

Endpoint distinctiveness facilitates analogical mapping in pigeons



Carl Erick Hagmann, Robert G. Cook*

Tufts University, USA

ARTICLE INFO

Article history:

Available online 15 November 2014

Keywords:

Pigeons
Categorization
Relational learning
Analogy
Dimensional mapping

ABSTRACT

Analogical thinking necessitates mapping shared relations across two separate domains. We investigated whether pigeons could learn faster with ordinal mapping of relations across two physical dimensions (circle size & choice spatial position) relative to random mapping of these relations. Pigeons were trained to relate six circular samples of different sizes to horizontally positioned choice locations in a six alternative matching-to-sample task. Three pigeons were trained in a *mapped condition* in which circle size mapped directly onto choice spatial position. Three other pigeons were trained in a *random condition* in which the relations between size and choice position were arbitrarily assigned. The mapped group showed an advantage over the random group in acquiring this task. In a subsequent second phase, relations between the dimensions were ordinally reversed for the mapped group and re-randomized for the random group. There was no difference in how quickly matching accuracy re-emerged in the two groups, although the mapped group eventually performed more accurately. Analyses suggested this mapped advantage was likely due to endpoint distinctiveness and the benefits of proximity errors during choice responding rather than a conceptual or relational advantage attributable to the common or ordinal mapping of the two dimensions. This potential difficulty in mapping relations across dimensions may limit the pigeons' capacity for more advanced types of analogical reasoning.

This article is part of a Special Issue entitled: Tribute to Tom Zentall.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

Categorization is fundamental in a variety of knowledge domains. Appreciating the mechanisms underlying categorization across different species is key to understanding the evolution of cognition and intelligence and its importance in organizing behavior. In particular, it has been valuable to distinguish among different classes of conceptual behavior (Zentall et al., 2008). It has been well and long established, for example, that a wide variety of animals can learn to make perceptual classifications based on shared visual attributes among a set of pictures or objects (Hernstein et al., 1976). More recently, considerable attention has focused on how animals learn relational concepts (Cook and Wasserman, 2006). Here it is the matching or difference relationship among two or more stimuli that is critical. This kind of categorical discrimination can be thought of as the abstraction of information within a *first-order relation* across stimuli. In this latter domain, Zentall and his colleagues were particularly important in advancing early attempts

to identify relational learning in pigeons (Zentall et al., 1980a,b; Zentall and Hogan, 1974, 1976, 1978). Since then, abundant evidence has shown that humans, monkeys, dolphins, and birds can learn rule-like categories based on such first-order relations in several contexts (e.g., Cook, 2002; Mercado et al., 2000; Pepperberg, 1987; Wasserman et al., 2001; Wright et al., 1983, 1988; Young and Wasserman, 2001).

Success in identifying the capacity of various animals to form perceptual classes and to learn first-order conceptual relationships has engendered a number of attempts to look for more advanced forms of categorization. The ability to categorize *second-order relations*, or the *relations between relations*, expands the knowledge that can be generalized and applied across domains. For example, the ability to form abstract concepts based on second-order relations allows for *analogical reasoning*. Analogical reasoning has been proposed to be critically important to the development of human intelligence (Gentner et al., 2001). To form an analogy requires the perception and evaluation of first-order relations and the recognition of the sameness and difference of these relations across multiple domains (French, 1995; Gentner and Markman, 1997; Thompson and Oden, 2000). As a result, analogies are derived from common relational structures across domains, not just from overlapping or distinguishable features among stimuli. Thus, analogical reasoning comes from not only being able to compare and

* Corresponding author at: Department of Psychology, Tufts University, 490 Boston Avenue, Medford, MA 02155, USA. Tel.: +1 617 627 2546; fax: +1 617 381 3189.

E-mail address: Robert.cook@tufts.edu (R.G. Cook).

contrast features within specific domains, but across domains and feature dimensions by cognitively and computationally mapping their internal structures or relations on to one another (French, 2002). Humans develop analogical reasoning relatively early in childhood. For instance, Rattermann and Gentner (1998) had children solve analogical completion tasks. Children that were 3–4 years old relied on object similarity, whereas by five years old, the children had undergone a “relational shift,” allowing them to map the domains of one relationship to another. In part, the development of relational language seems to be important to relational learning.

Because of its possible ties to language, studying analogical reasoning in non-human animals has been of particular interest. Various tests of analogical reasoning in animals have produced mixed results. Typically, analogical reasoning is tested in animals by examining whether they can recognize and transfer the second-order same or difference relations of two or more first-order relations. Studies exploring analogical reasoning have used first-order relations typically built from shapes and colors in a relational matching task. On second-order *same* trials, the items across two physically distinct sets of stimuli share the same relation (both same or both different). On second-order *different* trials, the two physically distinct sets of stimuli have different relations (one same and one different).

Chimpanzees (*Pan troglodytes*) have provided the strongest and most abundant evidence for the existence of analogical reasoning among animals (Flemming et al., 2008; Flemming and Kennedy, 2011; Gillan et al., 1981; Haun and Call, 2009; Thompson and Oden, 2000; Thompson et al., 1997). Using symbols to represent the concepts “same” and “different,” for example, Sarah demonstrated analogical reasoning even when a simpler associative strategy would have sufficed (Oden et al., 2001). Thompson and Oden (2000) suggested that analogical judgment of second-order relations by Sarah was possible only with the development of a symbolic concept system. However, Flemming and Kennedy (2011) showed that three chimpanzees could use relative information to show analogical reasoning without symbolic training. Here the animals saw food being placed under one of three different sized cups. When tested with a different set of plastic cups with the same size relations, the chimpanzees used relational rather than absolute size information to choose the correct cup based on the prior size relations. This outcome indicates the chimpanzees could map the ordinal size relations of one set of cups onto the size relations of another set.

Evidence for analogical reasoning in monkeys has been less robust, but the experiments have helped elucidate the perceptual and cognitive demands of analogical reasoning (Flemming et al., 2008; Thompson and Oden, 1995). Fagot et al. (2001) successfully trained two baboons (*Papio papio*) to discriminate 16-item displays of icons that were either all the same or all different in a relational matching task. These animals successfully transferred to novel displays. Further tests suggested that entropy played an important role in these results. Flemming et al. (2011) found that providing differential reward enhanced the ability of macaques (*Macaca mulatta*) to perform a relational MTS tasks. To reduce the role of perceptual grouping, Fagot and Parron (2010) tested baboons with pairs of color rectangles in a relational matching task. When the colored rectangles were located close together, baboons successfully transferred their relational matching discrimination to novel color sets. However, any gap between the stimuli dropped the discrimination to chance levels. Fagot and Thompson (2011) used pairs of shapes. Only six out of 29 symbol-naïve baboons could learn a relational MTS task, although five of these six monkeys could then transfer this skill to novel stimuli. Flemming et al. (2013) subsequently determined that categorical abstraction took priority over

perceptual similarity in a relational task consisting of four-item displays for both humans and baboons.

Among new world monkeys, the results are less promising but the research is far from complete. Capuchins (*Cebus apella*) show little evidence of analogical reasoning abilities when asked to perform relational MTS (Thompson et al., 2007), except perhaps under specific stimulus conditions (Truppa et al., 2011). Kennedy and Frigaszy (2008) tested four capuchin monkeys with a task similar to Flemming and Kennedy’s (2011) relative cup size search task. Only one of the four capuchins tested was able to perform this task by mapping across the shared dimension of size.

Few non-primate species have been tested with similar analogical reasoning tasks. Cook and Wasserman (2007) tested pigeons in a relational matching task. Using same and different displays consisting of 16 computer icons each, pigeons successfully learned this task by matching samples to test stimuli consisting of physically different sets of icons that had the same first-order relationship (same to same; different to different). More importantly, the pigeons transferred this discrimination to novel stimulus sets at above chance levels of accuracy (although not to the same degree as observed with apes). As new stimulus sets were added to their training and testing repertoire, the pigeons showed savings by learning the new sets more rapidly than previous ones. Cook and Wasserman argued that such results suggested pigeons might have the rudimentary perceptual and cognitive foundations for analogical reasoning.

To better understand the evolutionary origins of analogical cognition and whether it exists in non-primates, we thought it would be valuable to see if some of the cognitive subsystems or components necessary for analogical reasoning were present in pigeons. By better understanding the simpler task of how the different parts of an analogy are processed, it might serve as a platform for better testing more full-fledged analogical capacities. One key step in making an analogy requires mapping a relationship from a *source* to a *target* domain (French, 1995). In humans, relations among these domains can be very complex and highly multidimensional. To test the pigeons, we sought to simplify the relations, by asking if and how they could learn the relational mapping of one ordinal dimension onto another. If an observer can use the structure of one dimension to guide behavior along another, then the capacity to eventually form more complex analogies may also be present.

The mapping of ordered dimensions has previously been investigated in humans and animals using number and space. The spatial-numerical association of response codes, or SNARC effect, occurs when the smallest numbers in a set are implicitly coded as mapping onto an endpoint of a spatial position. Each increasing numerical value is then mapped onto each successive location. Drucker and Brannon (2014) examined the SNARC effect in rhesus monkeys with a vertical array of five homogeneous shapes. The monkeys were trained to pick the second item from the top, and showed robust transfer to novel shapes, colors, inter-item spacing, and positioning. When presented with a horizontal array, for instance, the monkeys chose the second position from the right. Similar findings in infants (de Hevia and Spelke, 2009) and chicks (Rugani et al., 2010, 2011) suggest that number–space mapping is an evolved cognitive trait rather than one developed based on cultural reading norms.

The goal of the present experiment was to examine whether pigeons would benefit from the mapping of the ordinal structure of one physical dimension onto a physically different dimensions. If so, it would suggest they possess one of the cognitive components needed to provide the scaffolding for more advanced analogical reasoning. The two physical dimensions selected consisted of the size of six yellow circular samples and the right to left spatial position of six identical red square choice locations. The dimensions

of size and location were chosen to prevent any physical similarity that might benefit training over and above their potentially common ordinal relations. We tested two groups of pigeons with these dimensions. The *mapped group* received the direct ordinal mapping of one dimension onto a different physical dimension. In this case, as the size of the sample increased (small to larger) it mapped directly onto its choice response locations (e.g., left to right). In the *random group*, the assignment of the sample circle size and response location was arbitrarily and randomly determined for each bird, so any direct common mapping between the two dimensions was unavailable. We predicted that if the pigeons in the mapped group could benefit from the ordinal psychological relationship between the two physical dimensions, this group would learn their matching-to-sample task faster and at a higher level of accuracy than the *random group*.

The experiment had two phases. The first phase examined the acquisition of this complex six-item matching-to-sample task with the mapped and random groups. Following the completion and evaluation of the above prediction for the first phase of training, we changed the mappings of the task for each group to re-examine the same question. For this second phase, the assignment of circle size and response location was reversed for the mapped group. Pigeons that had learned a right to left response mapping for each circle size were now switched to a left to right mapping, for example. This change altered all of the prior sample-choice location assignments, but retained the critical relational ordering among the dimensions for the mapped group. In contrast, the random group of pigeons received a new and arbitrary set of size-to-choice response location assignments. Again, if the pigeons could take advantage of the reversed structural pattern across the two physical dimensions, the mapped group should relearn this “new” discrimination faster than the random group. If the mapped group had been relying on this relational structure during the acquisition phase, it was anticipated that the mapped group would show much earlier reversal of its discrimination than the random group, since the latter group would have to learn an entirely new set of associations to perform the task in this second phase.

2. Method

2.1. Animals

Six naïve male pigeons (five Silver King & one White Carneaux), *Columba livia*, were tested. They were maintained at 80–85% of their free feeding weights with free access to grit and water in a colony room maintained on a 12 h LD cycle.

2.2. Apparatus

The pigeons were tested in an illuminated black operant chamber (38 cm wide × 36 cm deep × 38 cm high). Stimuli were presented on a CRT color monitor at a resolution of 1024 × 768 pixels visible through a 29 × 22 viewing window in the infrared LED touchscreen (EloTouch Systems, Fremont, CA) mounted in front of the monitor that detected pecks. Correct responses were reinforced from a central food hopper. The food hopper was centrally located in the front panel and flush with the floor. Side hoppers were located in the right and left walls, but were not used during this experiment. A 28-V houselight was located in the ceiling of the box and was illuminated at all times, except when an incorrect choice was made. All experimental events were controlled by computer.

2.2.1. Stimuli

The sample stimuli consisted of six yellow (RGB = 255,255,0) circles of varying sizes. The circle size was increased logarithmically in

diameter from 0.25 to 4 cm – 0.25, .44, .76, 1.32, 2.3, and 4 (cf. Peissig et al., 2006). On each trial, the circular sample was located centrally on the computer display. Each sample was assigned to one of six red (RGB = 255,0,0) response locations. Each response location was 2.27 cm × 2.27 cm in size. They were arranged horizontally 6.8 cm below the center of the centrally presented sample. They were separated from each other by 3.4 cm and occupied a horizontal spatial extent of 20 cm. To prevent confusion with the sample stimulus, the ready signal was a centrally located white plus sign that was 2.72 cm × 2.72 cm in size on each axis.

2.3. Procedure

The pigeons were initially trained to peck the display. Over several sessions, they gradually learned to peck in sequence the ready signal, a sample, and the correct response location presented in isolation to obtain food reward. These elements were added one at a time starting first with the ready signal, then ready signal + sample, and finally ready signal + sample + correct test only. All six circle sizes were presented equally often over this time and number of pecks required to advance past the sample gradually increased. Once reliable responding was established over several sessions, discrimination training began.

2.3.1. Phase 1 – discrimination acquisition

Discrimination training began with the inclusion of all six response locations on each trial. Each trial started with a single peck to the white plus ready signal. The ready signal was then turned off and replaced by one of the six yellow circular samples. The sample remained on until the pigeon pecked it on average 10 times (VR-10; range = 7–13). Upon completion of the VR, the sample was turned off and the six response locations illuminated below it. A choice was defined as a single peck to any of the six response locations. If this response was correct, the pigeon received 2.5 s access to the mixed grain in the central food hopper. If the response was incorrect, the pigeon received a 30 s dark timeout. Trials were separated by a 2 s inter-trial interval. Each daily session consisted of 10 trials per circle size (60 total trials). Each session's trial order was randomly scrambled. To minimize possible response bias during acquisition, a correction procedure for incorrect responses was used during the early part of each session. Two randomly chosen trials out of the first four trials of each circle size could be repeated up to four times if the pigeon failed to choose the correct response. All correction trials were excluded from the data analysis.

Two groups of three pigeons each were trained. In the *mapped group*, each sample circle size was mapped ordinally to the respective horizontal spatial position of the six choice locations. Two pigeons had the six small to large circles mapped from the left to right among the six locations. The other pigeon was mapped from right to left. In the *random group*, each sample circle size was randomly assigned to one of the six choice locations. Each of these three pigeons had a different assignment of circle size and choice location. Acquisition training was conducted for 70 total 60-trial sessions.

2.3.2. Phase 2 – discrimination reassignment

At this point, the relations between circle size and choice location were changed for each group. For the *mapped group*, each sample circle size retained its ordinal mapping to choice locations, but this mapping was reversed with respect to spatial position of response location (i.e., right to left became left to right). This changed mapping altered all of the sample-choice location assignments, but retained the relational ordering in its simple reflection of the previous sample-to-choice mapping. For the random group, each pigeon received a new and different random assignment of circle size to choice location at the beginning of the second phase.

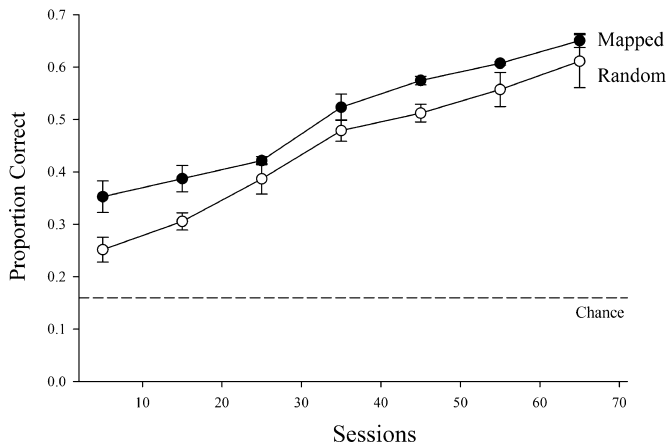


Fig. 1. Mean proportion of correct choice responses for the mapped and random groups during acquisition as a function of 10-session blocks. Error bars depict SEM.

All other aspects of daily testing remained the same as during the acquisition phase. Reassignment training was conducted for 70 total 60-trial sessions.

3. Results

3.1. Phase 1 – discrimination acquisition

During the experiment the mapped group learned their discrimination faster than the random group. This can be seen in Fig. 1, which shows mean choice accuracy for each group during acquisition displayed in 10-session blocks. All three pigeons in the mapped group showed consistently better accuracy over the first 30 sessions of training, with this difference between the groups diminishing somewhat with training.

Averaged across all 70 sessions of training, the individual pigeons of the mapped group displayed higher choice accuracy (51.4%, 48.3%, 50.9%) than the three pigeons in the random group (46.9%, 45.6%, 40.7%). Over the entirety of training, the mapped

group contained the two best-performing pigeons, while the random group contained the two worst performing pigeons. A mixed ANOVA (group \times 10-session blocks) on choice accuracy confirmed the presence of a main effect of Sessions, $F(6, 24) = 39.7$, $\eta^2 = 0.88$, as all six pigeons learned their assigned task. The between-groups main effect neared significance, $F(1, 4) = 7.2$, $p = .055$, $\eta^2 = 0.32$. This difference in acquisition is consistent with the pre-experimental hypothesis that the shared ordinal mapping across the two dimensions would benefit the acquisition of the mapping group compared to the random group.

To better understand why the mapped group learned faster and performed better, a series of analyses was conducted that further examined the effects of each dimension on performance. One important difference between the groups was their performance as a function of circle size. Displayed in Fig. 2 is a comparison of acquisition for each of the groups as a function of the size of the sample circle. For the purposes of this figure, the largest and smallest, the next two intermediate sizes, and the two interior sizes have been grouped together. The reason for this grouping is because the endpoints appeared to be the easiest for the birds to learn. Both groups of pigeons learned the extreme values of the size dimension faster than the interior ones. Further, the mapped group learned the two endpoints of the size dimension consistently faster than the random group. This same benefit was reduced or eliminated among the four interior values of the size dimension, as both groups showed equivalent rates of acquisition for these sizes.

Fig. 3 depicts choice accuracy for each group as a function of the six circle sizes over the last 20 sessions of acquisition. Each group showed a U-shaped function as they generally performed better with the largest and smallest sized samples relative to the intermediate values of this dimension. A mixed ANOVA (group \times circle size) on mean choice accuracy over the last 20 sessions revealed a significant main effect of size, $F(5, 20) = 5.1$, $p < 0.004$, $\eta^2 = 0.52$. There was no main effect of group or its interaction with size. Pairwise comparisons revealed that accuracy with the largest and smallest sizes were significantly better than with the next smaller or larger sized circles, respectively. The greater accuracy with the smallest circle was present for all six pigeons, and the higher accuracy with the largest circle relative to its next adjacent value was found in five

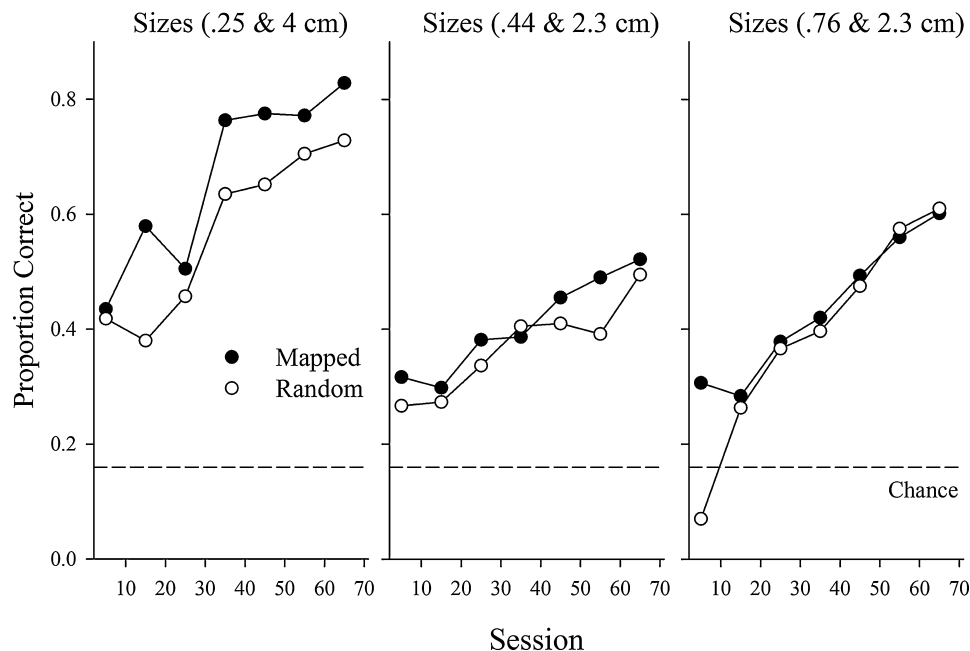


Fig. 2. Mean proportion of correct choice responses for the mapped and random groups during acquisition as a function of 10-session blocks. Each panel shows performance as a function of different groups of sample size. See text for more details about these groups.

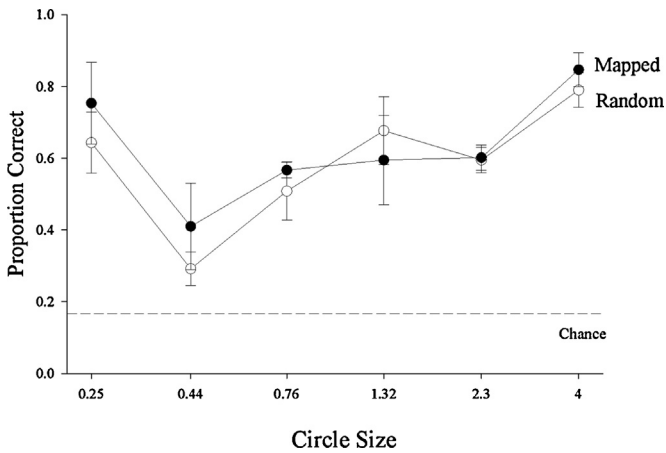


Fig. 3. Mean proportion of correct choice responses for the six sample sizes over the last 20 sessions of acquisition. Error bars depict SEM.

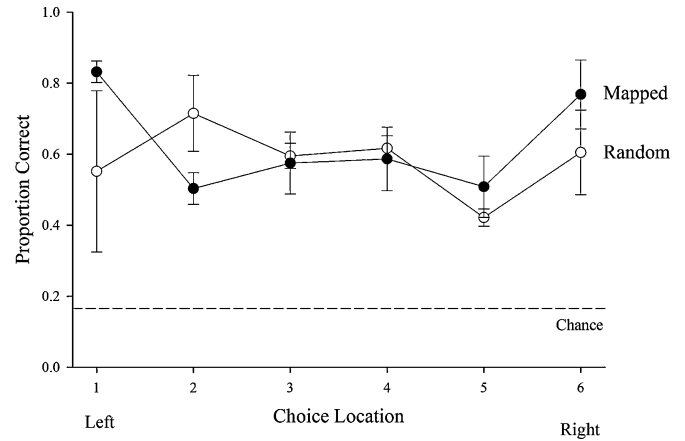


Fig. 4. Mean proportion of correct choice responses across the six choice locations over the last 20 sessions of acquisition. Error bars depict SEM.

of the six birds. Over the last 20 sessions, a quadratic contrast of these six values neared significance, $F(1, 4) = 5.3, p = .08, \eta^2 = 0.56$. Conducted over all 70 sessions, this same quadratic contrast across circle size was significant, $F(1, 4) = 14.2, \eta^2 = 0.77$. This advantage for the endpoint circle sizes in both groups suggests these values were distinctive regardless of their specific choice mapping. Nevertheless as shown in Fig. 2, it is with these two sizes where the two best-performing pigeons in the mapped group most strongly outperformed the two poorer birds from the random group, especially over the latter portions of acquisition. The best-performing bird from the random group was essentially equivalent to the poorest performing bird in the mapped group in this regard.

We next examined the effects of choice location for each group. Shown in Fig. 4 is choice accuracy for each group as a function of the six correct response locations over the last 20 sessions of acquisition. Because of the ordinal mapping between circle sizes on to these response locations in the mapped group, its function retains the same U-shaped function just described. The random group, on the other hand, shows no trend in accuracy as a function of choice location, suggesting that the interior response locations had no specific disadvantage relative to the two outside

endpoints. A repeated measures ANOVA (correct location) on mean choice accuracy using just results from the random group over the last 20 sessions revealed no significant main effect of location, $F(5, 20) = 0.43$, consistent with a hypothesis that none of the choice locations were more distinctive than the others.

Finally, we wanted to examine nature of the errors made in responding to each choice location. Shown in Fig. 5 are the mean numbers of responses recorded to each of the six response location as a function of the correct location over the last 20 sessions of this phase. The two panels show these data for the mapped group in the left panel and random group in the right panel. Each group was similar in that the vast majority of incorrect responses were simple proximity errors, with locations nearest the correct one being the most consistent source of error. This was true across all six response locations. On incorrect trials, the average distance away from the correct location was 1.15 positions for the ordered birds and 1.73 positions for the random birds. That these values are small for both groups suggests that response errors were predominantly made at the time of response execution and were not specifically tied to how the sample was encoded.

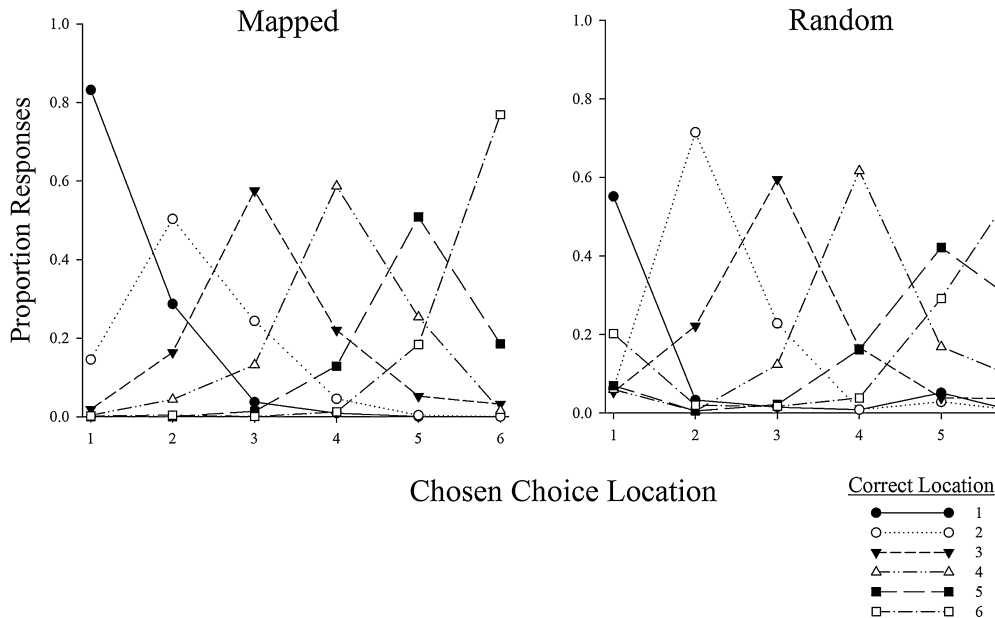


Fig. 5. Proportion of choices at each choice location as a function of the correct location for each group. Data are from the last 20 sessions of acquisition.

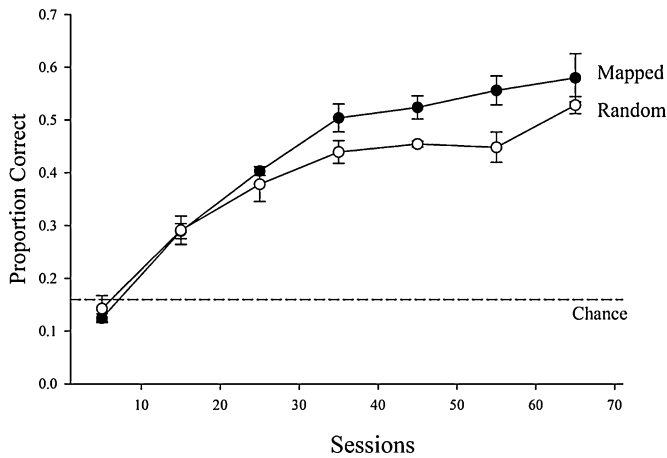


Fig. 6. Mean proportion of correct choice responses for the mapped and random groups during the reassignment phase as a function of 10-session blocks. Error bars depict SEM.

3.2. Phase 2 – discrimination reassignment

The “reversal” or reassignment of circle size to new response locations disrupted accuracy in both the mapped and random groups. Fig. 6 shows mean choice accuracy for each group following reversal displayed in 10-session blocks. Over the first 30 sessions of reversal, both groups showed equivalent rates of acquiring their discrimination with the sample-choice assignments. Over the next 40 sessions of the reversal phase, the mapped group again began to show superior performance relative to the random group. A mixed design ANOVA (group \times 10-session blocks) parallel to that done for acquisition revealed that performance improved over sessions, $F(6, 24) = 75.4$, $\eta^2 = 0.91$. The analysis indicated no main effect or interaction across groups. Over the latter half of reversal training the mapped group again showed better accuracy than the random group. This was due again to the two best-performing pigeons being in the mapped group, while the two worst performing pigeons

were in the random group. The remaining pigeon in each condition performed similarly and intermediate to these four birds.

Overall, in comparison to the acquisition phase, the reacquisition of matching accuracy proceeded along at a comparable rate. The mapped group showed no marked advantage in relearning the discrimination relative to the random group early in training. A mixed ANOVA comparing the acquisition and reversal phases (group \times phase \times 5-session block) revealed a marginally significant main effect of group, $F(1, 4) = 7.1$, $p = .057$, $\eta^2 = 0.22$, as the mapped group outperformed the random group in both phases. Learning did not happen exactly the same way across the two phases as there was a significant phase \times session interaction, $F(13, 52) = 3.52$, $p < 0.001$, $\eta^2 = 0.22$. This latter interaction was due the poorer performance at the beginning of the reversal phase and generally lower accuracy in this phase compared to the acquisition phase.

As in acquisition, the difference between the groups during reversal was influenced by circle size. Displayed in Fig. 7 is a comparison of reversal reacquisition for each of the groups as a function of the size of the circle. Again the largest and smallest, the next two intermediate sizes, and the two interior sizes have been grouped together as done in Fig. 2. Two things are worth noting. First, the overall effect of training with the endpoints (leftmost panel) mirrors the difference observed in both groups. The mapped group's better performance late in training relative to the random group was mediated by better performance on the two endpoints of the size dimension. Second, the groups also differed in how they performed with the most interior sizes (rightmost panel). During acquisition there was little difference between groups with these sizes, but the mapped group showed a marked advantage over the entirety of the reversal phase with these sample-choice mappings. This latter pattern was likely due to proximity errors made by the pigeons during responding. Because of this, the mapped group came to benefit from these errors as these middle sizes under the new reversed reinforcement rules were still near their previous choice location. The random group did not have this response advantage, as their new choice assignments for these sizes were randomly further away.

We examined the effects of circle size and response location in the same way as at the end of acquisition, by using data from

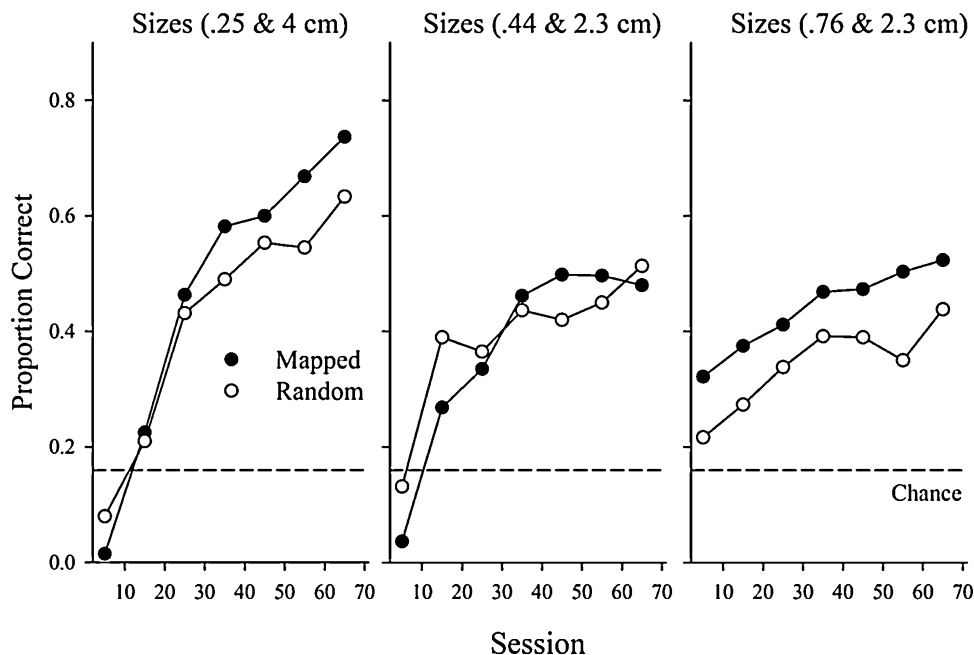


Fig. 7. Mean proportion of correct choice responses for the mapped and random groups during the reassignment phase as a function of 10-session blocks. Each panel shows performance as a function of different groups of circle size. See text for details about these groups.

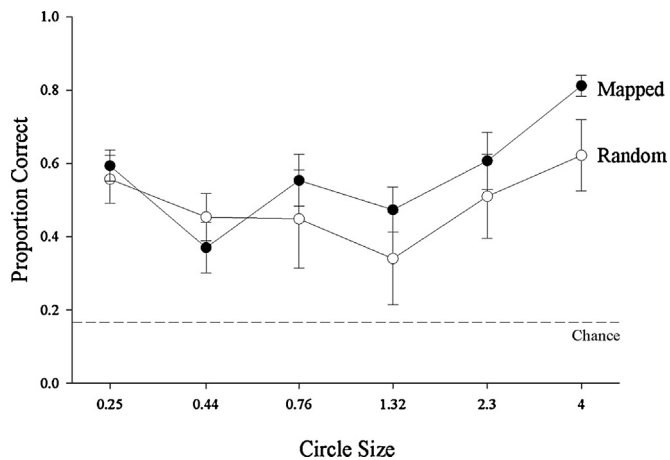


Fig. 8. Mean proportion of correct choice responses for the six circle sizes over the last 20 sessions of the reassignment phase. Error bars depict SEM.

the last twenty sessions of the reversal phase. Fig. 8 depicts choice accuracy for each group as a function of the six circle sizes over the last 20 sessions of the reversal phase. Again both groups exhibited U-shaped accuracy functions across the six circle sizes. A mixed ANOVA (group \times size) revealed that there was a significant linear, $F(1, 4) = 9.7$, $\eta^2 = 0.55$ and quadratic, $F(1, 4) = 7.8$, $\eta^2 = 0.66$ component in the effect of size on accuracy. There was no significant effect of group or its interaction with size.

Choice accuracy for each group as a function of correct choice location produced a U-shaped function for mapped group again. By the end of the reversal phase, the random group also exhibited a U-shape function with the two exterior choice locations producing the best performance. A one-way ANOVA (location) using just the random group, however, revealed no significant main effect of location, nor a significant quadratic component. Response errors again tended to be only one position away from the correct location and highly similar to the pattern of data in Fig. 5. On incorrect trials, mapped and random birds averaged choices that were 1.25 and 1.68 positions away from their correct location.

4. Discussion

The prominent outcome of this experiment is that both during acquisition and at the end of the reassignment phase, the pigeons in the mapped group showed dependably higher levels of accuracy than pigeons in the random group. This benefit for the mapped group is consistent with a predicted analogical mapping account of these results as outlined in Section 1. This hypothesis suggested that ordered relational mapping between source and target domains provides cognitive benefits that would facilitate learning. Such an account would be consistent with the prior evidence that pigeons can learn a relational matching-to-sample task (Cook and Wasserman, 2007), and would be highly suggestive of the existence of potentially analogical-like processes in birds. We think several features of the results, however, suggest a more cognitively restrained account might be sufficient.

Upon more detailed examination of the results, we hypothesize that the ordinal mapping between the sample and choice domains was not the primary reason for the mapped group's superior performance. Specifically, the mapped group benefited from the redundant, but apparently independent, effects that are best attributable to the endpoints of the two ordered dimensions. In particular, the distinctive endpoints of the size dimension and their assignment to the outermost response locations were the most critical factor in producing the consistent performance advantage found in the mapped group. If analogical processes were

generally and exclusively operating, its advantages should have extended across the entire range of each dimension, and not just the restricted endpoints.

Both the mapped and random groups showed similar U-shaped functions in their discrimination of the dimension of circle size. At the end of each phase, both groups performed better with the two endpoints of the size dimension relative to the intermediate ones. The superior performance of the mapped group of pigeons seems more attributable to the fact that these easiest values of the size dimension were then assigned to the ends of the response location continuum. Beyond the advantages of this endpoint distinctiveness across dimensions, the mapped group never showed any superiority with the interior values of the size dimension or the response location dimension that could be attributed to any possible mapping advantage. For such interior values, the performance of the mapped group never markedly diverged from that of the random group, except during reversal.

Here the mapped group would have been advantaged by the nature of the choice errors made by all birds during the experiment. Because the pigeons primarily made proximity errors in their choice responding, any incorrect encoding related to the processing of the circle's size would have benefited the mapped group to a greater degree than the random group. If a circle's size was mistakenly encoded, the birds in the mapped group would still be near the correct response location, increasing the probability of a correct response by accident. This "off-by-one" benefit would not be present in the random group because of the unordered mapping of circle size and response location. Together, these additional factors seem to provide an adequate account of the mapped group's better performance without resorting to an account that invokes second-order relational mapping across dimensions.

Finally, it is important to note that the mapped birds did not show their performance benefit until the latter stages of their discrimination reversal. We had anticipated that if the birds were engaged in relational mapping that they might be able to more quickly and analogously remap the assignment of circle size onto the reflected response locations in comparison to the random group, who would have been limited to learning entirely new associations by memorization. No such anticipated advantage at the beginning of reversal was observed, however, it seemed both groups of birds were relearning in the same way. Over the first 30 sessions after the reassignment, both groups of birds exhibited similar rates of re-acquiring the complex matching-to-sample task. Although more research is needed, the present results do not suggest that the pigeons showed any marked cognitive advantage from having two physically distinct, but ordered dimensions, directly mapped onto one another. In line with this trend, Lazareva and Wasserman (2006) found that stimulus orderability similarly added no benefit for pigeons learning a transitive inference task. Without a capacity to see the common ordinal relationship between dimensions, it would be difficult for pigeons to engage in the kind of analogical reasoning that is so critical to human intelligence.

These results contrast with the implications of those of Cook and Wasserman (2007), in which pigeons showed an ability to recognize and transfer sameness and difference across physically different displays of visual icons in a relational matching task. Cook and Wasserman's results suggest at the very least that the pigeons were able to recognize some common feature shared across these perceptually different displays. Because the pigeons could simultaneously see all the icons of a particular display in those experiments, it is possible that they were able to use shared perceptual or entropy-based information about the relative regularity of the same and different displays to possibly mediate their recognition across physically different displays (although perceptual tests were conducted to evaluate these possibilities with little support).

One possible reason for the potentially contrasting results is that in the present experiment, the successive sample presentation of the different sized circles one at a time made seeing its inherent relations less directly available to perception, while the simultaneous presentation of the choice locations made seeing its spatial relations easy. Such simultaneity may promote processing the relations within a dimension for pigeons. Another consideration is that pigeons do not see either of these dimensions as having any ordinality, so they are not perceived as being on a continua. Either way, the current experiment may reveal an important cognitive limitation in how pigeons think about dimensional correspondence. One important advance would be to reexamine Cook and Wasserman's (2007) relational MTS experiments using successive presentation of the icons rather than simultaneous ones.

If pigeons lack the capacity to recognize the shared relational patterns among different dimensions, it generally may be difficult for them to detect rules among complex multidimensional structures. Smith et al. (2011) recently conducted experiments in which pigeons were tested in their ability to learn rules in a two-dimensional categorization task developed by Ashby to test the structure of human categorization (Ashby and Ell, 2001). In marked contrast to humans, the pigeons showed no difference in their ability to learn a dimensional rule-based task relative to a more complex multidimensional informational integration task. Humans and other primates take advantage of the inherent dimensionality of these stimuli in rule-based tasks to learn them much faster than information integration (Smith et al., 2010, 2012). This pattern of results suggests that pigeons may use a unitary, nonanalytic mechanism in learning both of these kinds of tasks. Though the current dimensional mapping task and the Ashby categorization task are different in many respects, their outcomes point to a difficulty in pigeons taking advantage of the larger global structure or relations within dimensions to integrate information across dimensions.

It may, of course, be that size magnitude and spatial position are not easily recognized as being similar in structure for pigeons. It will be important to test other dimensions to see if those could be more successful in supporting common mapping. It is common in humans that time is often encoded using a spatial-like metaphor (Casasanto and Boroditsky, 2008; Smilek et al., 2007). As a result, longer durations of the sample's appearance might better facilitate mapping with space. Examining this ability across different modalities would also be very interesting, such as seeing if auditory pitch implicitly maps onto brightness, spatial position, or size magnitude, as it does in humans (Spence, 2011). We think being able to break down the components of analogical reasoning into separate, but linked, tasks is one highly valuable approach to investigating this still elusive phenomenon in animals.

Acknowledgements

The conduct and preparation of these experiments were supported by a grant from the National Eye Institute (EY022655). The authors thank Muhammad Qadri for his helpful comments on an earlier draft of this paper. Robert.Cook@tufts.edu. Home Page: <http://www.pigeon.psy.tufts.edu>.

References

- Ashby, F.G., Ell, S.W., 2001. The neurobiology of human category learning. *Trends Cogn. Sci.* 5, 204–210.
- Casasanto, D., Boroditsky, L., 2008. Time in the mind: using space to think about time. *Cognition* 106, 579–593.
- Cook, R.G., 2002. The structure of pigeon multiple-class same-different learning. *J. Exp. Anal. Behav.* 78, 345–364. <http://dx.doi.org/10.1901/jeab.2002.78-345>.
- Cook, R.G., Wasserman, E.A., 2006. Relational learning in pigeons. In: Wasserman, E.A., Zentall, T. (Eds.), *Comparative Cognition: Experimental Explorations of Animal Intelligence*. Oxford University Press, London, pp. 307–324.
- Cook, R.G., Wasserman, E.A., 2007. Learning and transfer of relational matching-to-sample by pigeons. *Psychon. Bull. Rev.* 14, 1107–1114.
- de Hevia, M.-D., Spelke, E.S., 2009. Spontaneous mapping of number and space in adults and young children. *Cognition* 110, 198–207.
- Drucker, C.B., Brannon, E.M., 2014. Rhesus monkeys (*Macaca mulatta*) map number onto space. *Cognition* 132, 57–67.
- Fagot, J., Parron, C., 2010. Relational matching in baboons (*Papio papio*) with reduced grouping requirements. *J. Exp. Psychol. Anim. Behav. Process.* 36, 184.
- Fagot, J., Thompson, R.K.R., 2011. Generalized relational matching by guinea baboons (*Papio papio*) in two-by-two-item analogy problems. *Psychol. Sci.* 22, 1304–1309.
- Fagot, J., Wasserman, E.A., Young, M.E., 2001. Discriminating the relation between relations: the role of entropy in abstract conceptualization by baboons (*Papio papio*) and humans (*Homo sapiens*). *J. Exp. Psychol. Anim. Behav. Process.* 27, 316–328.
- Flemming, T.M., Beran, M.J., Thompson, R.K.R., Kleider, H.M., Washburn, D.A., 2008. What meaning means for same and different: analogical reasoning in humans (*Homo sapiens*), chimpanzees (*Pan troglodytes*), and rhesus monkeys (*Macaca mulatta*). *J. Comp. Psychol.* 122, 176.
- Flemming, T.M., Kennedy, E.H., 2011. Chimpanzee (*Pan troglodytes*) relational matching: playing by their own (analogical) rules. *J. Comp. Psychol.* 125, 207.
- Flemming, T.M., Thompson, R.K.R., Beran, M.J., Washburn, D.A., 2011. Analogical reasoning and the differential outcome effect: transitory bridging of the conceptual gap for rhesus monkeys (*Macaca mulatta*). *J. Exp. Psychol. Anim. Behav. Process.* 37, 353.
- Flemming, T.M., Thompson, R.K.R., Fagot, J., 2013. Baboons, like humans, solve analogy by categorical abstraction of relations. *Anim. Cogn.* 16, 519–524.
- French, R.M., 1995. *Subtlety of Sameness*. MIT Press, Cambridge, MA.
- French, R.M., 2002. The computational modeling of analogy-making. *Trends Cogn. Sci.* 6, 200–205.
- Gentner, D., Holyoak, K.J., Kokinov, B.N., 2001. *The Analogical Mind: Perspectives from Cognitive Science*. MIT Press, Cambridge, MA.
- Gentner, D., Markman, A.B., 1997. Structure mapping in analogy and similarity. *Am. Psychol.* 52, 45.
- Gillan, D.J., Premack, D., Woodruff, G., 1981. Reasoning in the chimpanzee. I. Analogical reasoning. *J. Exp. Psychol. Anim. Behav. Process.* 7, 1–17.
- Hau, D., Call, J., 2009. Great apes' capacities to recognize relational similarity. *Cognition* 110, 147–159.
- Hernstein, R.J., Loveland, D.H., Cable, C., 1976. Natural concepts in pigeons. *J. Exp. Psychol. Anim. Behav. Process.* 2, 285–305.
- Kennedy, E.H., Frigaszy, D.M., 2008. Analogical reasoning in a capuchin monkey (*Cebus apella*). *J. Comp. Psychol.* 122, 167.
- Lazareva, O.F., Wasserman, E.A., 2006. Effect of stimulus orderability and reinforcement history on transitive responding in pigeons. *Behav. Process.* 72, 161–172.
- Mercado III, E., Killebrew, D.A., Pack, A.A., Macha, I.V.B., Herman, L.M., 2000. Generalization of 'same-different' classification abilities in bottlenosed dolphins. *Behav. Process.* 50, 79–94.
- Oden, D.L., Thompson, R.K.R., Premack, D., 2001. Can an ape reason analogically? Comprehension and production of analogical problems by Sarah, a chimpanzee (*Pan troglodytes*). In: Gentner, D., Holyoak, K.J., et al. (Eds.), *The Analogical Mind: Perspectives from Cognitive Science*. MIT Press, Cambridge, MA, USA, pp. 471–497.
- Peissig, J.J., Kirkpatrick, K., Young, M.E., Wasserman, E.E., Biederman, I., 2006. Effects of varying stimulus size on object recognition in pigeons. *J. Exp. Psychol. Anim. Behav. Process.* 32, 419.
- Pepperberg, I.M., 1987. Acquisition of the same/different concept by an African Grey parrot (*Psittacus erithacus*): learning with respect to categories of color, shape, and material. *Anim. Learn. Behav.* 15, 423–432.
- Rattermann, M.J., Gentner, D., 1998. More evidence for a relational shift in the development of analogy: children's performance on a causal-mapping task. *Cognitive Dev.* 13, 453–478.
- Rugani, R., Kelly, D.M., Szelest, I., Regolin, L., Vallortigara, G., 2010. Is it only humans that count from left to right? *Biol. Lett.* 6, 290–292.
- Rugani, R., Vallortigara, G., Vallini, B., Regolin, L., 2011. Asymmetrical number-space mapping in the avian brain. *Neurobiol. Learn. Mem.* 95, 231–238.
- Smilek, D., Callejas, A., Dixon, M.J., Merikle, P.M., 2007. Ovals of time: time-space associations in synaesthesia. *Conscious. Cogn.* 16, 507–519.
- Smith, J.D., Ashby, F.G., Berg, M.E., Murphy, M.S., Spiering, B., Cook, R.G., Grace, R.C., 2011. Pigeons' categorization may be exclusively nonanalytic. *Psychon. Bull. Rev.* 18, 414–421. <http://dx.doi.org/10.3758/s13423-010-0047-8>.
- Smith, J.D., Beran, M.J., Crossley, M.J., Boomer, J., Ashby, F.G., 2010. Implicit and explicit category learning by macaques (*Macaca mulatta*) and humans (*Homo sapiens*). *J. Exp. Psychol. Anim. Behav. Process.* 36, 54.
- Smith, J.D., Berg, M.E., Cook, R.G., Murphy, M.S., Crossley, M.J., Boomer, J., Ashby, F.G., 2012. Implicit and explicit categorization: a tale of four species. *Neurosci. Biobehav. Rev.* 36, 2355–2369.
- Spence, C., 2011. Crossmodal correspondences: a tutorial review. *Atten. Percept. Psychophys.* 73, 971–995.
- Thompson, R.K.R., Hagmann, C.E., Dotov, D.G., Templer, V.L., 2007. Can capuchin monkeys (*Cebus apella*), like humans, discriminate relations-between-relations? Maybe. . . Maybe not. In: Paper Presented at the 14th International Conference on Comparative Cognition, Melbourne, FL.
- Thompson, R.K.R., Oden, D.L., 1995. A profound disparity revisited: perception and judgment of abstract identity relations by chimpanzees, human infants and monkeys. *Behav. Process.* 35, 149–161.

- Thompson, R.K.R., Oden, D.L., 2000. Categorical perception and conceptual judgments by nonhuman primates: the paleological monkey and the analogical ape. *Cogn. Sci.* 24, 363–396.
- Thompson, R.K.R., Oden, D.L., Boysen, S.T., 1997. Language-naive chimpanzees (*Pan troglodytes*) judge the relations between relations in a conceptual matching-to-sample task. *J. Exp. Psychol. Anim. Behav. Process.* 23, 31–43.
- Truppa, V., Mortari, E.P., Garofoli, D., Privitera, S., Visalberghi, E., 2011. Same/different concept learning by capuchin monkeys in matching-to-sample tasks. *PLoS ONE* 6, 1–9.
- Wasserman, E.A., Fagot, J., Young, M.E., 2001. Same-different conceptualization by baboons (*Papio papio*): the role of entropy. *J. Comp. Psychol.* 115, 42–52.
- Wright, A.A., Cook, R.G., Rivera, J.J., Sands, S.F., Delius, J.D., 1988. Concept learning by pigeons – matching-to-sample with trial-unique video picture stimuli. *Anim. Learn. Behav.* 16, 436–444.
- Wright, A.A., Santiago, H.C., Urcuioli, P.J., Sands, S.F., 1983. Monkey and pigeon acquisition of same/different concept using pictorial stimuli. In: Commons, M.L., Herrnstein, R.J., Wagner, A.R. (Eds.), *Quantitative Analyses of Behavior*, vol. 4. Ballinger, Cambridge, MA, pp. 295–317.
- Young, M.E., Wasserman, E.A., 2001. Evidence for a conceptual account of same-different discrimination learning in the pigeon. *Psychon. Bull. Rev.* 8, 677–684.
- Zentall, T.R., Edwards, C.A., Hogan, D.E., 1980a. The role of identity in both matching and oddity learning in the pigeon. *Bull. Psychon. Soc.* 16, 172.
- Zentall, T.R., Hogan, D., 1974. Abstract concept learning in the pigeon. *J. Exp. Psychol.* 102, 393–398.
- Zentall, T.R., Hogan, D.E., 1976. Pigeons can learn identity or difference or both. *Science* 191, 408–409.
- Zentall, T.R., Hogan, D.E., Edwards, C.A., Hearst, E., 1980b. Oddity learning in the pigeon as a function of the number of incorrect alternatives. *J. Exp. Psychol. Anim. Behav. Process.* 6, 278–299.
- Zentall, T.R., Hogan, E., 1978. Same/different concept learning in the pigeon: the effect of negative instances and prior adaptation to transfer stimuli. *J. Exp. Anal. Behav.* 30, 177–186.
- Zentall, T.R., Wasserman, E.A., Lazareva, O.F., Thompson, R.K.R., Rattermann, M.J., 2008. Concept learning in animals. *Comp. Cogn. Behav. Rev.* 3, 13–45. <http://dx.doi.org/10.3819/ccbr.2008.30002>.