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Visual Object Complexity Limits Pigeon Short-Term Memory*

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Abstract

The study of visual memory has repeatedly shown qualitatively similar visual short-term memory (VSTM) systems between many human and nonhuman species. In studies of human VSTM using change detection, increasing visual object complexity has an inverse effect on accuracy. In the current study, we assessed the functional relationship between visual object complexity and memory performance in visual change detection in pigeons and humans. Visual object complexity was quantified for each object type within each species using visual target search. Change detection performance was inversely related to object complexity in both species, suggesting that pigeon VSTM, like human VSTM, is limited by visual object complexity. Human participants were able to use a verbal-labeling strategy to mitigate some of the effect of visual object complexity, suggesting a qualitative difference in how the two species may solve certain visual discriminations. Considering the visual complexity of novel objects may help explain previous failures to transfer relational rules to novel visual objects.

Keywords

visual short-term memory; visual target search; change detection

Of the many lasting impacts Tony Wright has had on the fields of human and nonhuman memory, his emphasis on estimating functional relationships via broad parametric manipulation is perhaps the most important. His work demonstrating cross-species similarities in list memory (for a review, Wright, 2007) is a striking example of how testing a broad range of the parameter space can reveal surprising functional relationships. We have adopted a similar parametric approach in our recent work investigating visual short-term memory (VSTM) in pigeons, humans, and nonhuman primates (e.g., Elmore et al., 2011; Elmore, Magnotti, Katz, & Wright, 2012; Wright et al., 2010). The goal of the current study was to look for a functional relationship between object complexity and VSTM in pigeons and compare it to an analogous function from humans.

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Humans and pigeons alike rely on VSTM to accomplish a variety of tasks ranging from navigating a crowded environment to locating food; the large degree of qualitative similarity in visual processing is therefore not surprising. Work in our laboratories and others has shown that, like human VSTM, pigeon and nonhuman primate VSTM is sharply limited in terms of available resources (e.g., Elmore et al., 2011; Gibson, Wasserman, & Luck, 2011; Heyselaar, Johnston, & Pare, 2011) and susceptible to proactive interference (e.g., Wright, Katz, & Ma, 2012).

An increasingly common way to study VSTM across species is the change detection procedure. In the version we employ (e.g., Wright et al., 2010), trials begin with the presentation of a sample array containing items from a particular object type (e.g., colored circles, clip art), followed by a brief probe delay. After the probe delay, a probe array is presented containing two items, one of which has changed to another item from the object type. The participant's goal is to choose the item that changed (or equivalently, is "different") from the sample array. Performance in the task requires participants to a) successfully encode some portion of the sample array, b) retain this information throughout the probe delay, and c) determine which item in the probe array was not contained in the sample array.

Although VSTM is often conceptualized as being comprised of a fixed number of objects (e.g., Luck & Vogel, 1997; Zhang & Luck, 2008; but see Bays & Housain, 2008; van den Berg, Shin, Chou, George, & Ma, 2012), a consistent finding in studies of human VSTM is a large effect of object complexity (Alvarez, & Cavanagh, 2004; Eng, Chen, & Jiang, 2005). As the objects become more complex, accuracy (and subsequent capacity estimates) significantly decreases. Importantly, the complexity of a given object type can be independently assessed by using a target search task (also known as a visual search task).

Alvarez and Cavanagh (2004) presented participants with alternating blocks of change detection and target search using objects of varying complexity, ranging from colored squares (low complexity) to shaded cubes (high complexity). For each object type, search rate slopes were obtained from the target search response time data and paired with the corresponding change detection data. Across 6 object types, search rate explained over 99% of the variance in change detection performance. The authors claimed that this relationship demonstrated that the amount of information stored in VSTM was related not only to the number of objects in memory, but also to the complexity of the objects being stored.

Along similar lines, Eng et al. (2005) related target search and change detection across object types in humans. To rule out encoding-related explanations for the complexity-capacity relationship, participants were given variable amounts of time to study the sample array (including one self-paced condition). Their results showed that the complexity-capacity relationship is weakened (but does not disappear) when the sample array viewing time is increased, suggesting that encoding limitations do play a role in change detection for complex objects. The authors noted, however, that as sample-array viewing time is increased, alternative strategies become available (e.g., chunking, verbal coding) that may change how the objects are processed.

An alternative account offered by Awh, Barton, & Vogel (2007) is that the difficulty of *comparing* the sample and probe arrays (rather than just the *encoding* of the sample array) is responsible for the decreased accuracy in change detection with complex objects. They showed participants sample arrays of mixed object types and allowed objects to have cross-category changes (e.g., a Chinese character changing to a cube). The accuracy difference between object types was only significant for within-category changes, despite identical encoding and storage demands. They concluded that the primary driver of the negative

relationship between object complexity and accuracy must therefore be the sample/probe array comparison (Awh et al., 2007). Regardless of the exact reason for the decrease in accuracy, if pigeon VSTM is qualitatively similar to human VSTM, then pigeons should show a similar effect of complexity on change detection performance.

We recently assessed the degree to which pigeons transferred performance from color change detection to other domains (Elmore et al., 2012). Although pigeons have previously transferred change detection performance to novel colors in a previous study (Wright et al., 2010), transfer performance on novel shape changes was poor. Even after extensive training with shape training, performance never reached the same level as color change detection performance. Although the primary conclusion concerning restricted-domain relational learning explains the transfer test results (Elmore et al., 2012), the inability of pigeons to learn shape change detection may be related additionally to the increased visual complexity of shapes as compared to colors. Previous work has shown that visual search slopes can provide an independent, quantitative assessment of object complexity that describes decreases in VSTM performance (Alvarez & Cavanagh, 2004; Eng et al., 2005).

Experimental Overview

To test the visual complexity hypothesis, in Experiment 1 we trained 2 birds in a visual target search task using the objects from our previous change detection experiments. Although previous human studies comparing target search and change detection relied on within-subject comparisons, using different pigeons was essential to eliminate carryover effects caused by the opposing natures of the two tasks—our target search task is equivalent to a change detection task with 1 sample item and rewarding responses to the object that matches the sample array (rather than the one that changed). To help ensure our forced-choice task, small-n design, and between-subject manipulation were not uniquely driving any observed relationship between change detection and target search, Experiment 2 was conducted to obtain target search slopes from humans in the task from Experiment 1. These slopes were then compared with results obtained in the human variant of our forced-choice task (Elmore, Passaro, & Wright, *this issue*).

Experiment 1

The main purpose of Experiment 1 was to establish target search functions with color, shape, and polygon object types. Search functions provide a quantitative estimate of object complexity that can then be compared with change detection performance from identical object types (cf. Alvarez & Cavanagh, 2004; Eng et al., 2005). The method we developed for target search was therefore designed toward achieving a close match with our previous change detection work.

Method

Subjects

Two White Carneaux Pigeons (*Columba livia*) with previous experience in a *same/different* procedure served as subjects. Testing was conducted 5 days per week. The pigeons were maintained at 80–85% range of their free-feeding weights, with free access to grit and water in their individual home cages. A 14:10-h light:dark cycle was maintained in the room containing individual home cages.

Apparatus

The pigeons were tested in a (35.9 cm wide × 45.7 cm deep × 51.4 cm high) custom wooden chamber. A hopper delivered mixed grain through a cutout centered below a 17-in. Eizo

T550 color monitor (resolution of 800×600 pixels). A pressure-fitted infrared touchscreen (Carroll Touch, Round Rock, TX) was used to measure responses. A house light (Chicago Miniature 1829, 24 V) was located in the center of the ceiling and was illuminated only during intertrial intervals (ITIs). A rear fan provided ventilation and white noise.

Objects

Object types consisted of 8 colored circles, 8 white shapes, and 8 white irregular polygons, as shown in Figure 1. One pigeon was initially trained with 72 irregular polygons, but training was switched to the 8 items following poor acquisition, and we show only the 8 used for extensive training. Additionally, because of poor shape acquisition, 4 shapes (the first four from the left in Figure 1) were used by the end of shape training. Objects were chosen to be identical to those used in previous change detection studies in both pigeons and humans (Elmore et al., 2012; Eng, et al., 2005; Wright et al., 2010). Each object subtended a visual angle of $3.25^\circ \times 3.25^\circ$. All target objects were presented in the center of the screen. All objects presented in the probe array were located along the edge of two invisible concentric circles, with 6 locations on each circumference, creating 12 possible locations. The diameter of the inner circle subtended 72° , and the diameter of the outer circle subtended 111° . Additionally, the locations were rotationally offset from one another by 30° . Before presentation, the locations of probe objects were randomly jittered along both axes according to a Uniform distribution ranging from -0.2° to 0.2° .

Experimental control

All experimental events were controlled with custom software. Computer-controlled relay interfaces (Metrabyte, Freemont, CA) operated the food hopper and house light.

Procedure

Two-alternative forced-choice training—The first phase of target search training began with a two-alternative forced-choice (2AFC) task using the 8 colored circles. Trials began with 15-s ITI during which the house light was turned on. After the house light was extinguished, a single colored circle was presented as the target in the center of the display. An observing response (FR1) to the circle produced a brief (500ms) blank delay followed by a probe array containing two colored circles, located at random positions on the polar grid. Responses to the colored circle that matched the sample item produced 3-s access to mixed grain. Responses to the non-matching colored circle (hereafter, the distractor) were followed by a correction procedure consisting of a 15-s dark timeout and repetition of the trial. The target and distractor were selected randomly without replacement from the 8-color set for each trial. Similarly, the locations of the probe array items were selected randomly without replacement from the set of 16 possible locations. The random selection of the probe item locations instead of three fixed locations distinguishes our training procedure from other match-to-sample procedures we (and many others) have used previously (e.g., Bodily, Katz, & Wright, 2008). Subjects completed 96 trials within each session. The observing response to the target object was steadily increased over sessions to an FR10. After reaching a performance criterion of 80% correct the correction procedure was removed. Subjects were then required to have a single session with 80% correct without the correction procedure before moving to probe array expansion.

Probe array expansion—After reaching the performance criterion with the 2AFC task, the subjects completed sessions with equal mixtures (32 of each) of trials with probe array sizes 1, 2, and 3. If accuracy dipped below 70%, the correction procedure was re-instated until accuracy went above 70%. The distractor items in the probe array were chosen randomly without replacement from the set of colors remaining after the target color was

selected. Training continued until accuracy reached 80% (without correction procedure) on probe array size 3 trials, and then subjects were given sessions with equal mixtures (24 or each) of trials with probe array sizes of 1, 2, 3, and 4. In this manner, probe array size was increased via subsequent expansions so that eventually subjects were completing sessions with equal mixtures (16 of each) of trials with probe array sizes of 1, 2, 3, 4, 5, and 6 during the final condition of probe array training. When probe array size was expanded to 5, an equal mixture was not possible, and the extra trial was assigned as probe array size 1. Once performance reached 80% on probe array size 6 trials, subjects received a series of shape transfer tests.

Shape transfer series—After training with the color objects, subjects were transferred to a shape target search task via a series of 3 transfer tests, similar to the shape transfer tests used in our pigeon change detection study (Elmore et al., 2012). For each transfer test, eight of the probe array size 2 trials used shape objects rather than colored circles. The assignment of the 8 shape objects to target/non-matching object was done pseudo-randomly so that each object was a target and non-matching probe item once per session. Additionally, no transfer trials were reversals of other transfer trials within the same session. For example, if one transfer trial used pentagon as target and heart as non-matching probe, then a trial with heart as target and pentagon as probe was never selected. Transfer tests were comprised of 6 sessions each and were conducted on consecutive days (18 days total). The correction procedure was never used during a transfer test.

In the first transfer test, the target item was still defined by its color, but rather than a circle, the shape was one of 7 novel shapes (see Figure 1). Non-matching probe items had distinct colors but matched on shape. For example, if the target was a red pentagon, the non-matching probe item could be a yellow pentagon. The second transfer test used targets defined by both color and shape. For example, if the target was a red pentagon, the non-matching probe item could be a yellow heart. The final transfer test used targets defined by shape only. For example, if the target was a red pentagon, the non-matching probe item could be a red heart.

Shape training—Subjects were given shape-only training immediately following the shape transfer series. Shape training began with probe array size 2 trials (2AFC), as in color training. To aid in the discrimination, only 4 shapes were used in training. The correction procedure was reinstated on the third day of shape training. After performance reached 80% the correction procedure was removed, and training continued until performance was at least 80% without correction procedure. Probe array size was expanded to four using the same criteria as color probe array expansion.

For J15313, after reaching the acquisition criterion for probe array size 2 trials, we integrated the remaining 4 untrained shape objects into the training set through 2 consecutive 6-session transfer tests. Each session in the first transfer tests contained 8 trials using only the 4 remaining shape objects. Each session in the second transfer test contained 16 transfer trials, evenly split into Target-Trained, Distractor-Untrained and Target-Untrained, Distractor-Trained types. We use the term untrained for the 4 shape objects used in these transfer tests to recognize that the objects are not, strictly speaking, novel, as they were used in the initial shape transfer test. After the two transfer tests with the untrained shape objects, training continued with probe array size 2 trials using all 8 shape objects. Correction procedure was used beginning with session 3. From this point the probe array was expanded up to size 3, using the same criteria as with the color objects. Because J15313 could not meet the performance criteria to move to probe array size 4, we changed the object set back to the original 4 shape objects. Using just these 4 shapes, the subject was able to reach probe array size 4. After reaching probe array size 4, we alternated blocks of shape

and color sessions in an attempt to increase performance. This training did not show any strong effect after extensive use (118 sessions).

Polygon transfer—After reaching 80% for a probe array size of 4 with the shape objects, subjects were given 6 sessions containing 8 transfer trials using polygon objects. All other procedural details were identical to the shape transfer tests.

Polygon training—Training with the polygon objects began with the use of 72 items and probe array sizes of 2 initially, but the set size was reduced to 4 polygons when J15313 did not reach high rates of accuracy in the task. Correction procedure was reinstated on the third session of polygon training. After subjects reached 85% accuracy, correction procedure was removed and a new criterion of 80% accuracy was set. After reaching this new criterion, subjects were given a single 6-session transfer test using 4 unfamiliar polygon objects from the 72-item set. After the transfer test, subjects received training sessions comprised of 8 polygon objects. After integrating the 8 polygon objects, training followed the procedure used for 8-color training, expanding the probe array up to size 4.

Results & Discussion

Color training—Both subjects finished the initial 2-item, match-to-sample training within 20 sessions (J15313: 17 sessions; O13667: 19 sessions). J15313 reached the 80% performance criterion for probe array size 6 after 32 sessions, while O13667 needed 46 sessions.

Shape transfer—After training with the color objects, both subjects were given the shape transfer series. As can be seen in Figure 2, both subjects performed well in the first two shape transfer tests, in which the target was still defined by color. Paired-sample *t*-tests comparing mean baseline and transfer accuracy across the 6 transfer sessions for each transfer type (Color, Novel Color and Color + Shape) and each subject confirmed this pattern [magnitude of all $t(5) < 1.97$, $ps > .1$]. Once the target was defined solely by shape, however, neither subject's mean accuracy was above chance, as confirmed by per-subject one-sample *t*-tests [magnitude of both $t(5) < .83$, $ps > .44$]. Additional analyses using the non-parametric Wilcoxon signed-rank test confirmed this pattern of transfer performance. These results suggest that both subjects were reliably using color to solve the discrimination and could not transfer this performance to a shape-only discrimination.

Shape training—J15313 required 41 sessions to reach the performance criterion of 80% without correction procedure with a probe array of 4 shape objects. O13667 required 55 sessions to reach the performance criterion of 80% without correction procedure with a probe array size of 4 objects. J15313 received an additional 166 sessions in an attempt to reach higher probe array sizes without success. Acquiring the shape discrimination was clearly more difficult than the color discrimination for the pigeons.

Polygon transfer and training—Results for the transfer to polygon objects are shown in Figure 2. Similar to shape transfer, no evidence was found for transfer, as shown by per-subject one-sample *t*-tests testing transfer accuracy across the 6 sessions against chance performance [magnitude of both $t(5) < 1.40$, $ps > 0.221$]. Non-parametric Wilcoxon signed-rank tests also confirmed that transfer performance was not significantly different than chance performance. Although this difference could be explained by restricted domain relational learning, we also note that the protracted shape training shows that discriminability may be an issue in locating targets defined solely by their shape.

Once J15313 proceeded to training with a set size of 8 polygons he needed 64 sessions to reach the 80% performance criterion for the 4-item probe arrays. It may be expected that successive acquisitions of new object sets may get progressively faster, as the subject learns more generally about the target search task. Because of the large difference between color and shape acquisition, however, it is clear that object discriminability remains an important factor. The next step is to compare search rates across the object types, to look for converging evidence about the role of complexity in pigeon VSTM.

Search rates across object types—Search rates were estimated for each subject by obtaining a least squares fit to the median response times for correct trials from each of the last 6 sessions of training with each object type. One subject (O13667) only had 4 sessions with all color probe array sizes; therefore only 4 sessions are used for this analysis. Figure 3 shows the resultant search slopes for each subject by object type. Across subjects color objects were located the fastest, with neither slope being significantly different from 0 [O13667: $F(1, 22) = 2.94, p = .100$; J15313: $F(1, 34) = 1.77, p = .192$], although there is some indication of an increase in both subjects. Both subjects showed reliably positive slopes for shape target search [O13667: slope=95.8, $F(1, 22) = 56.72, p < .001$; J15313: slope=121.7, $F(1, 22) = 19.52, p < .001$], and J1531 showed a reliable positive slope for polygon target search [slope=50.0, $F(1, 22) = 7.02, p = .015$]. Because of the visually apparent non-linearity in some of the search slopes, additional tests using a log transform on probe array size were conducted. We found reliable log-linear relationship between probe array size and color search times for O13667 [$F(1, 22) = 4.60, p = .043$], and between probe array size and polygon search times for J15313 [$F(1, 22) = 9.51, p = .005$]. No other log-linear relationships were reliable.

Because we did not counterbalance the order of object type training (or use a between subjects design as in Experiment 2), it is possible that the relative ease of polygon search as compared to shape search is due to the previous training with the shape stimuli. If this were the case, however, we would expect better transfer performance to polygons (Figure 2) or much faster acquisition. Future work should consider how target search performance transfers across object type domains.

Comparison with change detection—Figure 4 compares the average search slopes obtained from our target search task with the accuracies obtained in a series of transfer experiments (Elmore et al., 2012). The change detection data come from a series of transfer tests (using 2-item sample displays), rather than at the end of acquisition. The use of transfer data is important because our original question relates to reasons for failed transfer. If no relationship is found between target search rates and transfer performance, we could conclude that the lack of transfer is related mostly to the lack of relational learning during acquisition. On the other hand, a strong relationship between search rates and transfer performance would suggest that object complexity may be moderating performance on transfer tests.

The relationship is clearly linear, and although there are only 3 object types, the target search slopes explain over 98% of the variance in change detection accuracy. The graph does reveal the surprising finding that both the polygon search rate and accuracy both fall in-between the values for color and shape. This finding is somewhat counter-intuitive as we initially designed the shape objects to be “simple,” whereas the irregular polygons were thought to be more difficult. Converging evidence from both target search and change detection, however, suggest that pigeons perceived our shape objects as more complex than our polygon objects, within the set of objects they experienced. This discrepancy highlights the role of using target search to quantify visual object complexity, rather than relying on our own (species-specific) qualitative notion of object complexity.

As with the target search training, the single order of training in the change detection data (color, then shape, then polygon) leaves open the possibility that the better performance on polygon trials is explained by a general increase in performance. The lack of complete transfer from shapes to polygons (in both target search and change detection), however, suggests that pigeons had not learned a generalized change rule, but instead their relational domain was restricted to colors and the trained shapes.

Experiment 2

The goal of Experiment 2 was to collect target search data from humans in an analogous way as the pigeons in Experiment 1. We wanted to confirm the relationship found in previous human change detection studies (e.g., Alvarez & Cavanagh, 2004) would emerge using our task and a between-subjects manipulation. Finally, because of the difficulty of training pigeons to complete the task with highly complex objects, testing with humans allowed us to assess a wider range of object types across a large number of individuals.

Method

Participants

Participants were 48 students from Auburn University, who volunteered in return for course credit. Participants under 19 provided parental consent prior to the study, and all participants provided consent prior to beginning the experiment. The university's Institutional Review Board approved all experimental details.

Apparatus

Participants were seated approximately 30cm away from a 17-in touchscreen LCD monitor (1280×1064, 60Hz). The touchscreen displayed all objects and recorded all responses made by the participants. The room in which participants were seated was unlit; the only light in the room came from the computer monitor. All sequences of the experiment were controlled and recorded using custom software.

Objects

Objects consisted of the same items from Experiment 1, with the addition of 8 kaleidoscope items (see Figure 1). The visual angle for these objects was matched to the pigeons from Experiment 1.

Procedure

All participants were seated in front of the touchscreen. The experimenter read aloud task instructions and answered participant questions. Participants were randomly assigned to 1 of 4 visual object types (colors, shapes, irregular polygons, or kaleidoscopes). Participants completed 384 target search trials divided into 2 blocks of 192 trials, counterbalanced across participants for order. Each block contained 32 repetitions of 6 probe array sizes (1, 2, 3, 4, 5, and 6) pseudo-randomly ordered.

As in Experiment 1, each trial began with the presentation of a target object, and progressed to a blank probe delay after an observing response. The observing response was set to a single touch for humans. A 500-ms probe delay separated the target and probe array. All objects in the probe array appeared at the same time and remained onscreen until a choice was made. Correct responses were followed by a 1000-ms tone. A 2000-ms intertrial interval (ITI) separated subsequent trials. Between the two blocks, participants were allowed to rest as needed.

Results & Discussion

Target search slopes—Because participants were given explicit instructions, accuracies were uniformly high across probe array sizes and object types, and so we only consider response time in these analyses. Figure 5 shows how search times varied across probe array size and object types. The most notable difference when compared with Figure 3 is the lack of a strong distinction between the slopes for color and shape objects. Additionally, the polygon search times are slower than those for the shape objects.

We conducted a regression analysis on the median response times (correct trials only) for each subject across probe array size (probe array sizes 1 through 6; 1 parameter), object type (Color, Shape, Polygon, and Kaleidoscope; dummy-coded with color as the baseline level providing 3 parameters), and interaction terms (formed by crossing the dummy-coded variables with the slope parameter; 3 parameters). Fitting this joint model provides direct tests of the slopes/intercepts of each object type against the baseline color model, rather than against 0 (if individual models were fit to each object type). Overall, our linear model of object type and probe array size accounted for 71% of the variance in median correct response times ($R^2_{\text{adj}} = .707$). For the baseline color model, the best fitting intercept was 462.9ms [$t(280) = 16.41, p < .001$] and the slope was 24.29 ms/item [$t(280) = 3.353, p < .001$]. For shape objects, the analysis showed a marginally reliable 78.3ms increase in the intercept [$t(280) = 1.96, p = .051$], but no significant change in slope [$t(280) = .29, p = .776$]. For polygon objects, no change was found for intercept [$t(280) = 1.48, p = .140$], but the slope increased reliably by 26.2ms [$t(280) = 2.56, p = .011$]. Finally, for kaleidoscope objects, the intercept increased by a reliable 93.3ms [$t(280) = 2.34, p = .020$] and the slope by a reliable 72.2 ms/item [$t(280) = 7.25, p < .001$]. A generalized least-squares (GLS) model using an auto-regressive moving-average [ARMA(1, 2)] covariance structure showed comparable intercept/slope estimates and an identical pattern of parameter significance (including non-significance of the intercept increase for the shape object type, $p = .096$).

Comparison with change detection—As in Experiment 1, we next plotted the obtained target search rates with percent correct data from change detection (Elmore et al., *this issue*). The right panel of Figure 4 shows a roughly linear relationship between inverse percent correct in change detection and the search rates from target search. The deviation from linearity is caused by the relative similarity in change detection accuracy for polygons and kaleidoscopes, but a large difference in the target search slopes. Human participants were not tested with shape objects (Elmore et al., *this issue*) so there is no corresponding shape data point. The target search data would suggest, however, that performance with the shapes should be nearly identical to the color-objects performance.

General Discussion

Across two experiments, we obtained target search slopes for pigeons and humans and related these slopes to data from pigeon and human change detection. Although the pigeons' experiences were not perfectly equated, the stability of the search functions shows the utility of the method. Pigeons' change detection performance was linearly related to the target search slopes for the range of objects tested. The function for the humans was broadly consistent with previously published human target search/change detection work (e.g., Alvarez & Cavanagh, 2004; Eng et al., 2005), and generally replicates the effect found in our pigeon task. Several comparisons between the functions suggest both quantitative and qualitative differences, within the general finding of a cross-species, complexity-limited VSTM. We note, however, that because only two pigeons were used to obtain the mean target search slopes, any generalization to the broader species must be appropriately tempered.

Across pigeons and humans, color objects produced the fastest search rates and highest change detection accuracies. Additionally, search rates increased and change detection accuracies decreased for polygon objects for both species. A difference arises for the shape objects, as pigeons experienced a nearly 6-fold increase in search rates, but humans showed no difference between color and shape target search. The validity of pigeons' difficulty with shape target search was confirmed by a similar difficulty in shape change detection. One reason for this difference may be that humans can verbally label the shape objects. Applying a label or category to objects facilitates memory performance in change detection (e.g., Olsson & Poom, 2005), and may provide a more efficient representation for target search. When compared to search for polygons (another type of object defined by its boundary) a dissociation emerges: polygon search rates were faster than shape for pigeons, but slower than shape search rates for humans, strengthening the labeling/categorization benefit for target search. The use of a verbal labeling strategy shows a qualitative difference in how humans and pigeons (and likely other nonhumans) solve discriminations more generally.

A few differences between the training of the pigeons and the humans should be mentioned. First, only pigeons had a correction procedure during the training. The correction procedure was necessary to ensure accurate responding by the pigeons in both tasks. During change detection transfer sessions (the sessions used for comparison with polygon and shape target search slopes), however, correction procedure was not in place, and is therefore unlikely to play a large part in our primary comparison between change detection performance and target search slopes. Secondly, humans used larger sample arrays during change detection and were tested with different object types within a session. This difference makes direct comparisons between human and pigeon change detection or target search difficult, but do not change our overall point that visual object complexity impacts memory performance in pigeons.

Despite the noted methodological differences, the general similarities between and within target search and change detection for each species are suggestive of a common "limiting factor" in how each species utilizes VSTM. Combining the current quantitative estimates of visual object complexity with change detection (Elmore, Passaro, & Wright, 2012) results in stronger tests of current evolutionary-based theories of VSTM. Gibson et al. (2011) have suggested that pigeon VSTM may be limited by a fixed capacity of around 2 items, similar to the roughly 4-item fixed capacity advanced for human VSTM (e.g., Luck & Vogel, 1997). Because the current pigeon change detection data come from sample arrays of only two items, however, all of the items should fit within their capacity. Under this model, then, performance declines in change detection not because of a reduction in the number (or resolution) of the items stored, but rather because of the increase in sample/probe array confusability that results from the increase in object complexity.

Alternatively, our results also fit within the continuous view of VSTM (e.g., Elmore et al., 2011; van den Berg et al., 2012). If VSTM is a continuous, flexibly allocated resource, the performance decrease is explained by the difficulty of adequately encoding complex objects. A more complex object requires additional resources to be encoded with sufficient resolution to ensure a reasonable degree of accuracy. Differences between humans and pigeons with the least-complex objects (in the current study, colors) then arise from differences in the baseline noise levels of their respective VSTM systems.

Although the current results do not distinguish between discrete and continuous views of VSTM, they do provide more evidence of strong functional similarities between human and pigeon VSTM. Combined with recent work on nonhuman primate VSTM (Elmore et al., 2011; Heyselaar et al., 2011), it is becoming increasingly clear that a cross-species approach to VSTM can provide further insight and constraint on evolutionary theories of VSTM. The

development of such a theory will be buoyed by continued emphasis on accurate estimation of cross-species functional relationships via parametric manipulation.

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Highlights

- We trained pigeons and humans in a visual target search task using objects of varied complexity.
- Search rates from target search were inversely related to percent correct in change detection.
- Humans were able to use verbal-based strategies to solve the visual discrimination with some complex stimuli.
- Pigeon visual short-term memory shows effects of object complexity that are qualitatively similar to those found in human VSTM.

Figure 1.

Left. Example trial progression for Experiments 1 (pigeons) and 2 (humans). ITI: Intertrial Interval. *Right.* Objects used in Experiments 1 (except Kaleidoscopes) and 2 (all objects). For the Polygon and Shape objects, the first four objects were used as the initial 4-object sets during pigeon training (Experiment 1) before expanding to all 8 objects.

Figure 2.

Baseline and transfer performance across shape and polygon transfer series for 2 pigeons. For the polygon transfer, the baseline trials used shape objects for target/distractor. For all other tests, the baseline trials used the color objects for target/distractor. Error bars represent 1 standard error of the mean.

Figure 3.

Target search slopes by object type for 2 pigeons. Points represent the mean of the last 6 sessions' median response times for each object type. Linear slope coefficients are listed by the corresponding line for statistically reliable (i.e., different from 0) slopes. Error bars represent 1 standard error of the mean.

Figure 4. Relationship between inverse percent correct in change detection and search rates from target search for pigeons (left panel) and humans (right panel).

Figure 5.

Target search slopes by object type for the human target search experiment. Points represent the average across each individual's median response time. Linear slope coefficients are listed by the corresponding line for statistically reliable (i.e., different from 0) slopes. Error bars represent 1 standard error of the mean.