Categorization of birds, mammals, and chimeras by pigeons

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ABSTRACT

Identifying critical features that control categorization of complex polymorphous pictures by animals remains a challenging and important problem. Toward this goal, experiments were conducted to isolate the properties controlling the categorization of two pictorial categories by pigeons. Pigeons were trained in a go/no-go task to categorize black and white line drawings of birds and mammals. They were then tested with a variety of familiar and novel exemplars of these categories to examine the features controlling this categorization. These tests suggested the pigeons were segregating and using the principal axis of orientation of the animal figures as the primary means of discriminating each category, although other categorical and item-specific cues were likely involved. This perceptual/cognitive reduction of the categorical stimulus space to a few visual features or dimensions is likely a characteristic of this species' processing of complex pictorial discrimination problems and is a critical property for theoretical accounts of this behavior.

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It is well established that a number of animals can learn to discriminate and categorize a wide variety of ill-defined, open-ended, natural categories. Pigeons, for example, have learned to discriminate "natural" polymorphous noun categories such as flowers, cars, trees, chairs, cats, dogs, and people (Aust and Huber, 2001; Ghosh et al., 2004; Herrnstein, 1979; Herrnstein and Loveland, 1964; Wasserman et al., 1988). Besides supporting rapid learning, these types of categorical discriminations have been established to support transfer to novel exemplars similar to human conceptual behavior. Because of this similarity and its implications for the evolution of cognition, visual discriminations of this type have generated considerable interest since their inception.

One important issue in the analysis of visual categorization centers on what properties control discrimination and transfer performance. A shortcoming in many categorization experiments has been the scarcity of information about the nature of the cues regulating such discriminations. Without knowing what cues or features are being used by the animals, however, it is difficult to make inferences about the representation of these categories, their underlying computational mechanisms, or their similarity to human conceptual behavior (Cerella, 1986; Cook, 1993; Huber, 2001; Lea et al., 2006a). With these issues in mind, this paper describes

experiments focused on identifying the visual properties controlling the discrimination by pigeons of two representative pictorial noun categories – birds and mammals.

Research on natural categories has relied on photographs as the primary medium for testing such discrimination. A major limitation with this type of complex stimulus is that it is not easily manipulated. While this photographic complexity may be a key element in the formation of such discriminations, they correspondingly make it difficult to isolate the controlling cues. The availability of modern software for manipulating such images has resulted, however, in some progress. The most in-depth analysis of this type has been the series of experiments conducted by Aust and Huber (2001, 2002, 2003) examining the controlling properties involved with categorizing pictures of people from non-people by pigeons. Using a variety of different transformations (e.g., image scrambling and inversion, part deletion, gray scale) the results of these tests highlight the complexity of this analytic goal. Initial tests involving the scrambling of the entire image suggested that local cues associated with the people and image color were particularly critical (Aust and Huber, 2001). Subsequent research suggested that some portions of the human body (heads, hands) were more important than others (Aust and Huber, 2002) and that the spatial configuration of these parts may be at least partially encoded (Aust and Huber, 2003). The importance of the head has also been confirmed by the pecking and tracking of this part in a people-present/people-absent discrimination (Dittrich et al., 2010). Finally, their results suggested that both item-specific information about the individual exemplars and category-specific information about the class of items were both being encoded by the pigeons as

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determined by their different responses to tests with familiar and novel exemplars. Using a similar approach to examining the visual categorization of people, flowers, chairs and cars by pigeons, Lazareva et al. (2006b) found that different visual attributes controlled them. From tests involving stimulus inversion, blurring and scrambling, their results suggested that the categorization of flowers and people were controlled by the overall contour of the images, while cars and chairs were determined by local features.

The analysis of visual categorization by pigeons in this article has its origins in the research of Cook et al. (1990) using stimuli consisting of black and white line drawings of birds and mammals as the discriminative classes. These stimuli were drawn from edited collections (Harter, 1979; Iyari, 1979) of wood cuts and drawings from 19th century scientific journals and popular magazines. These images have the complex characteristics of photographed natural categories, but have several advantages as a medium. First, because of their original scientific and educational purposes, they capture the animals with considerable detail including, key visual features, characteristic or canonical poses and postures, and often include surrounding habitat for each animal. Combined with the considerable irrelevant variation produced by differences in perspective, subjective distance, and the number of animals depicted, these stimuli seemed well suited for the study of categorization. Second, because each image is a simple collection of individual pen strokes, each line can be independently altered allowing for easy manipulation of their features. Third, their black-and-white nature excludes color information. This is valuable because color often overshadows the processing of other features and dimensions of complex stimuli by pigeons. Thus, these stimuli provided an excellent mixture of the featural richness and variation of photographs, with the capacity for easy manipulation.

Cook et al. (1990) established that these line drawings were effective at creating categorical behavior. They found that these line drawings were easy to discriminate, produced robust transfer to novel exemplars of each category, and that speed of learning and degree of transfer varied with the number of training exemplars. Importantly, they also found that the degree of transfer appeared to be sensitive to the similarity of the items within each category as judged from human prototypicality ratings.

The goal of the present research was to identify the controlling features involved in the discrimination of these bird and mammal categories. We used a partitioning strategy to search the possible feature space involving a series of different image manipulations. These manipulations were tested as a pair of tests. The first test involved the manipulation of familiar exemplars while the second tested novel exemplars. This allowed us to assess both item-specific and category-specific information in the pigeons' reaction to the altered stimuli. The pigeons were trained and tested in a go/no-go discrimination task in which they had to discriminate between the categories by pecking at pictures of birds to be reinforced with food, while inhibiting pecking to pictures of mammals that were presented in extinction. Using this established discrimination, we then conducted a series of tests manipulating different aspects of the stimuli. The background, logic and rationale for these tests are described in the next section.

1. Stimulus analytic tests: background, rationale and logic

The purpose of Test 1 was to examine the degree to which the figure of an animal and/or the contextual natural backgrounds/habitats controlled the discrimination. This was important to determine because it has become established that pigeons can memorize the visual content of a very large numbers of pictorial items (Cook et al., 2005; Fagot and Cook, 2006; Vaughan and Greene, 1984). Further, earlier studies had suggested that small differences in the background of photographic images could also be detected and used by the birds (Greene, 1983). Cook et al. (1990) eliminated backgrounds from some of the training stimuli and showed that pigeons had little trouble continuing to discriminate these animal figures without the background, a finding consistent with the hypothesis that the pictured animals were of primary importance to the categorical discrimination. In those experiments, however, the pigeons were not tested with stimuli in which the figures were removed to evaluate how the background itself contributed to the discrimination. In the test conducted here, we removed the background from a larger set of familiar images, and included conditions where the animal in the drawing was removed, leaving only the background. This allowed us to determine whether or not the redundant contextual information contributed to the discrimination.

As detailed below, the results of the first test will show that the animal figure was indeed most important, so we next divided the animal figures into parts, examining the independent contributions of the head, body and legs. Tests 2A and 2B involved using chimera animals involving mixtures of these parts within and across the categories. By mixing and crossing together different portions of each category into a single "chimera" test animal, it was possible to judge which portions of the animal figures were making the greatest contribution to the pigeons' discrimination. Cook et al. (1990) had pilot-tested a few limited examples of such chimera stimuli. The results from three of the four exemplars tested suggested that the body of the animal, rather than features associated with the head, were most important. In the present study, we employ the same strategy but tested greater numbers of chimeras, constructed from a greater variety of animals, to better test and strengthen the conclusions from that earlier study. One set of tests involved exchanging the head and body of the animals from the two categories. The second set of tests involved manipulating the type and number of legs across the two categories.

The next two tests were designed to evaluate the relative contributions and roles of the global organization and local features of the animal figures. In Test 3A the animal figures were divided into three parts involving the head, trunk, and rear sections of the animals. To manipulate global information, conditions were tested in which these different parts were separated from each other by a spatial gap or simultaneously scrambled or inverted from their normal order of appearance. If the order and continuous nature of these different parts were critical, then these alterations to the global organization should be disruptive to the pigeons' performance.

In Test 3B the interior texture was replaced by a solid area of single brightness. This removed local information primarily leaving global shape as the basis for any discrimination. These test stimuli were presented over a range of brightness values, from complete silhouettes, through intermediate brightness values, to exclusively outlined contours. If the global form was exclusively controlling the discrimination, then the pigeons should have little difficulty with these altered forms. On the other hand, if local details in the interior of the animals were also a part of their representation of the categories, then this manipulation should disrupt performance.

Finally, Test 4 examined how the orientation of animal figures influenced the discrimination. Cook et al. (1990) had found that the pigeons were insensitive to either reflections or 180° rotations of the categories, suggesting that orientation was not particularly important. However, both tests had retained the primarily diagonal orientation of the birds and the basic horizontal orientation of the mammals. In Test 4, we included a more extensive and diagnostic set of figural orientations to reexamine the contribution of this global factor to the discrimination of both familiar and novel members of each category.

For purposes of economy, the general methods outline the shared elements of the procedures for the different tests. This is

followed by four different sections that include the specific details of each test, along with its results and a brief interpretation. Overall interpretations of the results are then considered in Section 4.

2. General methods

2.1. Animals

Five male White Carneaux pigeons, *Columba livia*, were tested. They were maintained at 80–85% of their free feeding weights with free access to grit and water. The pigeons had previously learned this bird/mammal discrimination 11 months earlier. They were re-familiarized with the discrimination using a combination of old and new exemplars of each category for approximately 1 month before testing commenced.

2.2. Apparatus and stimulus materials

Testing was conducted in a computer-controlled (Cromenco Z-2D) operant chamber. Stimuli were rear projected onto a 12 cm × 18 cm translucent projection screen using a slide projector (Kodak 760H). This screen was located 23 cm behind a clear Plexi-glas 9 cm × 9.3 cm response key centrally located in the front wall of the chamber. Stimulus duration was controlled by a computer-controlled shutter located in front of the projector lens. A food hopper was centrally located 7.5 cm below the response key and delivered mixed grain. A house light was located in the ceiling and was illuminated at all times.

All exemplars for both categories were photocopied from two edited collections of animal line drawings (Harter, 1979; Iyari, 1979). These items were then photographed with a SLR camera (Nikon FE2, 1/30th of a second at F 5.6, Kodachrome 64 slide film) and presented as 35 mm slides. A blue filter (Tiffen 80B) was used to compensate for the incandescent lighting used to illuminate the images during photography. The stimulus manipulations described below were performed on photocopied images prior to being photographed. When projected, the stimuli subtended a vertical visual angle of approximately 25°.

2.3. Procedure

2.3.1. Baseline categorization

Throughout all tests, the pigeons were maintained on a baseline categorization discrimination consisting of daily session (40 S+ and 40 S− presentations). The bird category was designated the S+ category and the mammal category designated the S− category for all five pigeons. Each trial consisted of a randomly determined category exemplar presented for 30 s. Pigeons were rewarded for pecks to the S+ category on a variable interval schedule (VI-45) that resulted in reinforcement on 66% of trials on average. Pecks to the S− category were not reinforced (i.e., extinction). Sixteen different orders of slide presentations were tested and employed different combinations of forward and backward projector motion to prevent any sequential memorization. Between tests, these baseline items were irregularly changed to incorporate new exemplars of each category to limit item memorization. Trials were separated by variable inter-trial intervals of 3–15 s that were independent of the randomized forward and backward positioning of the slide tray between trials.

2.3.2. Stimulus analytic test sessions

The general procedures were essentially identical for each of the tests. The primary variable was the nature of the stimulus manipulation tested, with minor adjustments in the details of session organization depending on the number of conditions and exemplars tested. Each test session consisted of 80 trials. The first 20 trials

were used as a warm-up period during which only baseline category stimuli were shown. Test stimuli were randomly placed into the remaining 60 trials with the constraint that at least two baseline trials occur between test trials. Test images replaced randomly selected baseline images in the slide tray. All temporal parameters were identical to the baseline sessions. These tests were conducted as *probe trials* during which no reinforcement was allowed. These probe trials allowed for the uncontaminated measurement of peck rate without the presence of food presentations. The rationale and details of the different analytic tests are described next.

3. Specific test procedures and results

3.1. Test 1: analysis of figure/ground – procedures

This test examined the contribution of the animal figure relative to its surrounding background. Because the original images were naturalistic in origin, there were correlations between the animal category and its setting. For each session, a set of category exemplars were modified, choosing baseline images with visible background characteristics. In the *figure* condition, the entire background was removed, leaving just the solitary animal. In the *Ground* condition, the animal figure was deleted, leaving just the background. Illustrative examples of each of the conditions are displayed in Fig. 1. In total, twenty exemplars (10 birds/10 mammals) were tested in these figure-only and background-only conditions. Each session tested two bird and mammal exemplars in each condition as unreinforced probe trials. Over 10 sessions, each of these exemplars was tested twice in each condition.

To test the role of *figure* vs. *ground* in categorical transfer performance, the pigeons were tested with novel exemplars. In total, 16 novel exemplars (8 birds/8 mammals) were tested in the *figure*, *ground* and a *complete image* transfer (neither property deleted) conditions. Each session tested one novel bird and mammal exemplar in each of these three conditions once as an unreinforced probe trial. Testing was conducted for a total of eight sessions.

3.2. Test 1: analysis of figure/ground – results

The left panel of Fig. 2 shows the mean peck rate to the baseline, figure, and ground conditions testing familiar exemplars. The baseline categorization continued to be well discriminated as indicated by the higher peck rates by all five pigeons to exemplars of the bird category (black bars) compared to the mammal category (gray bars). The *figure* condition supported virtually equivalent levels of discrimination. In contrast, the *ground* condition supported a much lower level of discrimination than either of these conditions. As to be expected from this pattern, a repeated measures ANOVA (Category × Condition) confirmed a significant interaction between category and condition, $F(2, 8) = 31.1$ (an alpha of $p < .05$ was used to judge the significance of statistical tests). Separate two-tailed paired t-tests (df = 4) comparing peck rates to each category within each condition confirmed the existence of significant categorical discrimination in the baseline and *figure* conditions ($ts > 2.76$). For the *ground* condition, there was little or no evidence for discrimination among the categories, $t(4) = 2.4$, $p = .07$.

The right panel of Fig. 2 shows the mean peck rate to the baseline, complete, figure, and ground conditions in the test with novel exemplars. Again, the baseline categorization continued to be well discriminated. The novel figure condition supported similar levels of discrimination among the categories. The complete figure transfer condition supported transfer, but not to the same degree as the baseline or novel figure conditions (see below). The novel ground condition supported no discrimination, with essentially equivalent peck rates to each category. Again, a repeated
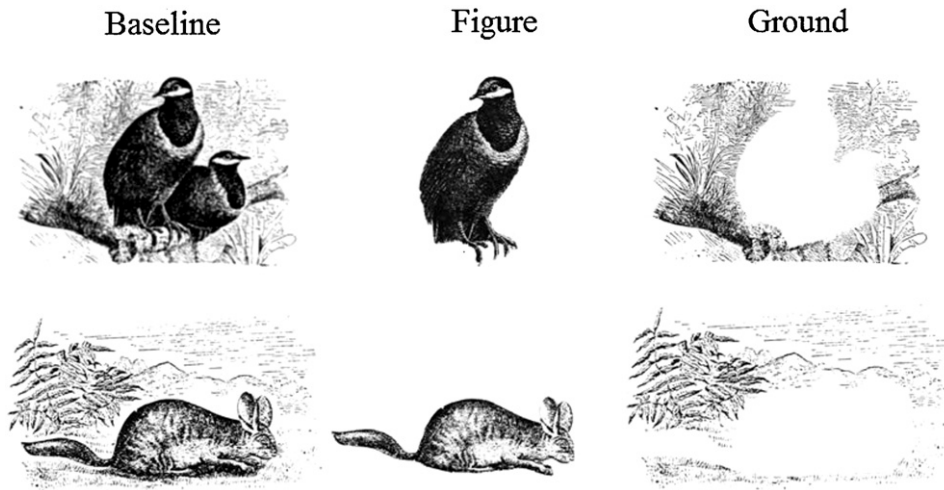
Fig. 1. Illustrative examples of the baseline, figure, and ground conditions of both categories used in Test 1.

measures ANOVA (Category × Condition) confirmed there was a significant interaction between category member and condition, $F(3, 12) = 11.7$. Separate paired *t*-tests comparing categorical discrimination in each condition revealed significant differences in peck rate to each category for the baseline, $t(4) = 5.3$ and novel figure conditions $t(4) = 7.1$. The moderate transfer results for the complete figure condition were due to one pigeon performing at near chance in this specific condition. With this bird included, the differences between the categories were not significant, $t(4) = 2.2$, $p < .09$. When excluded, the other four pigeons did show significant discrimination transfer, $t(3) = 3.4$. All five pigeons performed poorly in the novel ground-only condition and there were no significant differences among the categories for this condition.

Thus, the pigeons' discrimination of the categories was almost exclusively controlled by the animal figure in both tests. Some pigeons may have learned a little something about the item-specific background features associated with familiar bird and mammal exemplars, but this learning did not generalize to novel images where features of the background potentially correlated with each category (e.g., trees versus open ground) were not sufficient. In fact, the presence of the background cues may have impeded generalization to novel animal figures as suggested by the better transfer

performance observed in the novel figure condition in which they were absent. The next test tried to understand better what parts of the animal were most important.

3.3. Test 2A: analysis of figural components (head and body chimeras) – procedures

This test examined the contribution of the animal figure's body vs. its head to the discrimination. This was done by testing chimera animals created from conflicting information from both categories by combining the head of an animal from one category with the body of an animal from the other category and control animals combining heads and bodies from different exemplars of the same category. Four chimera conditions were created. These consisted of *control bird/bird* exemplars made from the head and body of two different birds, *control mammal/mammal* exemplars combined from two different mammals, *bird/mammal chimeras* (head/body) combining the conflicting head of a bird with the body of a mammal, and *mammal/bird chimeras* combining the conflicting head of a mammal with the body of a bird. In making the chimeras, the head and body components of eighteen different animals were used. Care was taken in combining these parts to make creatures with
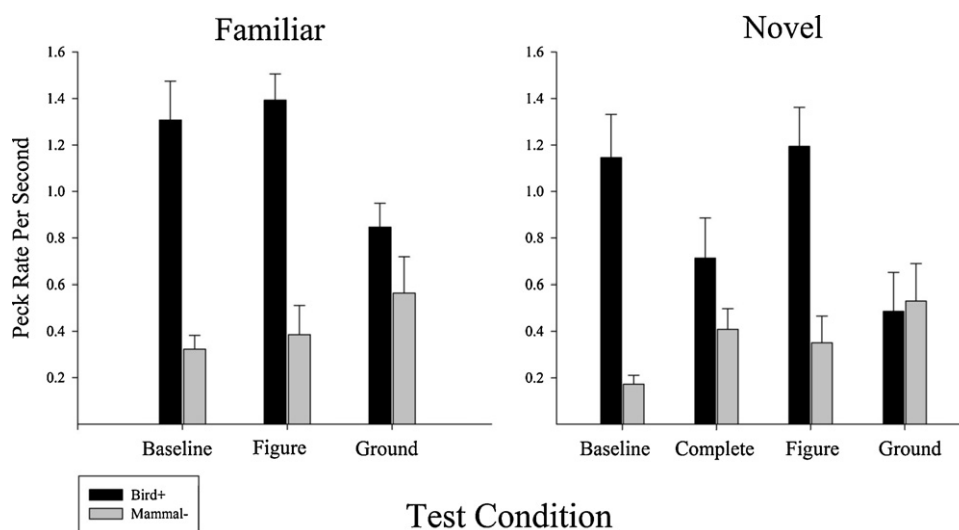

Fig. 2. Mean peck rate to the different test conditions examined in Test 1. The left panel shows these results for tests involving familiar exemplars. The right panel shows the results for tests involving novel exemplars. Error bars represent the SEM of each condition.
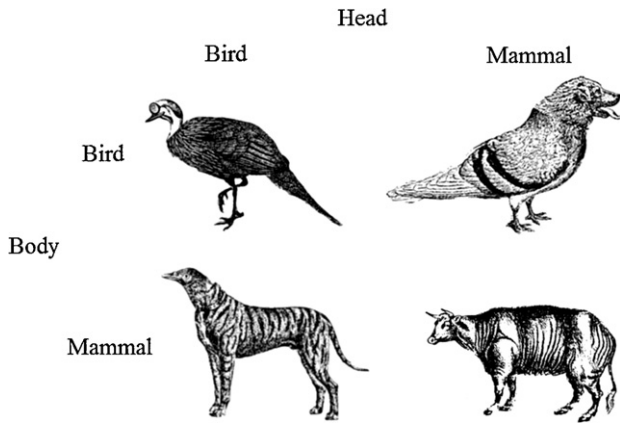
Fig. 3. Illustrative examples of the different chimera test conditions for combinations of both categories examined in Test 2A.

smooth contours and reasonable proportions. The background was also removed for these and future test stimuli. Illustrative examples of the conditions are displayed in Fig. 3. Each session tested two examples each of the four conditions. The control bird/bird and mammal/mammal test trials were differentially reinforced as they contained all the properties of the categories they represented. The two chimera conditions were tested as non-reinforced probe trials. Nine test sessions were conducted.

To test the role of these properties in determining categorical transfer performance, the pigeons were next tested with novel chimera exemplars. Thus, the only difference from the previous head vs. body test was that the chimera stimuli were made from parts of birds and mammals to which the pigeons had not previously been exposed. Each session tested novel exemplars in each of the four conditions twice. All test trials randomly appeared within a session and were tested as non-reinforced probes, including the control conditions. This test was conducted for six sessions, at which point the test images were reflected to face the opposite direction and another similar six-session test block conducted. Reflecting the images was done to minimize the effects of the prior exposure and maintain its novelty.

3.4. Test 2A: analysis of figural components (head and body chimeras) – results

The left panel of Fig. 4 shows the mean peck rates to the baseline and familiar chimera test conditions. The baseline categorization continued to be significantly discriminated and provides a good reference point for interpreting the birds' reactions to the chimeras. The pigeons exhibited excellent discrimination to those chimeras where the head and the body came from the same category. The peck rate in the bird/bird chimera condition was much greater and significantly different from that in the mammal/mammal chimera condition, $t(4) = 7.1$. In fact, this chimera discrimination was equivalent to that of the baseline condition as peck rates in the bird/bird chimera condition were not significantly different from the baseline bird category. Likewise, peck rates in the mammal/mammal chimera condition were found not to be significantly different than in the baseline mammal condition. Together, these results indicate that recombining heads and bodies of animals from within the same category did not alter the discrimination.

Results from the conflict chimera condition indicated that features associated with the body, and not the head, controlled the discrimination. Here the peck rate to the mammal-head/bird-body condition was not significantly different from that of the baseline bird condition while being significantly different from the baseline mammal condition, $t(4) = 9.0$. Correspondingly the peck rate to the bird-head/mammal-body condition was significantly different from the baseline bird condition, $t(4) = 7.2$, and even better discriminated than the baseline mammal condition, $t(4) = 2.9$. Finally, discrimination of the two consistent chimera conditions was not any better than that observed between the two conflict conditions. Overall, the results indicate that the head made little contribution to the discrimination.

The right panel of Fig. 4 shows the mean peck rates to the baseline and novel chimera test conditions. For the novel chimeras that maintained a consistent categorical structure, the pigeons' discrimination continued to be excellent, although slightly reduced from baseline levels. Peck rates to the novel bird/bird chimera condition were significantly different from those of the novel mammal/mammal chimera condition, $t(4) = 12.9$. Peck rates to the novel bird/bird condition were not significantly different
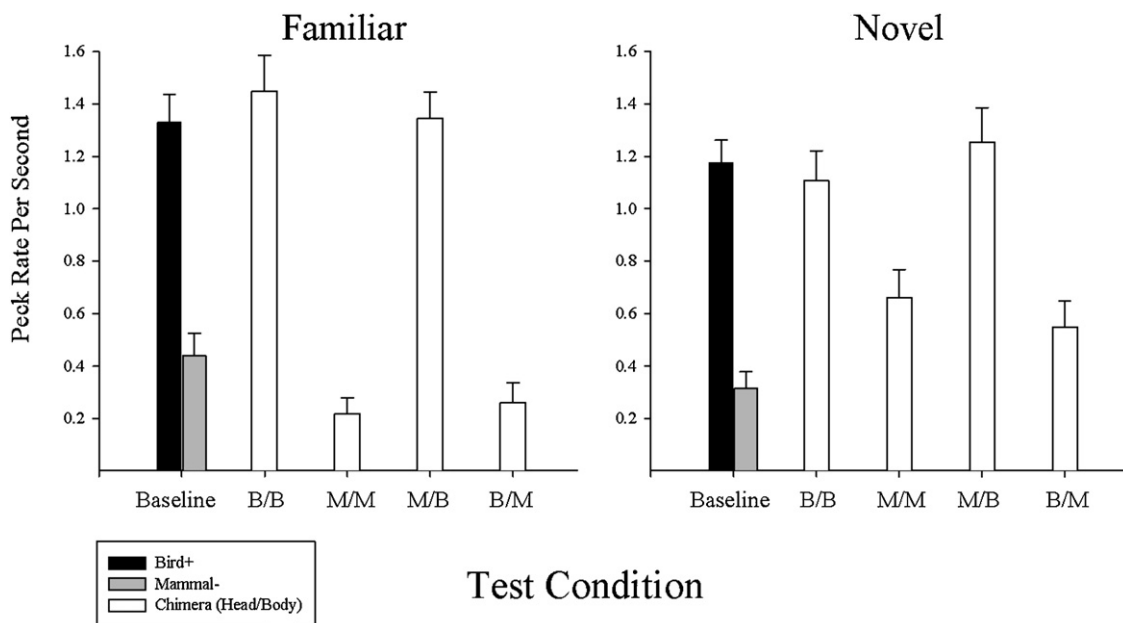

Fig. 4. Mean peck rate to the different test conditions examined in Test 2A. The left panel shows these results for tests involving familiar exemplars. The right panel shows the results for tests involving novel exemplars. Error bars represent the SEM of each condition.

relative to the baseline bird condition, but peck rates to the novel mammal/mammal condition were not suppressed to an equivalent degree in comparison to the baseline mammal condition, $t(4) = 5.3$. This difference suggests that the novelty of the test items was detected.

Results from the novel conflict chimera condition again supported the conclusion that the body, and not the head, controlled the discrimination. Here peck rates to the novel mammal-head/bird-body condition were not significantly different from that of the baseline bird condition, but were significantly different from the baseline mammal condition, $t(4) = 12.2$. This result indicates that when categorical features within the stimuli were in conflict, it was the body that prevailed and ultimately determined the classification. Consistent with these results were the peck rates to the novel bird-head,/mammal-body condition. In this condition, the peck rates were significantly different from the baseline bird condition, $t(4) = 7.2$, and only slightly, but significantly, higher than the baseline mammal condition, $t(4) = 3.2$.

Both of these tests clearly indicate that the pigeons were consistently classifying the chimera conflict stimuli based on properties of the body, and not the head, regardless of their familiarity with the stimuli. Our results converge with Ghosh et al.'s (2004) finding with pigeons that body-associated cues were more important in a similar chimera test examining the categorical discrimination of cats and dogs by pigeons. The next test explored some properties of that might be responsible for this control by the "body."

3.5. Test 2B: analysis of figural components (number and type of legs) – procedures

One major difference between mammals and birds concerns their typical number of legs. The next test examined the contribution of the number of the exemplar's limbs to the categorical discrimination. This was done by testing chimera animals with varying number of legs. One manipulation involved making the number of legs match those of the other category. In the *quadrupedal bird* condition, a set of birds had a matching set of their legs added to the front part of their bodies to give them four legs. In the *bipedal mammal* condition, a set of mammals had their front legs removed to make them have two legs (somewhat similar to birds). The second manipulation involved making chimera animals that had the number and type of legs from the other category. In the *bird/mammal* (body and head/legs) condition, a set of birds had a matched set of legs from a mammal placed on their bodies. In the *mammal/bird* (body and head/legs) condition, a set of mammals had a matched set of legs from a bird placed on their bodies. Again, in constructing these stimuli, care was taken to combine these parts in a proportional manner with smooth contours (although this was more difficult than for the head/body manipulation). Illustrative examples of the conditions are shown in Fig. 5. Each session tested two examples of each of the four conditions, plus two trials that tested the original baseline figures (five from each category) used to construct the stimuli. All 12 of these tests randomly appeared within a session and were tested as non-reinforced probe trials. Ten test sessions were conducted.

To test the role of these properties in determining categorical transfer performance, the pigeons were again tested with novel exemplars of these conditions. Thus, the only difference from the previous test was that the stimuli were made from novel bird and mammals parts. Each session tested novel exemplars in each of the four conditions twice, plus two trials that tested the unaltered novel bird and mammal exemplars (six from each category) used to construct the stimuli. All 12 test trials randomly appeared within a session and were tested as non-reinforced probes. Six different sets of these conditions were tested. This testing was conducted for
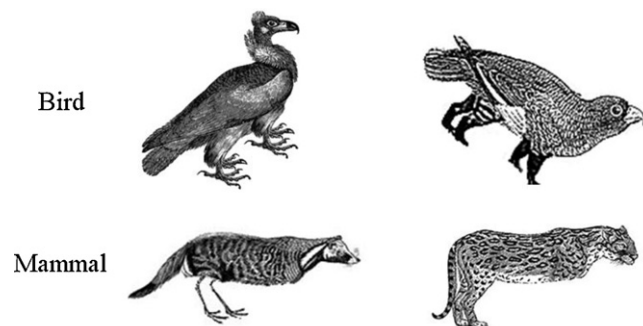

Fig. 5. Illustrative examples of the different chimera leg conditions for both categories examined in Test 2B.

12 sessions, with each set tested twice (the second time right/left reflected).

3.6. Test 2B: analysis of figural components (number and type of legs) – results

Overall, the number of legs present on the body made little substantive contribution to the pigeons' categorical discrimination. The left panel of Fig. 6 shows the mean peck rates to the baseline and test conditions. When the bird-bodied test figures with either four bird (B/B) or four mammal legs (B/M) were compared with paired t-tests (dfs = 4) to the baseline bird discrimination there were no significant differences in peck rates, indicative of their classification as bird-like. Similarly when the mammal-bodied test figures with either two mammal (M/M) or two bird legs (M/B) were compared to the baseline mammal discrimination there were no significant differences in peck rates among these conditions, indicative of their classification as mammal-like. The peck rates for the consistent mixed body and legs conditions (B/B and M/M) suggested slightly better control than when inconsistent chimera mixtures were used (B/M and M/B), but statistical comparisons found this to be unreliable.

The right panel of Fig. 6 shows the mean peck rates to the transfer and test conditions for tests involving novel figures. Again the pigeons showed significant transfer when tested with novel figures of each category, $t(4) = 4.4$. When the bird-bodied test figures with either four bird (B/B) or four mammal legs (B/M) attached to them were compared with paired t-tests to the transfer bird discrimination there were no significant differences in peck rates, indicating the classification of these novel figures as bird-like. Comparison of the overall levels of responding to the novel mammal-body test figures with either two mammal (M/M) or two bird legs (M/B) attached to them were consistent with their classification as mammal-like. However, when compared with paired t-tests to the transfer mammal discrimination there were significant differences in peck rates for both the M/M, $t(4) = 5.2$, and M/B conditions, $t(4) = 2.8$. However, both of these conditions supported significantly lower peck rates than either the B/B or M/B four legs conditions, all $ts(4) > 2.8$. This observation, in addition to the generally lower peck rates to two legged figures, indicate their classification of these modified novel figures as mammal-like. Thus, both tests consistently suggest that the number and type of legs attached to the body are not the properties responsible for the present categorical discrimination.

3.7. Test 3A: analysis of global and local features (figural separation) – procedures

The next tests examined the contribution of global form and local features of the animal to the discrimination. The first test
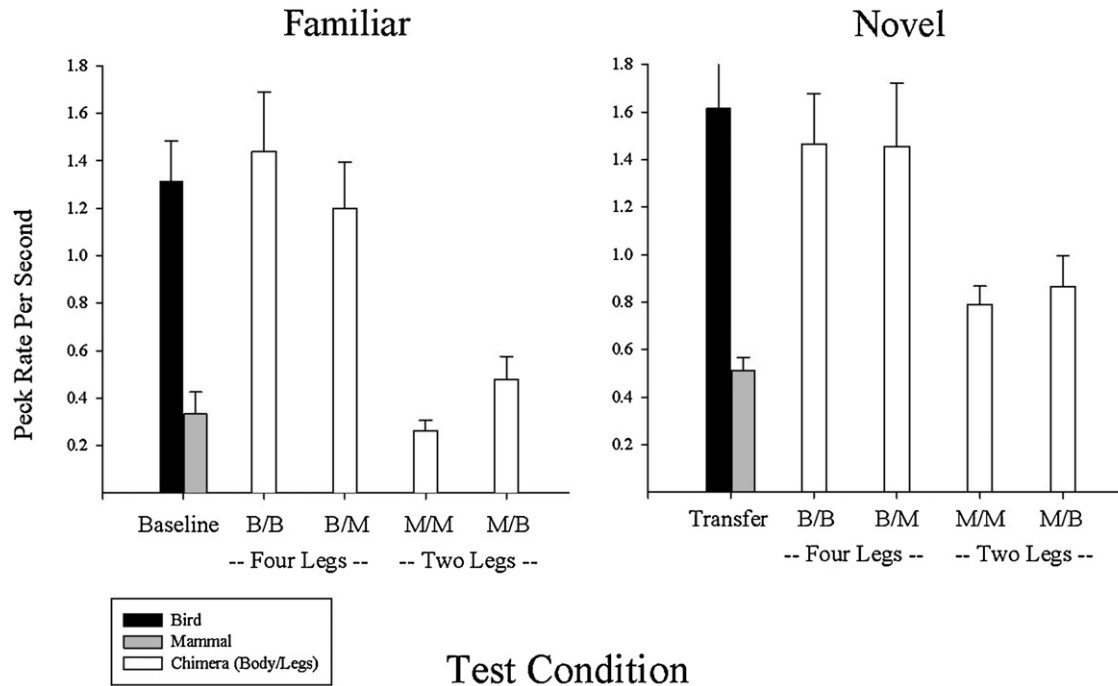
Fig. 6. Mean peck rate to the different test conditions examined in Test 2B. The left panel shows these results for tests involving familiar exemplars. The right panel shows the results for tests involving novel exemplars. Error bars represent the SEM of each condition.

examined how separating and scrambling different portions of the exemplars influenced discrimination. The global form of nine birds and nine mammal figures with their backgrounds removed were separated in three approximately equivalent segments containing the head, torso, and rear of each animal. From these parts four different conditions were created. These consisted of the *separated* condition, where the parts were separated by approximately 2 cm from each other along the animal's principal and canonical orientation, and the *close and scrambled* condition in which the three parts were scrambled, but placed adjacently to each other. In the *separated and scrambled* condition the head and rear parts were exchanged while in the *random and scrambled* condition the three parts were positioned randomly with the restriction that the normal order could not appear. Illustrative examples of these conditions are displayed in Fig. 7. Each session tested two baseline exemplars (one bird/one mammal) in each of the four conditions. All eight test trials randomly appeared within a session and were tested as non-reinforced probes. Nine test sessions were conducted.

Following this, the pigeons were tested with novel exemplars. Each session tested novel exemplars in each of the four conditions twice, plus two trials that tested the novel bird and mammal exemplars used to construct the stimuli. All ten test trials randomly appeared within a session and were conducted as non-reinforced probes. Six different sets of these conditions were tested. This testing was conducted for 12 sessions, with each set tested twice (the second time right/left reflected).

3.8. Test 3A: analysis of global and local features (figural separation) – results

The results for this test are slightly more complex than those from earlier tests in that the outcomes of the manipulation appeared to depend on familiarity of the figures. The left panel of Fig. 8 shows the mean peck rates to the baseline and test conditions with the familiar stimuli. Here the global organization of the

body parts had little effect on discrimination of familiar stimuli of each category. The baseline categorization continued to be clearly and significantly discriminated, $t(4) = 5.1$. The same was also true for all four test conditions as the bird category supported significantly higher peck rates than the mammal category regardless of its spatial organization, $ts(4) > 2.7$. When compared with baseline responding and across tests of items within the same category, there were no significant differences among the conditions confirming that peck rates were equivalent across conditions. Thus, independent of whether the body region of the animal had been separated, scrambled, or both, there was no effect on the discrimination of highly familiar items of bird/mammal categories.

The right panel of Fig. 8 shows the mean peck rates for the transfer and test conditions with the novel exemplars. These averages are computed based on four of the five pigeons that were tested, because one pigeon did not transfer to the novel figures in this test and pecked at very low rates to all of these transfer stimuli. For the other four pigeons, the transfer stimuli of complete figures supported significant categorical discrimination, $t(3) = 3.9$, again. Spatial separation of body segments reduced discrimination between categories as peck rates decreased with birds and increased with mammals. Although responding to the bird category was numerically higher, there was no significant differences in peck rates between the two categories for either separated test condition, $ts(3) < 2.1$. When the same figures were compacted close together, however, significant differences between the two categories emerged with peck rates to novel bird conditions greater than mammal conditions, $ts(3) > 4.1$. This was true regardless of how the position of the segments were scrambled within this compact figure.

This pattern of results suggests that the global configuration of the animal figures was more important than the specific arrangement of the local parts, especially for novel stimuli. Across all conditions, scrambling the local segments did not impact the discrimination when compared to unscrambled stimuli. When the segments were more widely separated, however, the categorical
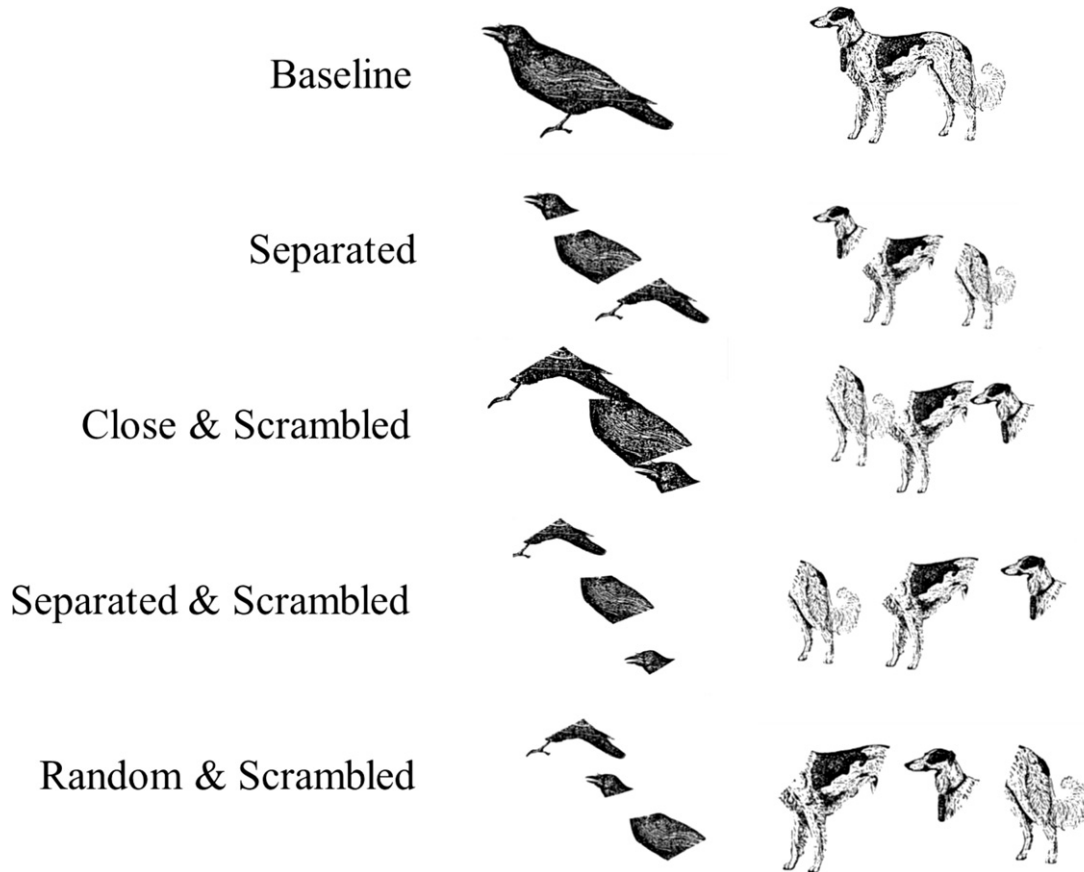
Fig. 7. Illustrative examples of the different test conditions for both categories examined in Test 3A.

discrimination of the novel stimuli was reduced. This result implies that pigeons had more difficulty recognizing the critical categorical cues, except when the segments were close together. In contrast, the results of the first test with the familiar items suggested that any such spatial and organizational factors were less important, perhaps because other categorical and item-specific cues had been well encoded and were still available despite the different spatial manipulations.
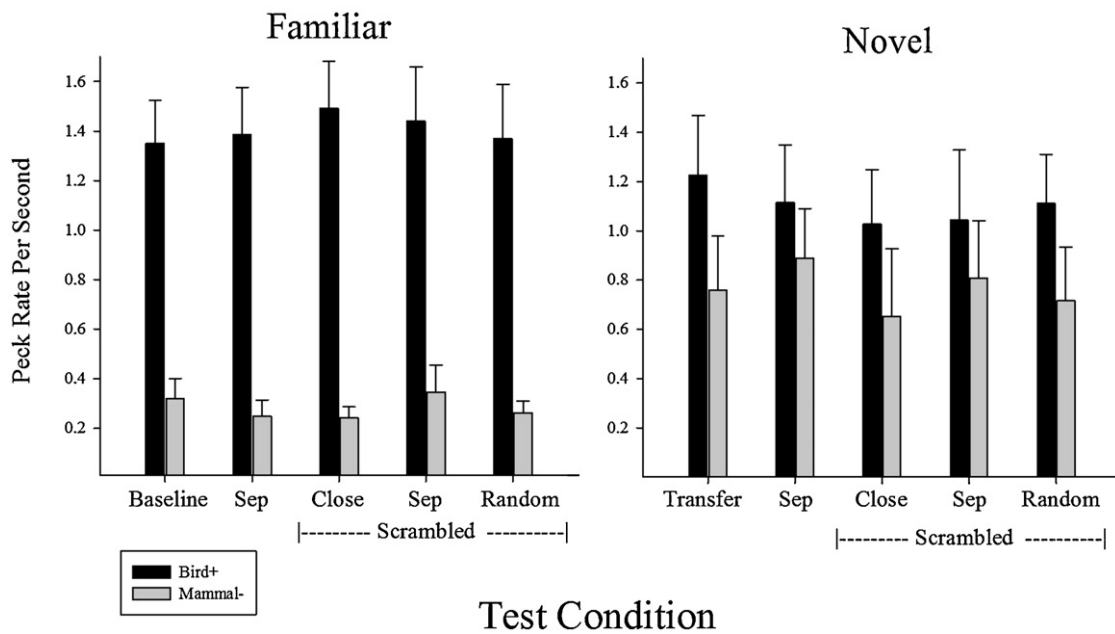

Fig. 8. Mean peck rate to the different test conditions examined in Test 3A. The left panel shows these results for tests involving familiar exemplars. The right panel shows the results for tests involving novel exemplars. Error bars represent the SEM of each condition.
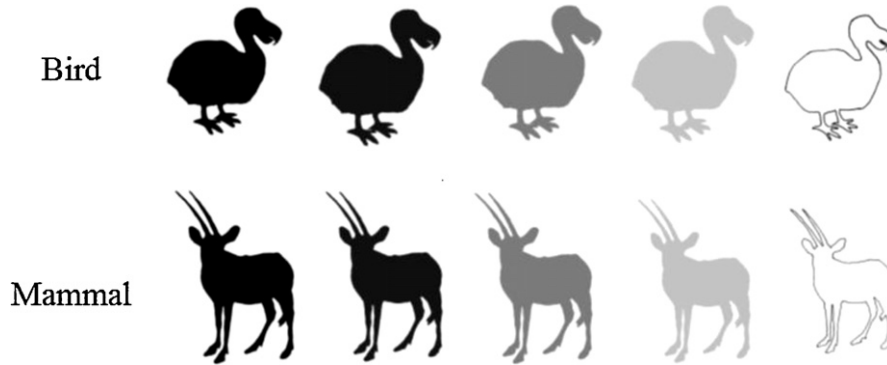
Fig. 9. Illustrative examples of the different brightness conditions for both categories used in Test 3B.

3.9. Test 3B: analysis of global and local features (figural uniformity) – procedures

The next test examined how eliminating the local interior detail within stimuli affected performance. The interior detail of eight familiar birds and eight familiar mammals (backgrounds removed) were replaced by uniform gray-scaled textures. The texture patterns of 100% 70%, 50%, 30%, and 0% gray scale levels were used to vary the amount of contrast in the image. Five different trial types ranging from black silhouette to outlined contour were created. Illustrative examples of the conditions are displayed in Fig. 9. Each session tested two baseline exemplars (one bird/one mammal) in each of the five conditions. All 10 test trials randomly appeared within a session. Twenty-four test sessions of this type were conducted. Unlike the other tests, these test trials were differentially reinforced as we were concerned that their distinctive nature might cause the pigeons to learn that stimuli without local details never yielded reward. No test with novel exemplars was conducted because of their poor performance with the familiar exemplars.

3.10. Test 3B: analysis of global and local features (figural uniformity) – results

Eliminating the interior featural detail by making the animal figures uniform in appearance produced by far the most mixed set of reactions from the pigeons among the different tests. The right panel of Fig. 10 shows the mean peck rates for the transfer and test conditions for all five pigeons. The summed test results for all five subjects suggest that only with intermediate gray levels was their categorical discrimination maintained to some degree. The pattern across conditions in Fig. 10 is due to the impact of only two pigeons, however, as the three remaining subjects showed no effect of interior brightness. Both of these pigeons were able to perform a diminished, but significant, discrimination of figures with gray stimuli of intermediate to black values (silhouette). A repeated measures ANOVA (Brightness level × Category) on peck rates for these two birds confirmed the presence of an interaction between these two factors, $F_{(1,4)} = 11.9$. For both of these pigeons, there were significant differences between bird and mammal conditions at the 70%, and 100% levels across sessions, $ts_{(23)} > 2.5$. Of these two, one pigeon could also discriminate at the 50% level, $t_{(23)} > 2.3$, and the other was very close, $t_{(23)} = 2$, $p = .07$. Neither of these two pigeons could discriminate categories at the 30% level or the 0% outline figures, exhibiting equivalent peck rates for each category. These results indicate that these two pigeons needed a certain level of brightness that approximately matched or exceeded the average brightness of the original stimuli to perform the discrimination accurately.

The other three birds performed differently. The pigeon that performed poorly in the prior test with separated and scrambled body parts, again responded at very low rates to all of these test stimuli in both categories. This result suggests that the elimination of the interior local detail strongly impacted this pigeon's ability to recognize them as reinforced stimuli. The remaining two pigeons exhibited more typical levels of responding to these stimuli, but also showed no discrimination of the categorical test stimuli at any of the five gray-scale levels. A repeated measures ANOVA (Brightness level × Category) on peck rates for these three birds revealed no significant interaction between these two factors, unlike the first two pigeons, or significant main effects of either Category or Brightness level. The absence of any discrimination of the categories by these three pigeons suggests that the interior local details or black and white textural variation within the animal figures were part of their representation of the categories. When removed and made uniform, these pigeons could no longer discriminate the figures based on the silhouette contour of the familiar training stimuli, regardless of its relative brightness.

3.11. Test 4A: analysis of figural orientation – procedure

The final test examined the role of stimulus orientation to the discrimination. This was done by reorienting the principal axes of the categories to different degrees of rotations. Three conditions were tested. These consisted of *reversed to other category* exemplars made from rotating birds 45° down to a horizontal orientation typical of most mammals and rotating mammals 45° up to the diagonal
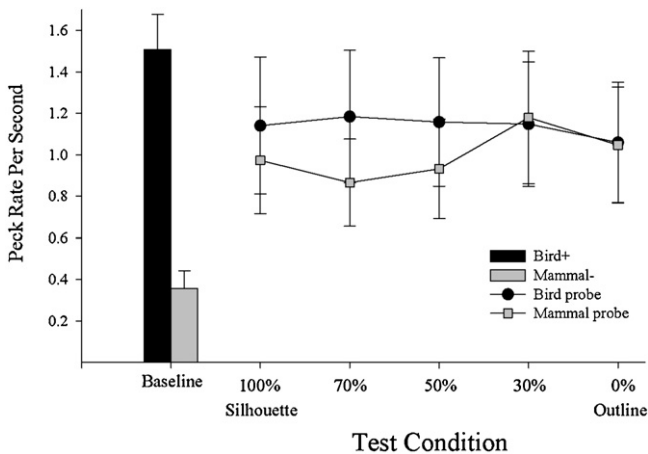

Fig. 10. Mean peck rate to the different brightness conditions examined in Test 3B. Error bars represent the SEM of each condition.
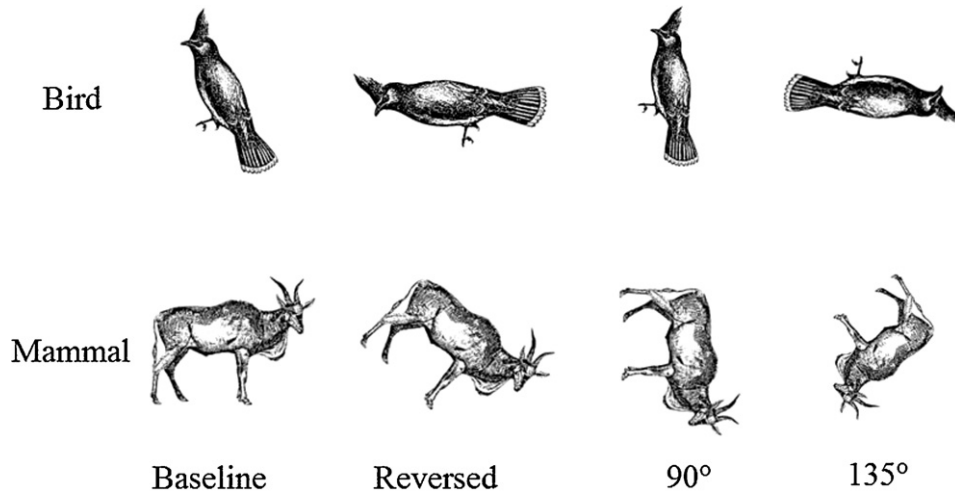
Fig. 11. Illustrative examples of the different orientation conditions for both categories examined in Test 4.

orientation typical of birds; *90° condition* where the principal axes of the animals from each category were at 90° relative to horizon, and the *135° condition* where the principal axes of the animals from each category were rotated to be 135° relative to its original axis. Illustrative examples of each of the conditions are displayed in Fig. 11. Ten test sessions were conducted, with each testing two familiar birds and mammals in the different orientation conditions. All test trials randomly appeared within a session and were tested as non-reinforced probes. Finally, the pigeons were again tested with novel exemplars. Six test sessions were conducted, with each testing two novel birds and novel mammals in the different orientation conditions. All test trials randomly appeared within a session and were tested as non-reinforced probes.

3.12. Test 4: analysis of figural orientation – results

Reorienting the animal figures had an effect on the pigeons' ability to perform their categorical discrimination with both familiar and novel stimuli. The left panel of Fig. 12 shows the mean peck

rates for the baseline and orientation conditions for all five birds. For the two conditions that rotated the familiar stimuli to 90° or 135°, this manipulation effectively eliminated the pigeons' discrimination of the familiar stimuli, indicating that their orientation was critical. The reversed orientation condition produced mixed results with familiar stimuli, with two pigeons able to partially maintain the original discrimination (the reason for the difference in the figure), while the remaining three pigeons dropped to chance levels of discrimination. Not surprisingly, a repeated measures ANOVA (Orientation [Baseline and Tests] × Category) on peck rates for all birds confirmed the significant interaction of Orientation and Category, $F(3, 12) = 5.0$. Subsequent paired *t*-tests among the different conditions confirmed the significant difference in peck rate between the categories for the baseline condition, $t(4) = 3.1$, but not for either the reversed, 90° and 135° conditions where orientations were altered.

Reorienting novel animal figures was equally effective as disrupting the discrimination, as all five birds now had difficulty with those figures during novel transfer testing. The right panel of Fig. 12 shows the mean peck rates for the transfer and orientation
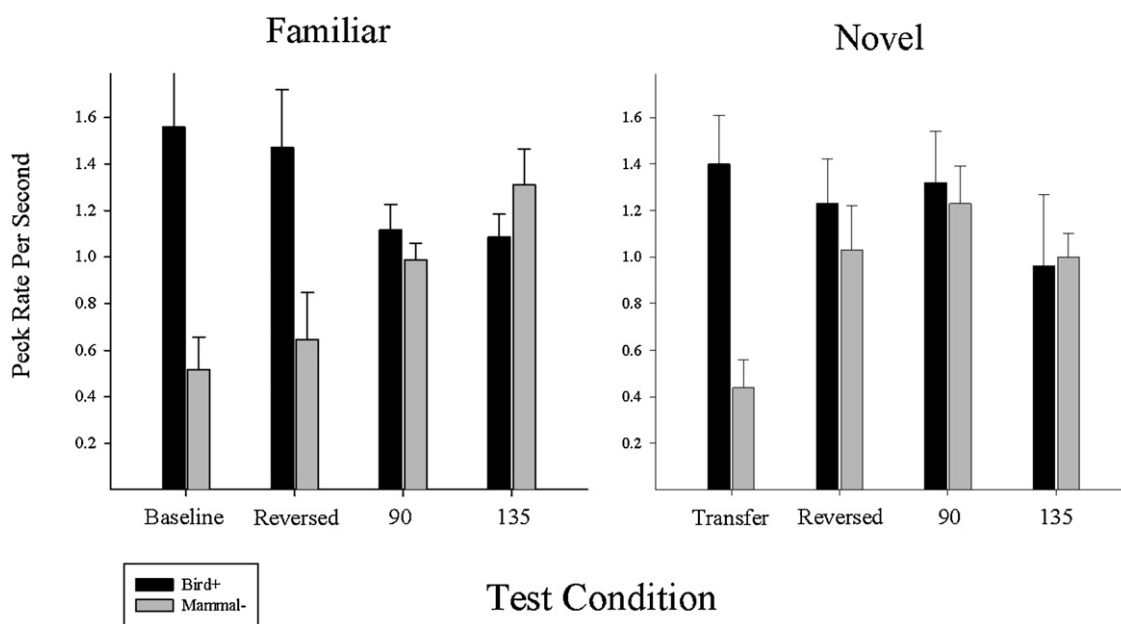

Fig. 12. Mean peck rate to the different orientation conditions examined in Test 4. The left panel shows these results for tests involving familiar exemplars. The right panel shows the results for tests involving novel exemplars. Error bars represent the SEM of each condition.

conditions for all five birds. Baseline performance continued to be good, as was transfer performance to the novel exemplars of each category. Changing the orientations of these novel figures, however, created problems as evidenced by the poor discrimination across the three orientation test conditions. A repeated measures ANOVA (Orientation [Transfer and Tests] × Category) on peck rates for all birds confirmed the existence of a significant interaction of Orientation and Category, $F(3, 12) = 3.9$. Subsequent paired t-tests among the different conditions confirmed a significant difference in peck rate between categories for the transfer condition, $t(4) = 5.2$, but not among any of the three conditions where orientation was altered.

4. General discussion

The current results paint one of the most complete descriptions yet of the visual factors controlling a categorical discrimination by pigeons. Our pigeons exhibited the major hallmarks used to identify and invoke accounts involving categorical representation. They were able to accurately discriminate large numbers of polymorphous exemplars from two open-ended visual categories and show significant and consistent transfer across multiple tests with novel exemplars of these categories. From the totality of the results from the different stimulus manipulations, it appears that these two categories were visually discriminated by the pigeons by segregating the textured animal figures from the background and extracting the orientation of the principal axis of the animal's body.

Several outcomes suggested that bodily orientation was critical to the categorical discrimination. The most direct evidence was the results from the final orientation test, where reorienting the animal figures disrupted the discrimination. The chimera tests that recombined the categories with either conflicting heads or legs and showed that body (and in its typical orientation) – not heads or legs – controlled the discrimination (see also Ghosh et al., 2004). The figure/ground test suggested that transfer performance might even be better when the background was removed. Eliminating the background's clutter and noise may have made orientation of the animal more prominent.

Tests with the body divided, scrambled, and spatially separated, also suggested a body-related computation, like orientation, was critical. Scrambling the body parts had little effect on performance, most likely because this manipulation did not change the basic orientation of the figure. However, when these same body-part manipulations were made to novel bodies, the discrimination suffered, suggesting that familiarity was necessary to recognize these parts across their separation. Taken together, these different results suggest a conclusion that the principal body axis was the primary cue underlying their categorical discrimination and transfer.

Analyses looking at the orientation of the baseline exemplars additionally confirmed a role for bodily orientation. For the 80 baseline exemplars tested during the extended number of sessions in Test 3A, the average orientation of the bird exemplars was 44° from the horizontal axis of the picture, while the mammal exemplars averaged 17°. Looking at overall peck rates for all items as a function of orientation revealed a significant correlation across categories ($r(78) = .51$) but not within categories (bird: $r(38) = .17$; mammal: $r(38) = .12$), possibly due to within-category orientation similarity.

The results also indicate that cues other than orientation had some effect on the pigeons' processing and representation of these stimuli. First, the pigeons were clearly performing some kind of figure/ground segregation (Cook and Hagmann, 2012; Lazareva et al., 2006a). The various and complex backgrounds present in these stimuli contributed little to the discrimination and perhaps even interfered with it because they masked the figural orientation of the animals. Because of their original intention as public illustrations,

the vast majority of the images were in landscape format, making the orientation of the entire image useless to category identification. This suggests the pigeons were extracting the "object" from the illustration perhaps by identifying the most central, enclosed, dense pattern in the stimulus. Second, the pigeons' discrimination clearly depended upon the 'fill' or interior features of the body figure. We showed that outlines of the animal figures alone were not sufficient to maintain the discrimination, despite orientation being a readily available cue in these cases. Similar failures to find transfer from shaded to outlined figures have been found with pigeons in other contexts (Aust and Huber, 2002; Cabe and Healey, 1979; Peissig et al., 2005). In our experiments, when the interior detail or texture of the figures was removed and replaced with uniform areas of different brightness, the discrimination of categories did suffer for the majority of the birds. Moreover, reorienting the figures to the other category's typical orientation produced a general disruption in performance (as opposed to misclassification), suggesting that more than simple body orientation was involved in these classifications by pigeons.

Together the results suggest that the pigeons' representation of categories depended upon having a certain absolute level of texture, detail, or brightness being present in the interior of the figure. This would be consistent with the idea that surface information may also more important in defining objects for these animals (cf. Cook et al., 2012; Loidolt et al., 1997; Peissig et al., 2005). Finally, item-specific memorization also played a role similar to that found in several other experiments (e.g., Aust and Huber, 2001). In several tests, discriminations of the familiar figures survived stimulus manipulations, such as figural separation, that interfered with discrimination of novel items. This suggests that there were miscellaneous, and likely idiosyncratic, item-specific features that were memorized about the familiar stimuli over and above the categorical factors that mediated novel transfer.

While the evidence that pigeons can solve a wide variety of complex pictorial classifications is bountiful, the results of the current study raise important questions about the meaning of such results. Part of the initial excitement and importance attributed to such findings was the implication that human-like concept learning was a cognitive ability shared widely in the animal kingdom. Yet, the body of evidence in the current study suggests the hypothesis that the pigeons reduced the apparent complexity of this categorical discrimination to a simple set of a few critical visual features. While the nature of the controlling properties has been examined for only a handful of categories with different species, the results are similar in showing that the complex categorical discrimination seems to be reduced to a simple set of critical visual features (e.g. Aust and Huber, 2002; Brooks et al., in press; D'Amato and Van Sant, 1988; Lazareva et al., 2006b; Troje et al., 1999). If such cases are representative of the general processing of pictorial stimuli by nonhuman animals, then one could question whether we been truly studying concept learning with this preparation over the last 50 years. The answer to this question has numerous implications.

Disregarding for the moment its relations to human concept learning, the results of this field-wide research effort have been very important in revealing the nature of the discrimination learning process, especially in pigeons. What the evidence clearly indicates is that pigeons, and potentially other animals, are exquisitely sensitive to discovering and extracting relevant information from highly complex multidimensional displays. No matter how complex and polymorphous the categories are (e.g., abstract art, Watanabe et al., 1995), if the pictures contain features correlated with the categories, then pigeons appear quite capable of finding, isolating, and using them. Whether or not they have conceptualized such solutions, there is certainly no doubt that their visual/cognitive equipment is second to none when it comes to feature discovery and identification. For computers, the latter is

a particular difficult problem (Rumelhart and Zipser, 1985). It is only when challenged by categories lacking such coherent featural similarity that we see a breakdown in this exceptional feature extraction ability in pigeons, such as in the case of discriminating living versus non-living items (Roberts and Mazmanian, 1988).

This perceptual/cognitive reduction of the stimulus space to a few dimensions is seemingly characteristic of this species' processing of complex pictorially-based categorization problems. One of the chief difficulties of past experiments using compound stimuli having multiple dimensions is getting the birds to move away from this approach. Several experiments had found that pigeons have a difficult time learning artificial polymorphous concepts that require their simultaneous processing of multiple dimensions of the stimuli for their solution (Lea et al., 1993, 2006b). This is not to say they cannot attend to multiple features, but they seem generally resistant to doing so. When such featural solutions fail, pigeons can always fall back on their considerable capacity to memorize patterns and configurations (Cook and Fagot, 2009; Cook et al., 2005; Fagot and Cook, 2006; Vaughan and Greene, 1984), which gives the birds the capacity to acquire pseudo-categories, and likely many other types of complex discriminations.

This pattern suggests that pigeons have two sources for information during learning; one tied to features correlated with class membership, and the other tied to the features of each item. The category-related and item-specific sources are both valuable and it is their balance and relative competition that determines the rate of learning and the eventual nature of the representation used as the basis for the discrimination. These sources may lead to a cascade of apparent strategies used by pigeons when faced with solving complex discriminations. If item-specific information is deemphasized by having large number of similar items grouped together, then categorical-like behavior emerges, likely based on a reduced dimensionality of the stimuli. On the other hand, if the processing of such absolute information is demanded, by say the randomized assignment of stimuli to responses, then the pigeons memorize large amounts of item-specific information. Of course, both can be made part of the same experiment and you see both sources in action. Using artificial multidimensional stimuli, Cook and Smith (2006) found that dimensional abstraction seemed to precede item memorization. That pigeons also learn consistent categories relations faster than pseudo-categorizes further suggests that the memorization of items is secondary or emerges more slowly than abstraction-based analysis. The duality and competitive nature of these factors in discrimination learning has been captured in a variety of models that pivot around these distinctions (Anderson and Betz, 2001; Nosofsky et al., 1994; Soto and Wasserman, 2010). Although the computational mechanisms are different, these models attempt to capture the constant interplay between these two sources of information. Understanding better how pigeons rapidly discover and identify the key features in complex pictures, along with identifying the conditions that allocate control between common and item-specific features, remain important topics for investigation.

The question of whether we have been investigating categorization in animals remains unanswered. At one level, the answer is clearly yes. The last several decades of research has substantially advanced and expanded our understanding of how discrimination learning operates and revealed the remarkable ability of pigeons to process complex stimulus situations. The natural behavior of this animal on the street would unlikely lead one to suspect that its small brain contained such remarkable and powerful computational resources. Beyond their superficial similarities, however, it is not clear yet that the mechanisms involved are comparable to those responsible for conceptual behavior in humans. Two possibilities seem likely. The first is that with more detailed examinations, we will establish that human conceptual abilities operate in a way different from those in pigeons. A second possibility is that we have perhaps overestimated the sophistication of human thought on this issue, and that at their core, the process of feature discovery and classification operate very similarly at least when challenged to processing complex pictorial information of varying visual similarity (e.g., Gluck and Bower, 1988).

Acknowledgments

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