due to the limited capacity of VSTM, participants should have shown a diminished ability to correctly report whether the two displays were the same or different when both features had to be remembered and reported. Yet, their performance was equivalently accurate in both conditions suggesting that VSTM stores integrated, bound representations of objects instead of independent lists of object features.

Similar to the primate visual system, the avian visual system processes visual information along at least two separate dimensions (shape and motion) localized in different brain areas (Laverghetta and Shimizu 1999; Shimizu, Patton, and Husband 2010). Thus, it seems logical to assume that, just like the primate brain, the avian brain should be able to switch from coding individual features to representing unitary, bound objects. Although binding in avian low-level vision is relatively well-established (Cook 1992; Cook et al. 1997; Cook, Cavoto, and Cavoto 1996), its participation in VSTM is less clear.

The problem of binding originally arose in the context of low-level perception: Once the visual system encodes elemental features, it must at some level establish which features belong to which object. Feature integration theory posits that elemental features of the object are detected early and in parallel, whereas binding of these features to construct *object files* requires attention, occurs later, and proceeds serially (Treisman 1998, 2006). Consequently, visual search for an object that can be detected by an elemental feature (e.g., a red target among green distractors) is predicted to be faster and more accurate than search for an object defined by a conjunction of features (e.g., a red square target among green squares and red circles). Just like humans, pigeons were reported to be more accurate and faster in detecting targets in elemental displays than in conjunctive displays, demonstrating that the avian visual system detects and encodes elemental features early and, possibly, preattentively (Cook et al. 1997; Cook, Cavoto, and Cavoto 1996; Cook 1992). But, does it combine these elemental features into an object file? And, if it does, then are these object files similar to those found in humans?

According to feature detection theory, the process of creating object files can sometimes lead to illusory conjunctions. For example, the brief presentation of a display containing a red X, a blue X, and a green T occasionally produces a report of a blue X or a red T; in other words, when people are prevented from focusing attention on individual objects, they sometimes join object features incorrectly (Treisman and Schmidt 1982). Similarly, Katz, Cook, and Magnotti (2010) found that pigeons occasionally committed binding errors indicative of illusory conjunctions. For example, having been trained to select the left hopper when a red U and a green T are presented, a bird might incorrectly select the left hopper when a green U and a red T are presented due to erroneous conjunctions between color and shape.

What about binding in avian VSTM? Recent research suggests that human visual working memory stores two to four object files containing bound features such as color, location, or shape (Treisman 2006; Vogel, Woodman, and Luck 2001; Luck and Vogel 1997). Storing object files instead of individual object features seems intuitively plausible due to the limits of a small VSTM capacity (Cowan 2000; Miller 1956). Object files can be thought of as a form of chunking, a well-known basic principle of human memory that allows us to increase

the number of correctly encoded and recalled items. Pigeons also have a comparably small VSTM capacity (Gibson, Wasserman, and Luck 2011; Wright, this issue) and use chunking in serial learning tasks (Terrace 1987). We do not yet know, however, whether pigeons also store bound representations of objects in their short-term memory.

Some indirect evidence suggests that pigeons can learn a task that is impossible to solve without correctly binding the features belonging to the same stimulus. George and Pearce (2003) trained pigeons to respond to a compound target stimulus (e.g., horizontal red lines on the left and vertical green lines on the right) and to refrain from responding to a distractor (e.g., vertical red lines on the left and horizontal green lines on the right); in other words, the pigeons had to simultaneously attend to both color and orientation dimensions in order to solve these discriminations. Subsequent tests demonstrated that pigeons learned this task by using feature-bound stimulus representations rather than by using a form of a template matching. However, being able to learn the task that requires binding does not necessarily imply that pigeons use bound representations of objects in their VSTM in other discrimination tasks, as people do.

In our study, we chose a change detection task as a means of studying feature binding in pigeons. Previous research has shown that pigeons can learn a traditional change detection task (Wright et al. 2010). Moreover, just as in humans, pigeons' ability to detect changes improves when more items in the display change, indicating an ability to maintain multiple items in VSTM (Gibson, Wasserman, and Luck 2011; Wright, this issue). Because the change detection task has been successfully used to study feature binding in humans (Vogel, Woodman, and Luck 2001), we anticipated that it would also be effective for studying feature binding in pigeons.

2. Experiment 1

In our first experiment, we trained pigeons to respond to one key when two consecutive displays remained unchanged and to respond to another key when the second display differed from the first, a classic change-detection task. Once the pigeons had acquired the discrimination, we conducted several tests designed to explore whether pigeons performed this task by storing independent lists of features or integrated, bound object representations.

2.1. Method

2.1.1. Subjects—The subjects were 4 feral pigeons (*Columba livia*) housed in individual cages in the Psychology vivarium at The University of Iowa. The birds were maintained at 85% of their free-feeding weights by the delivery of food pellets during experimental sessions and by mixed grain after experimental sessions. Grit and water were freely available in the home cages. The pigeons had served in unrelated studies prior to this experiment. One bird did not learn the task even after extensive training; therefore, the final sample comprised 3 birds.

2.1.2. Apparatus—The experiment used $36 \times 36 \times 41$ cm operant conditioning chambers detailed by Gibson, Wasserman, Frei, and Miller (2004). The boxes were located in a dark room with continuous white noise. The stimuli were presented on a 15-in LCD monitor

(NEC MultiSync LCD1550V, Melville, NY) located behind an AccuTouch resistive touch screen (Elo TouchSystems, Fremont, CA). A food cup was centered on the rear wall level with the floor. A food dispenser delivered 45-mg food pellets through a vinyl tube into the cup. A houselight (an incandescent 28V-0.1 Amp lamp, Eiko, model 1820, Taiwan, with filament type C-2F) on the rear wall provided illumination during the session. Each chamber was controlled by an Apple® eMac® computer.

A single central 9×9 cm area in the center of the computer monitor was used to present the stimulus display; the rest of the central area was black. The response buttons were shown on the left and the right sides of the stimulus display. Responses that occurred beyond these areas were not recorded and could not advance the trial. The experimental procedure was programmed in HyperCard, Version 2.4 (Apple Computer, Inc., Cupertino, CA).

2.1.3. Construction of training stimulus displays—Figure 1 illustrates the construction of a stimulus display. Each stimulus display included four bars that could vary in color, orientation, and spatial location placed on a light grey background. At the beginning of each trial, the features of each of the four objects were randomly chosen to construct the initial display. On a training *no-change* trial, the same display was presented a second time. On a training *change* trial, a second display was constructed so that none of the object features used in the first display appeared in the second display.

For the color dimension, we used red (R: 255 G: 0 B: 0), yellow (R: 255 G: 255 B: 0), orange (R: 255 G: 128 B: 0), pink (R: 255 G: 0 B: 255), light green (R: 0 G: 255 B: 0), dark green (R: 0 G: 142 B: 35), light blue (R: 0 G: 255 B: 255), and dark blue (R: 0 G: 0 B: 255). To create the orientation dimension, the bars were rotated 0° , 22° , 45° , 67° , 90° , 112° , 135° , and 157° . Finally, a 3×3 matrix was used to create eight locations, with the center location excluded.

2.1.4. Procedure—Each trial began with the presentation of an orienting stimulus (a black cross on a white square; Figure 2). After one peck at the orienting stimulus, the pigeon was presented with the first stimulus display until a fixed number of responses (FR) to that display has been completed. All birds started training with a FR 1 requirement; thereafter, the number of required responses was gradually increased on bird-by-bird basis to increase exposure to the display and to make mistakes more punishing. If a bird failed to complete a session due to the stringent FR, then the number of required responses was decreased. At the end of training, bird 31B was required to complete 53 pecks; bird 37B was required to complete 18 pecks; and, bird 90B was required to complete 36 pecks. The median time to complete the FR requirement during last 10 training sessions was 20,600 ms (IQR = 18,971-22,767) for bird 31B, 700 ms (IQR = 667-18,896) for bird 37B, and 14,483 ms (IQR = 13,117-16,083) for bird 90B.

Upon completion of the FR, a black display was presented for a 900 ms (interstimulus interval, ISI) to disrupt any potential influence of iconic memory on the bird's choices. After that, a second display was presented, together with two choice keys. On a training *no-change* trial, the second display was identical to the first display. On a training *change* trial, all features of the second display were different from the first display; the objects were

placed in different locations, had different colors, and had different orientations. Birds 31B and 37B had to choose the left key on *no-change* trials and the right key on *change* trials; this assignment was reversed for bird 90B.

A correct choice was followed by food delivery and an intertrial interval (ITI). Much like the FR requirement, all birds started with an ITI of 5 s; this duration was gradually increased to reduce any intertrial interference. At the end of training, the ITI was set to 10 s for bird 31B, 8 s for bird 37B, and 13 s for bird 90B. An incorrect choice was followed by turning off the houselight for the duration of the ITI and repeating the same trial (an unscored correction trial). Correction trials were given until the bird made the correct choice.

Each training session comprised 32 blocks of 6 trials (3 *change* trials plus 3 *no-change* trials), for a total of 192 trials. Training continued until the performance criterion had been reached. The initial performance criterion was set at 80% correct choices or better on both *change* and *no-change* trials. However, only one bird reached this criterion in a timely fashion; thus, the criterion was lowered slightly to 75% for the two remaining birds. Once the criterion had been reached, the birds proceeded to testing.

2.1.4.1. Single dimension tests: Single Dimension tests contrasted a true *change* in a single feature (Replace trials) with an *exchange* of a single feature between objects (Switch trials). If a bird simply maintained separate lists of features in its memory, then it should have responded “change” on Replace trials and “no-change” on Switch trials. However, if the bird maintained a bound representation of each object in its memory, then it should respond “change” on both types of trials.

Figure 3 illustrates the construction of training and testing *change* trials in the Single Dimension tests. As before, the first display was constructed by randomly selecting four colors, orientations, and locations, and then randomly pairing them with each other. On Replace trials, the second display was constructed by replacing a single feature (e.g., color) of all four objects. On Switch trials, a single feature was switched across all objects, so that no truly new features were introduced.

Each testing session comprised 80 training *change* trials, 80 training *no-change* trials, and 20 testing trials that included 10 *no-change* trials, 5 Replace test trials, and 5 Switch test trials. During training trials, only correct choices were reinforced. During testing trials, any choice was followed by food delivery; no correction trials were given.

Single Dimension tests were presented in three runs: Color test, Orientation test, and Location test. Each test run was conducted for 10 consecutive sessions, so that each bird received 50 Replace trials and 50 Switch trials. The selected performance criterion had to be maintained during testing; if the bird’s performance fell below the training criterion, then it was returned to training until its accuracy improved.

2.1.4. Statistical analyses—All statistical analyses were conducted using multilevel generalized linear modeling (Pinheiro and Bates 2000) allowing us to use repeated measures regression with the binomial distribution that is more appropriate for dichotomized choice data than the traditional conversion into proportions (Dixon 2008; Young, this issue). The

session variable was treated as a continuous predictor, centered to avoid multicollinearity, and log-transformed. Each best-fitting model included fixed effects (independent variables similar to those in traditional analyses) and random effects (within-subject variables that allow for variability across subjects). Therefore, a within-subject variable could have both a fixed effect (indicating a general influence across all subjects) and a random effect (reflecting individual differences among subjects). We compared models that included only fixed effects with others that included both fixed effects and random effects, and retained the best model according to the Akaike information criterion (AIC; Akaike 1974). Because the binomial distribution was chosen for our choice data, the analysis returned z -values, rather than t -values. All analyses were conducted in R (R Core Team 2014) using the lme4 package (Bates et al. 2014). The graphs of fitted data were created using the lattice package (Sarkar 2008).

2.2. Results and Discussion

2.2.1. Training—Training took 103 sessions for bird 37B, 295 sessions for bird 31B, and 324 sessions for bird 90B. Figure 4 separately shows multilevel logistic regression fits of the proportion of correct choices during training on *change* and *no-change* trials for each bird. The best-fitting model producing these fits included a fixed effect of session, $z = 5.78$, $p < .0001$, and a trial (*change*, *no-change*) $\times$ session interaction, $z = 21.95$, $p < .0001$, indicating that these effects were consistent at the group level. The model also included a random effect of session and trial, indicating that the effect of these variables differed across individual birds. The fixed effect of trial was not statistically significant, $z = -1.47$, $p = .142$, suggesting that the difference between *change* and *no-change* trials was not consistent at the group level; however, the presence of a significant trial $\times$ session interaction indicated that *no-change* trials started at a higher level of accuracy and reached asymptote faster than *change* trials.

This result agrees with previous research reporting more accurate discrimination of displays containing identical items than displays containing different items (Young and Wasserman 2002). In other words, pigeons here appeared to find it easier to discriminate sameness across two snapshots in time, just as in prior work they found it easier to discriminate sameness among simultaneously presented items. Nonetheless, all pigeons reached the required training criterion (80% or 75% correct) on *change* trials prior to proceeding to testing.

2.2.2. Single dimension tests—Figure 5 shows the mean proportion of *change* responses on training and testing trials in the Single Dimension tests for each bird. Surprisingly, two out of the three birds predominately responded below chance on all Replace trials; the remaining bird responded below chance on Replace trials in the Orientation test and near chance level in Color and Location tests. In other words, even when the displays included novel features along one of the three dimensions, the birds still classified these images as “no-change.”

The best-fitting model for the Single Dimension tests included a random effect of trial (training, Replace, and Switch) suggesting that its effect varied across birds. The model also

included a fixed effect of trial, indicating that both Replace trials, $z = -16.81$, $p < .0001$, and Switch trials, $z = -16.93$, $p < .0001$, were significantly different from training trials. Finally, the model included a fixed effect of test run (Color, Location, and Orientation) and a test $\times$ trial interaction. To further explore the interaction, we conducted a separate analysis that excluded training trials. The best-fitting model for this analysis included both a random and a fixed effect of test run; specifically, overall accuracy in the Color test was significantly higher than in the Orientation test, $z = -2.74$, $p = .006$, but accuracy in the Color test did not differ from accuracy in Location test, $z = 1.66$, $p = .096$. More importantly, the follow-up model did not include an effect of trial, indicating that birds responded identically on Replace and Switch trials. In other words, the pigeons responded on both Replace and Switch trials as if they were more similar to *no-change* trials than to *change* trials.

3. Experiment 2

Because the pigeons had been trained to respond “change” when all three features on the second display were different from the first display, it is possible that a change in a single feature in Experiment 1 would not have been salient enough to generate reliable “change” responses. To address this possibility, in Experiment 2, we constructed Multiple Dimensions tests contrasting the *replacement* of features across two dimensions with a *three-feature switch* across all four objects, effectively creating four novel objects without introducing any new features. Therefore, if the birds maintain the bound representations of the objects in their VSTM, then they should respond “change” on Switch tests.

3.1. Method

3.1.1. Subjects and apparatus—We used the same three pigeons and the same apparatus as in Experiment 1.

3.1.2. Procedure—The overall procedure was similar to that described in the Experiment 1, with the exception of testing trials. Figure 6 illustrates the construction of the Multiple Dimensions tests. On Replace trials, two features (color and location, color and orientation, and orientation and location) of every object were replaced by novel features. On Switch trials, all of the features were switched across all of the objects; these trials were identical across all test runs.

The Multiple Dimensions tests were presented in three runs: the Color & Location test, the Color & Orientation test, and the Location & Orientation test. The composition and number of test sessions were the same as in the Single Dimension tests in Experiment 1.

3.2. Results

Figure 7 shows the mean proportion of change responses on training and testing trials in the Multiple Dimensions tests for each bird. All birds responded to Replace trials in the Color & Location test significantly above chance, indicative of perceived change in the second display. The Replace trials in Color & Orientation and Orientation & Location tests were responded to at or significantly below chance level indicating that the birds still classified them as “no-change.” More importantly, the pigeons consistently responded “no-change” on Switch trials in all tests. In other words, even when all of the features present in the first

display were recombined to create, in essence, four novel objects, the birds still responded as if they perceived these trials to be more similar to “no-change” trials than to “change” trials.

The best-fitting model included a random effect of trial as well as a fixed effect of trial, a fixed effect of test run (Color & Location, Color & Orientation, and Orientation & Location), and a trial $\times$ test run interaction. Similar to the Single Dimension test analyses, we next conducted a separate analysis on testing trials only. The best-fitting model in this analysis included a random effect of trial together with a fixed effect of trial and a fixed effect of test run, but no trial $\times$ test run interaction. Specifically, the birds were more likely to classify Replace trials as “change” in comparison to Switch trials across all test runs, $z = -6.97, p < .0001$. The birds were also more likely to respond “change” in the Color & Location test than in the Color & Orientation test, $z = -3.77, p = .0002$, or in the Orientation & Location test, $z = -4.92, p < .0001$; the difference between the Color & Orientation test and the Orientation & Location test was not statistically significant, $z = -1.47, p = .25$.

4. Experiment 3

Both Single Dimension and Multiple Dimensions tests in Experiments 1 and 2 revealed no evidence of binding; pigeons predominately responded to Switch trials as if they were *no-change* training trials. Interestingly, with the exception of the Color & Location test, the pigeons also responded to Replace trials as if they were *no-change* training trials, despite the presence of novel visual features. In other words, the birds appeared to behave as if they were evaluating a change in variability from the first to the second display (Wasserman, Young, and Cook 2004; Young and Wasserman 2001) instead of attending to a change in individual objects. So, for example, the change in only 4 features (4 objects $\times$ 1 feature) on testing change trials in the Single Dimension tests instead of 12 features (4 objects $\times$ 3 features) on training *change* trials was classified as “no-change.” Following the same logic, Switch trials would always be classified as “no-change,” as they do not involve the appearance of any new features. (Computing the change in variability is explained in greater detail in Experiment 4.)

It is also possible, however, that some features of our visual displays or training procedure might encourage attending to the change in the variability of a display instead of attending to the individual, integral objects even in humans. So, in Experiment 3, we trained human participants to perform the *change/no-change* discrimination and then gave them Single Dimension tests followed by Multiple Dimensions tests. Unlike pigeons, human participants were explicitly instructed to respond to changes in the display; however, they were trained in the same manner as pigeons, with *change* training trials involving a change in all of the objects.

4.1. Method

4.1.1. Participants—Twenty-eight undergraduate students (21 females, 7 males) at The University of Iowa participated in the experiment for course credit. All students had normal or corrected to normal vision. The participants’ data were used only if they: (1) reached the established discrimination criterion in training and (2) maintained this criterion during testing. Otherwise, students were dropped from the study. Four students (3 females, 1 male)

were excluded for these reasons; thus, the final sample included 24 students (19 females, 6 males).

4.1.2. Apparatus and procedure—The experiment used four Apple® iMac® computers with 15-in CRT displays located in the same room. The presentation of all stimuli was programmed in HyperCard, Version 2.4 (Apple Computer, Inc., Cupertino, CA). All stimuli were constructed as described in Experiment 1 (cf. Figure 1).

Before the experiment began, the participants received brief instructions stating that they would need to press one key on a computer keyboard if they saw a change in a stimulus display and another key if the display remained the same. The sequence of events during the trial was similar to that used with pigeons (Figure 2), with the following exceptions. Participants first had to press any key to initiate the trial when they saw an orienting stimulus (a white square with black cross in the middle). Then, the first display was shown for 1,500 ms, followed by the black display also presented for 1,500 ms (ISI). No responses were required during the first display presentation or during the ISI. Next, participants were presented with a second display without choice keys; instead, they had to press one of the keys on the keyboard to indicate their choice.

At the beginning of the experiment, the participants were required to complete 80 training trials composed of 20 blocks of 4 trials (2 *change* × 2 *no-change* trials). Later, the participants were given the Single dimension test that included the three types of test runs (Color, Location, and Orientation; Figure 3) presented concurrently. The Single dimension test consisted of 10 blocks of 18 trials, for a total of 180 trials. Each block was composed of a single Replace and Switch trial for each of the test runs (2 trial types × 3 test runs) plus 12 training trials. Thus, each participant was exposed to 10 Replace trials and 10 Switch trials for each test run by the end of the test.

In the final third of the experiment, the participants had to complete a single Multiple dimensions test that included Color & Orientation, Color & Location, and Orientation & Location tests (Figure 4). This test consisted of 10 blocks of 12 trials, for a total of 120 trials. Because Switch trials in the Multiple dimensions test were identical across test runs, each block was composed of one Replace trial for each of the three test runs and a single Switch trial (4 trials) plus 8 training trials. By the end of the test, each participant received 10 presentations of Replace trials for each test run and a total of 10 Switch trials.

4.1.3. Statistical analyses—As in Experiment 1, statistical analyses were conducted using multilevel generalized linear modeling with the binomial distribution. The block variable was treated as a continuous predictor, centered to avoid multicollinearity, and log-transformed. We also performed latency analyses during acquisition, but found no reliable relationships with the variables of interest; therefore, the results of these analyses are not presented here.

4.2. Results and Discussion

4.2.1. Training—Figure 8 shows the mean proportion of correct choices across blocks of 8 trials for the *change* and *no-change* trials. The best-fitting model for these data included

both a random and a fixed effect of block, $z = 10.33$, $p < .0001$, indicating that accuracy increased as training progressed, although the speed of learning differed across participants. The model did not include a fixed effect of trial or a block $\times$ trial interaction, demonstrating that participants responded equivalently on *change* and *no-change* training trials.

4.2.2. Single Dimension tests—Figure 9 shows the mean proportion of change responses on Replace and Switch trials for each test run. Unlike pigeons, people reliably responded “change” on Color Replace trials as well as on Location Replace and Switch trials. The proportion of change responses did not differ significantly from chance on Color Switch trials or on Orientation Replace and Switch trials; most importantly, the participants did not reliably classify any of these three types of trials as “no-change,” in contrast to pigeons’ responses (cf. Figure 6).

The best-fitting model included a fixed effect of test run, indicating that participants were less likely to make “change” responses in the Orientation test than in the Color test, $z = -2.83$, $p = .005$, while the Color test and the Location test were not significantly different, $z = -0.56$, $p = .58$. The model also included a fixed effect of trial and a trial $\times$ test run interaction. Specifically, participants were more likely to respond “change” on Replace trials than on Switch trials in the Color test, $z = -2.38$, $p = .02$, and the Location test, $z = -2.32$, $p = .02$, but they were equally likely to respond “change” on both types of trials in the Orientation test, $z = -0.54$, $p = .59$. Finally, the model included a random effect of trial $\times$ test run interaction indicating that the influence of both variables differed across individuals. The analysis of individual fits (Figure 10) showed that 5 out of 24 participants were highly likely to respond “change” across all test runs and both trial types, whereas another 5 participants responded “change” only on Replace trials in a single test (3 in the Color test and 2 in the Orientation test). The rest of the participants exhibited an intermediate pattern of responses. In summary, although a few participants tended to classify Replace and Switch trials as more similar to “no-change” trials, just as pigeons did, the majority of the participants classified these trials as more similar to “change” trials.

Overall, our results are in line with prior research that documents the relatively low salience of changes in object orientation compared to changes in the color or location of objects (e.g., Vogel, Woodman, and Luck 2001; Kerzel and Schönhammer 2013). The results of the Location test also hint at the possible binding of location with other object features, because people responded “change” significantly above chance on Switch trials in the Location test.

Unlike our pigeons, our human participants were explicitly instructed to respond to a change in the display. However, their training was identical to that of pigeons, with the “change” trials involving a change in all of the features of all of the objects. The participants were not explicitly informed about the presence of the testing trials nor were they instructed to attend to a change in a single dimension. Nonetheless, with the exception of the Orientation test, people reliably classified Replace trials as “change” trials. This behavior is consistent with people’s attending to individual objects in the display rather than evaluating a change in its variability from one time to the next. These results also accord with prior research on same-different discrimination (Young and Wasserman 2001, 1997). Specifically, the majority of human participants trained in this task respond “same” if all of the items in the display are

the same, but respond “different” if any single item differs from the rest; in contrast, pigeons exhibit a gradual transition from reporting “same” to reporting “different” across differing levels of entropy, consistent with control by variability rather than by a categorical same/different relationship.

4.2.3. Multiple Dimensions tests—Figure 11 shows the mean proportion of change responses on Replace trials in the Color & Location, Color & Orientation, and Orientation & Location tests as well as on Switch trials. Participants were more likely to respond “change” in all three tests in comparison to Single Dimension tests (cf. Figure 9); more importantly, they also classified Switch trials as “change” significantly above chance.

The best-fitting model for these data included a fixed effect of test, but no random effect of test, indicating that, unlike in the Single dimension test, “change” responses in the different test runs were consistent across participants. Specifically, the participants were more likely to respond “change” in the Color & Location test than in the Color & Orientation test, $z = -3.34$, $p = .0008$, or in the Location & Orientation test, $z = -4.17$, $p < .0001$. In addition, the participants were significantly less likely to respond “change” on Switch trials than on any of the Replace trials, $z = -6.83$, $p < .0001$.

Unlike pigeons, people responded significantly above chance on all Replace trials. More importantly, people also reliably responded “change” on Switch trials. In other words, when all of the features in the first display were recombined in the second display, people classified these displays as “change” trials showing a robust evidence of binding and little evidence of their being affected by a change in the variability of the second display.

5. Experiment 4

Here, we explicitly tested the hypothesis that pigeons (but not people) may be evaluating the change in variability of successively presented displays by manipulating the number of objects presented in each display. We used the number of novel features in the second display as a quantitative measure of this change. For example, on *change* training trials the second display contained 12 novel features (4 objects $\times$ 3 features), whereas on *no-change* training trials it contained 0 novel features.

When only 1 object was presented in the display (Figure 12), *no-change* trials still contained 0 novel features in the second display; however, there were now only 3 novel features (1 object $\times$ 3 features) in the second display on *change* trials. Critically, this variability score assumes the absence of binding as all features are treated identically, whether or not they belong to the same or to different objects. If pigeons (or people) attend to individual objects, then pigeons should continue to respond “change” on such trials. But, if they use the change in variability between the displays, then they should respond “no-change” on *change* trials, as the change in the variability of the second display (3 novel features) is more similar to *no-change* training trials (0 novel features) than to *change* training trials (12 novel features). Manipulating the number of objects in the display has been used to demonstrate control by variability in the same-different task in pigeons as well as in humans and nonhuman

primates (Young and Wasserman 2001; Young, Wasserman, and Garner 1997; Wasserman, Fagot, and Young 2001; Young et al. 1999).

5.1. Method

5.1.1. Subjects—Two of three pigeons used in the Experiment 1 served as subjects in this experiment. Sixteen students (13 females, 3 males) who did not participate in Experiment 3 were recruited from the introductory psychology pool at The University of Iowa. Three students (2 males, 1 female) did not meet the performance criterion and were excluded from data analysis; thus, the final sample included 13 students.

5.1.2. Testing stimuli—Figure 12 illustrates the construction of the stimuli. The *change* and *no-change* training trials remained identical to those in Experiment 1. On testing trials in Test 1, the number of objects shown in the first stimulus display varied from 1 to 4. On *change* testing trials, all of the objects were replaced by novel objects in the second display. In Test 2, the number of objects again varied from 1 to 4, but only 1 object was replaced by a novel object in the second display of *change* testing trials. In Test 3, the number of objects remained constant, but the number of objects replaced in the second display varied from 1 to 4.

5.1.3. Apparatus and procedure—The same apparatus was used as in Experiments 1 and 2 (for pigeons) and Experiment 3 (for human participants). The training and testing procedures were similar as well, with the few exceptions outlined below.

For pigeons, the Set Size tests were presented consecutively (first Test 1, followed by Test 2, and Test 3). The test session consisted of 4 blocks of 48 trials, for a total of 192 trials. Each block included 20 *change* trials, 20 *no-change* trials, and 8 testing trials (2 trial types $\times$ 4 set sizes). Each test lasted for 17 sessions, so that each bird received 68 trials with each type of testing trial.

Human participants were trained in the manner described in Experiment 3. Once training was completed, participants were presented with Test 1, followed by Test 2, and then Test 3. Test 1 consisted of 10 blocks of 24 trials (8 *change* trials, 8 *no-change* trials, and 8 testing trials), for a total of 240 trials. To keep the total number of trials across the three tests manageable, we excluded *no-change* testing trials from Tests 2 and 3 as they were most likely to be non-diagnostic. Therefore, these tests consisted of 10 blocks of 12 trials (4 *change* trials, 4 *no-change* trials, and 4 testing trials), for a total of 120 trials.

5.2. Results and Discussion

5.2.1. Pigeon results—Figure 13 shows the results of Test 1. Both pigeons consistently responded “no-change” across all *no-change* trials. However, the pigeons were more likely to respond “change” on *change* testing trials when the testing display contained 3 or 4 objects than when it contained 1 or 2 objects. In other words, the birds appeared to be affected by the change in variability from the first to the second display.

The best-fitting model for these data included a significant fixed effect of set size (1, 2, 3, or 4 objects), trial (change or no-change), and a set size $\times$ trial interaction as well as a random

effect of trial. To help interpret the interaction, we next conducted two separate analyses for *change* trials and for *no-change* trials. The best-fitting model for *no-change* trials did not include either a fixed or a random effect of set size, indicating that pigeons' responses did not depend on the number of objects in the display. In contrast, the best-fitting model for *change* trials included a fixed (but not random) effect of set size, showing that pigeons' responses were similarly affected by changes in the number of objects in the display. Specifically, the proportion of "change" responses on training trials was significantly higher than on 1-object trials, $z = -5.75, p < .0001$, and on 2-object trials, $z = -3.20, p = .001$, but it did not differ from 3-object trials, $z < 1$, or 4-object trials, $z = 1.27, p = 0.20$.

Figure 14 shows the results of Test 2. Both pigeons again responded accurately on *no-change* trials across all set sizes. In contrast, only one bird responded "change" to a display in which a single object was replaced by a novel object. All other trial types were reliably classified as *no-change* trials, again suggesting that the birds responded to the change in display variability.

The best-fitting model again included a significant fixed effect of set size, trial, and a set size $\times$ trial interaction as well as a random effect of trial. The follow-up model for *no-change* trials did not include a fixed or a random effect of set size, confirming that pigeons responded equivalently on *no-change* trials. The model for *change* trials included a fixed (but not random) effect of set size. Specifically, the proportion of "change" responses on training trials was significantly higher than on any of the *change* testing trials, $z = -5.37, p < .0001$.

Figure 15 illustrates the mean proportion of "change" responses in Test 3. When only 1 or 2 of the 4 objects were replaced, both birds reliably classified these displays as "no-change" trials. With 3 objects replaced, the birds chose "change" and "no-change" equally often. Only when 4 out of 4 objects were replaced, did the birds reliably report "change."

The overall best-fitting model again included the fixed effects of trial and number (1, 2, 3, or 4 objects changed) together with the trial $\times$ number interaction; the model also included random effects of number and trial. The follow-up model for *no-change* trials did not include a fixed or a random effect of number indicating that responses on *no-change* trials remained similar. The model for *change* trials had a fixed (but not random) effect of number; specifically, birds responded significantly less accurately in comparison to training trials on all 4 four-object test trials, $z = -9.54, p < .0001$.

To confirm that pigeons' responses were based on the change in variability between the displays, we quantified this change by calculating the number of novel features in the second display. For example, during training, the first display contained 4 objects $\times$ 3 features = 12 independent features. On training *no-change* trials, these features remained the same, so the number of novel features was 0. On training *change* trials, there were 12 unique features as every object was replaced by a novel one. In Test 1, the number of novel features in the second display was 0 for all *no-change* testing trials. However, on *change* testing trials this number depended on set size (3 for set size 1, 6 for set size 2, and 9 for set size 3). Note that

this variability score assumes no binding between the features belonging to the same object as all features are treated independently.

We also calculated this variability score for Replace and Switch trials in Single Dimension and Multiple Dimensions tests for both birds (cf. Experiment 1) and included them in our calculations. The training trials were excluded from this correlational analysis as asymptotic accuracy on these trials could produce a forced linear relationship.

Pearson's correlation coefficients between the proportion of change responses and the computed variability scores were 0.78, 95% CI [0.55, 0.90], for pigeon 31B and 0.86, 95% CI [0.70, 0.94], for pigeon 37B, both $ps < .0001$. The presence of strong and significant positive correlations between the computed variability score and the birds' likelihood of responding "change" clearly suggests that the pigeons were not binding features belonging to the same object; instead, they were responding to the extent of change from one display to another.

5.2.2. Human results—Figure 15 shows the mean proportion of "change" responses in Tests 1, 2, and 3 by human participants. Unlike pigeons, people exhibited a high proportion of "change" responses in all tests showing little evidence of being affected by the change in the variability of the second display.

Because the *change* testing trials were the most theoretically interesting, our analyses concentrated on the proportion of "change" responses on these trials as our dependent variable. For Test 1, the best-fitting model did not include either fixed or random effects of set size, indicating that people responded equally accurately despite the change in the number of objects in the display. In Test 2, the best-fitting model included a fixed (but not random) effect of set size. Specifically, people responded less accurately than in training when 1 object changed in the displays containing 2, 3, or 4 objects, $z = -1.97$, $p = .049$; when the display contained only 1 object, their responses were as accurate as in training, $z < 1$. Finally, the model in Test 3 had a fixed (but not random) effect of number; people responded less accurately than in training when only 1 out of 4 objects changed, $z = -3.94$, $p < .0001$, but their responses in the remaining tests did not differ from training trials.

Table 1 shows Pearson's correlation coefficients between the proportion of "change" responses and the variability scores for individual participants. Because different participants were studied in Experiment 2, the human data set did not include Single dimension and Multiple dimensions results. None of the 13 participants showed a statistically significant correlation between the variability score and the likelihood of responding "change," providing no evidence of control by the change in display variability. In summary, it appeared that humans, unlike pigeons, were attending to the individual objects in the display instead of the change in variability of the second display.

6. General Discussion

In four experiments, we deployed a change detection task to explore the possibility that pigeons store *object* representations in their visual working memory instead of storing independent *features*. In Experiments 1 and 2, we compared pigeons' behavior when

features of the objects in the second displays were replaced by novel features (Replace trials) and when features were merely exchanged among the objects (Switch trials). We found no difference between Replace and Switch trials; more importantly, we found that pigeons tended to classify Replace trials as “no-change” trials, suggesting that they might have been attending to the change in display variability from the first to the second visual display instead of attending to the changes in the individual, integral objects. In contrast, human participants in Experiment 3 responded “change” on Switch trials, thereby showing evidence of feature binding. Finally, in Experiment 4, pigeons (but not people) showed robust control by the change in variability between the stimulus displays, again indicating that they were not attending to changes in the individual, integral objects.

Although unexpected in our study, pigeons’ tendency to respond to the change in display *variability* instead of changes in the individual *objects* is consistent with prior research on same-different discrimination learning (Brooks and Wasserman 2010; Wasserman, Young, and Cook 2004; Young and Wasserman 2001, 2001). This result, however, does not necessarily mean that pigeons store lists of features rather than bound objects in their VSTM. Indirect evidence suggests that objects may indeed be a unit of attention in pigeons’ intermediate-level vision, just as they are in human vision. Pigeons appear to preferentially attend to figures rather than to backgrounds (Castro et al. 2010; Lazareva et al. 2006); they attend to organizational properties of objects (Matsukawa, Inoue, and Jitsumori 2004; Kirkpatrick-Steger and Wasserman 1996; Kirkpatrick-Steger, Wasserman, and Biederman 1996); and, they are able to learn an object-based discrimination task which requires their discriminating displays with two targets located on the same object from those with two targets located on different objects (Lazareva, Vecera, and Wasserman 2006; Lazareva et al. 2005).

It is possible that the nature of our discrimination task contributed to pigeons’ learning to attend to the change in overall variability of the display instead of the change in the individual objects. In initial training (Figure 2), pigeons were required to peck one button when the second display remained the same and to peck a different button when all features of all objects in the display changed. This training procedure did not explicitly require attending to the change in individual, integrated objects. A modified change detection task in which the pigeon is required to locate and peck an object (or objects) that changed might provide a better means for exploring feature binding in pigeons’ memory; such a task might encourage attention to a change in individual object(s). Future research should explore this intriguing possibility.

Whatever the outcome of that future work, it is clear that comparative research into visual perception is eminently possible with modern psychophysical procedures. Change detection paradigms seem to be especially well suited to this important realm of work in comparative perception and cognition.

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Highlights

We used a change detection task to study feature binding in visual short-term memory

Unlike people, pigeons showed no evidence of feature binding

Follow-up tests disclosed that pigeons relied on the change in display variability

A better task to study binding might require attending to changes in individual objects

Figure 1.

Construction of stimulus displays. Each display used four out of eight possible features from three dimensions (color, orientation, and location) on a light grey background (removed for illustrative purposes). A 3×3 matrix was used to create eight possible locations (the center location was never employed). The features were selected and combined randomly on each trial.

Figure 2.

The sequence of events during a *change* trial and *no-change* trial.

Figure 3.

Examples of *change* trials in Single Dimension tests. During Replace trials, a single feature of every object (e.g., color) was replaced by a novel feature. During Switch trials, all objects switched a single feature, but no new features were introduced to the second display.

Figure 4. Multilevel logistic regression fits of the proportion of correct choices during training on *change* and *no-change* trials shown by pigeons in Experiment 1.

Figure 5.

Mean proportion of “change” responses during Single dimension tests shown by pigeons in Experiment 1. Asterisks indicate a significant difference from chance level according to two-tailed binomial test for testing trials; all training trials were significantly different from chance. Error bars indicate the standard error of mean.

Figure 6.

Examples of *change* trials in Multiple Dimensions tests. On Replace trials, two features of all objects were replaced by novel features. On Switch trials, all object features were switched across all objects; thus, these trials were identical for all test runs.

Figure 7.

Mean proportion of "change" responses during Multiple dimensions tests shown by pigeons in Experiment 1. Asterisks indicate a significant difference from chance level according to two-tailed binomial test for testing trials; all training trials were significantly different from chance. Error bars indicate the standard error of mean.

Figure 8.

Mean proportion of correct choices during training on *change* and *no-change* trials shown by adult humans in Experiment 2. Error bars indicate standard error of means.

Figure 9.

Mean proportion of "change" responses during Single dimension tests shown by adult humans in Experiment 2. For training trials, the proportion of change responses was 0.99 ± 0.01 ($M \pm SD$) for change trials and 0.02 ± 0.02 for no-change trials. Asterisks indicate a significant difference from chance level according to two-tailed t-test, $t(24) = 2.68, p = 0.01$. Error bars indicate the standard error of mean.

Figure 10.

Individual multilevel logistic regression fits of the proportion of "change" responses during Single dimension tests obtained for adult humans in Experiment 2.

Figure 11.

Mean proportion of “change” responses during Multiple dimensions tests shown by adult humans in Experiment 2. For training trials, the proportion of change responses was 0.99 ± 0.001 ($M \pm SD$) for change trials and 0.01 ± 0.005 for no-change trials. All responses were significantly above chance according to two-tailed t-test. Error bars indicate the standard error of mean.

Figure 12.

Examples of *change* trials in Set size tests. In Test 1, the set size varied from 1 to 4 objects and all objects on the display were replaced by novel objects on *change* trials. In Test 2, the set size again varied from 1 to 4 objects, but only 1 object was replaced by a novel object on *change* trials. In Test 3, the set size was always 4 objects, but the number of replaced objects varied from 1 to 4.

Figure 13.

Mean proportion of "change" responses during Test 1 shown by pigeons in Experiment 3. Asterisks indicate a significant difference from chance level according to two-tailed binomial test for testing trials; all training trials were significantly different from chance. Error bars indicate the standard error of mean.

Figure 14.

Mean proportion of "change" responses during Test 2 shown by pigeons in Experiment 3. Asterisks indicate a significant difference from chance level according to two-tailed binomial test for testing trials; all training trials were significantly different from chance. Error bars indicate the standard error of mean.

Figure 15.

Mean proportion of “change” responses during Test 3 shown by pigeons in Experiment 3. Asterisks indicate a significant difference from chance level according to two-tailed binomial test for testing trials; all training trials were significantly different from chance. Error bars indicate the standard error of mean.

Figure 16.

Mean proportion of “change” responses during Tests 1, 2, and 3 shown by adult humans in Experiment 3. All trials were significantly different from chance level. Error bars indicate the standard error of mean.

Table 1

Pearson's correlation coefficients between proportion of change responses and the number of novel features on the second display (the variability score) for human participants in Experiment 3. The correlation coefficient for two out of 13 participants was effectively zero as these participants always responded "change" on all testing trials.

Participant	Pearson's r	95% CI	<i>p</i>
P1	-0.09	-0.26, 0.67	.320
P2	0.18	-0.35, 0.62	.504
P3	0.11	-0.41, 0.57	.688
P4	0.15	-0.38, 0.60	.589
P5	0.09	-0.42, 0.57	.719
P6	0.09	-0.42, 0.57	.719
P7	-0.14	-0.59, 0.39	.616
P8	0.14	-0.38, 0.60	.598
P9	0.17	-0.35, 0.61	.519
P10	0.17	-0.35, 0.61	.519
P11	0.44	-0.08, 0.77	.091