

SHORT COMMUNICATION

Simultaneous Pattern Discriminations by Pigeons Reveal Absence of Mirror-Image and Left-Right Confusions

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In a simultaneous discrimination task, pigeons were first trained with two patterns: one rewarding (A+) and the other unrewarding (B-) that contained the same components (the symbols: c, d, ■ and <) but displayed in a different spatial layout. They were then tested for their choices of patterns: (1) A+ vs. its mirror image (MI); (2) A+ vs. its left-right reversal (LR); (3) MI vs. other layouts (OL) of the symbols; (4) LR vs. OL. In the first two conditions, A+ was chosen over its MI and LR reversal (i.e., no MI or LR confusions were found). In the last two conditions, MI and LR were not chosen over the OL, that is, they were not treated as substitutes for the A+. On the contrary, the OL stimuli were chosen over the transformations of A+. In all cases, the discriminations revealed a failure to confuse the A+ with its transformations, as predicted from work showing that the position of pattern components is important in pattern recognition.

Mirror image (MI) confusions have been observed in many species. Humans confuse the MI of a visual stimulus with the original one until they are about seven years old (Corballis & Beale, 1976). For example, children often confuse letters “d” and “b” when they are in the process of learning to read and write. In adults, this phenomenon is infrequent even though MIs can be confused when they are presented in different orientations (Shepard & Metzler, 1971). Moreover, a spontaneous generalization (confusion) of a MI with the original stimulus is observed in cases where Left and Right (LR) is not a relevant dimension. For instance, Standing, Conezio, and Haber (1970) presented 2500 photographs of natural scenery to adults and then gave them a recognition test. The MIs of the recently presented photos were as easily recognized as the original ones.

Because a MI transformation involves reversing the left and right sides of a pattern, the MI confusion might be attributable to LR confusion (and for this reason, the patterns in our study were chosen so that the MI was different from the LR; see below). LR discriminations have been shown to be arduous for humans: adults show longer reaction times for LR mirror image discriminations than for Top-Bottom mirror image discriminations (Corballis & Cullen, 1986).

MI confusions and discriminations have also been studied in other species using a variety of procedures: octopuses (Sutherland, 1960), goldfish (Mackintosh & Sutherland, 1963), dogs, (Pavlov, 1927), rats (Kinsbourne, 1967, 1971; Lashley, 1938) rabbits (Van Hof, 1966, 1970), cats (Parriss, 1964; Sutherland, 1963), bumblebees (Korneluk & Plowright, 1995; Plowright 1997), and honeybees (Gould, 1988; Stack & Giurfa, 2001). The extent of MI confusion by pigeons remains

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unclear. Some authors (Cerella, 1990; Delius & Hollard, 1995; Hollard & Delius 1982) argue that pigeons recognize the MI of a pattern as different from the original, at least more so than humans. Indeed, the absence of a mental rotation effect (i.e., longer time reaction with orientation disparity) using MI stimuli in pigeons has been attributed to this superior discrimination of the MI from the original image (Delius & Hollard, 1995). Nonetheless, others have demonstrated that MI discriminations are more difficult to learn than a pair of arbitrary patterns, and so there must be some confusion between the MI and the original (Todrin & Blough, 1983).

In the present study we used a new procedure to address the question of whether there is a MI confusion with pigeons. The procedure was first used by Gould (1988) and subsequently used in other studies with honeybees and bumblebees (Korneluk & Plowright, 1995; Plowright, 1997; Stack & Giurfa, 2001) but not yet with vertebrates. The procedure comprises three steps: Training of a discrimination followed by two tests. First, a simultaneous binary choice task is given in which the positive stimulus (A+, reinforced) is presented together with a negative stimulus (B-, nonreinforced). The two stimuli contain the same pattern components but their spatial arrangement differs. Note that during training the MI is not seen by the pigeon. Following acquisition of this discrimination, the two tests consist of giving new choices of patterns, both of which are unrewarding. In the first test, A+ is presented with its MI (A+ vs. MI). A failure to discriminate at this point would show an “absolute ambiguity,” in Gould’s (1988) terminology: An inability to distinguish between the two. In the second test, the MI is presented with stimuli previously unseen to this point. These stimuli contain the same components as the A+ in other layouts (OL). A preference for the MI at this point would show a “facultative ambiguity”: the MI, although distinguishable from the A+, would be accepted by the animal as a substitute for the A+ in the absence of the A+. The elegance of this procedure lies in the conclusion of a “confusion” based on a rejection of the null hypothesis: A discrimination between the MI and the OL.

We used patterns taken from a previous study on bumblebees (Plowright, 1997) because the MI of the A+ (in which the A+ is “flipped”) was distinguishable from its LR (in which the left and right sides of the pattern are switched). The difference between the two is illustrated in Figure 1. In this way, true mirror image confusion could be distinguished from left-right confusion.

We had good reason to expect that our pigeons would not confuse the MI with any of the other stimuli. Our previous research (Landry & Plowright, 2001) has shown that the position of pattern components is crucial in the recognition process (see also Biederman, 1987; Wasserman, et al., 1993), but that the orientation of the components is unimportant. In our MI (Figure 1), the positions of the individual components all change location and so we predicted that the MI would be judged to be different from the A+.

Method

Subjects

Nine White King pigeons from Palmetto Plant in South Carolina were maintained at 85% \pm 2% of their free feeding weight. Five pigeons had served previously in unrelated studies (effect of competition on food choice) and the other four were naive. Four pigeons were excluded for reasons

given below, and so only data from five pigeons (three of which were naïve) are reported. Prior to the present experiment, the birds were trained to peck operant keys using a combination of hand shaping and autoshaping. The birds were kept in individual cages with unlimited access to water and grit. The room lights were on a cycle of 12 h on and 12 h off (Lights on at 06:00 h). Training and experimental sessions began at approximately 09:00 h, 5 days a week.

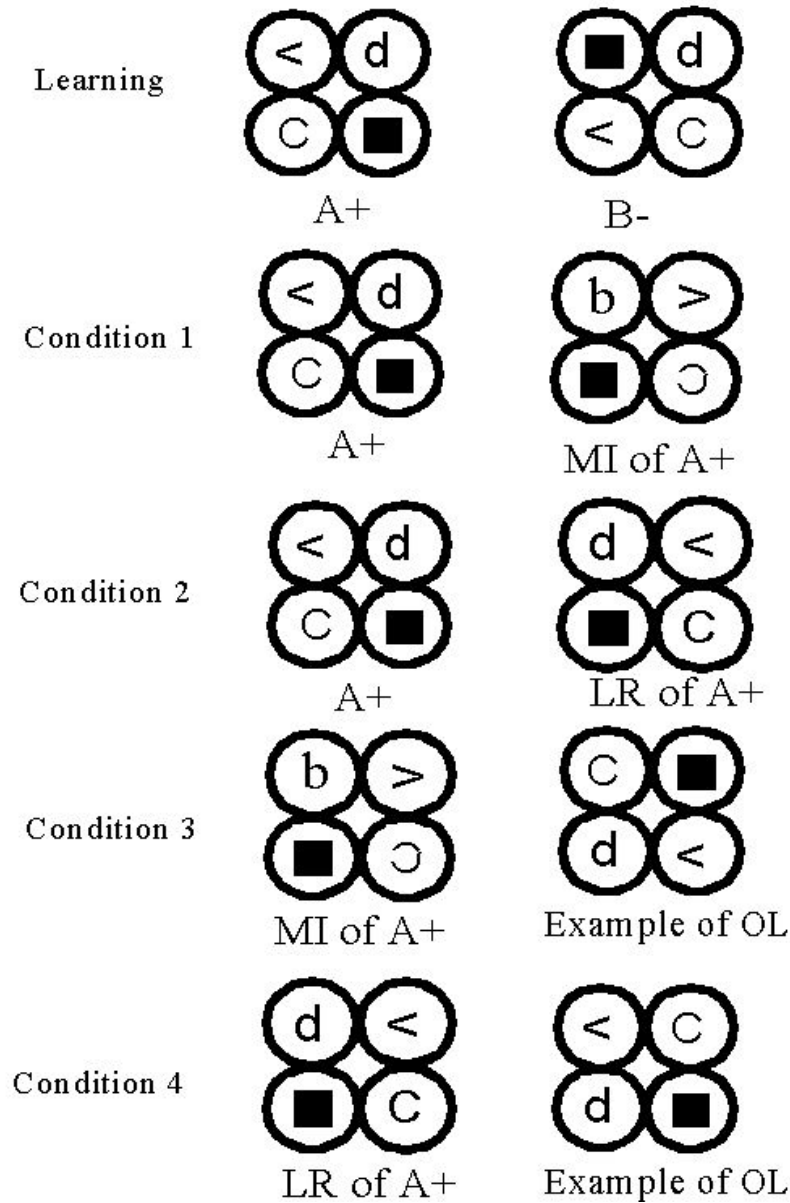


Figure 1. Stimuli used for training and for each of the four testing conditions. A+, B-, mirror-image of the A+ (MI), left-right reversal of A+ (LR) and examples of the other layout (OL) stimuli.

Apparatus

One operant chamber (32 x 32 x 30 cm) was used. On the side wall were three keys. Two clear plastic side keys (5 cm in diameter) covered with white paper on the back which served as a screen projector for the slides; one opaque white plastic center key (2 cm in diameter), was illuminated by a green light. Each side key was located 10 cm above a feeder opening into which were dispensed 40 mg BioServ food pellets. The operant chamber was controlled by a 386SX IBM computer via an Interface and MED-PC software (Tatham & Zurn, 1989).

Two projectors (Elmo Omnigraphic 301 AF) with an Elmo zoom lens 1:3.5 f = 100-150 mm and regular 80 slots Kodak carousels were used (only 40 slots were used in order to give an inter-trial interval between projections). The lens stood at 30 cm from the side keys outside the sound-attenuating box that enclosed the operant chamber. To focus the stimuli on the side keys, the lens had to be held (4 to 5 cm) in front of the projector by a retort stand. A fan and a white noise diffuser inside the sound-attenuating box helped to mask the outside noise.

Stimuli

The stimuli consisted of four black symbols each centred inside a black circular outline. The various arrangements of these symbols (A+, B-, MI, LR) are given in Figure 1. Two examples of the ten OL patterns are also given. The projected patterns were approximately 4.5 cm in diameter.

Procedure

Pretraining. Pigeons learned by hand shaping to peck the side keys on which were rear-projected images displaying four empty circles randomly projected on one side or the other. The bird had to peck the image in order to receive food. In a second phase of pretraining, the green center key would turn on and the pigeon had to peck it twice so that alternately one or the other of the two side keys would turn on and the bird had to peck the illuminated one to receive food. Approximately 300 trials were needed by each pigeon to obtain a sustained pecking response to the keys.

Discrimination Training. A simultaneous binary choice task was then introduced. After pigeons pecked the center key twice, A+ would appear on one side key, and the B- on the other. A+ and B- appeared equally often on each side. Two pecks on the A+ would extinguish the key lights and lead to four pellets of food being dispensed in the feeder, with the feeder light on for 4 s. Pecks on the B- were not reinforced but the feeder light would turn on for 4 s (to show the empty feeder). A new trial began after a 4-s inter-trial interval. A session consisted of 40 pairs of A+ and B-. After 35 sessions, no learning was apparent so correction sessions were introduced in which a peck to B- would make that key turn off and only pecking the A+ key could complete the trial. When pigeons chose the A+ more than 75% of the trials (i.e., 30 out of 40 trials) in a session for three consecutive sessions, correction trials were terminated. Regular discrimination sessions were then resumed until the birds also succeeded in pecking the A+ on more than 75% of the trials in a session for three consecutive sessions. Three pigeons did not learn the discrimination (after an average of 106 sessions these pigeons still chose the A+ only 50% of the time, whereas the others pigeons reached 70% success for the first time in an average of 53 sessions) and one was exhibiting aggressive behaviour and so they were removed from the experiment.

Testing. When the 75% discrimination criterion was achieved, four experimental conditions were conducted in which four test pairs of stimuli were randomly inserted in the last twenty trials of a regular 40-trial carousel (10 testing sessions were presented in order to complete 40 test trials for each condition). A choice of either of the patterns in a test pair was not reinforced, which is why these test stimuli were presented so infrequently. In the first condition the positive stimulus was pitted against its MI (A+ vs. MI). In the second condition, the positive stimulus was pitted against its LR (A+ vs. LR). These first two conditions were aimed at testing for an absolute ambiguity (Gould, 1988): Discrimination would show that there is no confusion when the pigeon can see both the A+ and the transformations. In the third condition, the other layouts (OL) were constructed by rearranging the four symbols. The MI was pitted against these other spatial layouts (MI vs. OL). In the fourth condition, the LR reversal of the positive stimulus was also presented with other layouts (LR vs. OL). The last two conditions were aimed at testing for a facultative ambiguity:

A preference for the MI and/or the LR would show that the transformations are treated as similar to the A+ in its absence. The order of presentation was changed periodically to prevent possible learning of sequences. The pigeons had to maintain a 75% success criterion in the 36 A+/B- trials of a session in order to ensure that the initial A+/B- learning was preserved. If the criterion was not attained, pigeons were returned to the correction procedure and then to discrimination sessions until they attained the criterion again for three consecutive days (the experimental sessions in which the criterion was not attained were not tallied).

Results

Pigeons reached the training criterion (without correction) in approximately 90 sessions (*Mean* = 88.80 *range* 74-125). Figure 2 shows the choice proportions for the 4 experimental conditions.

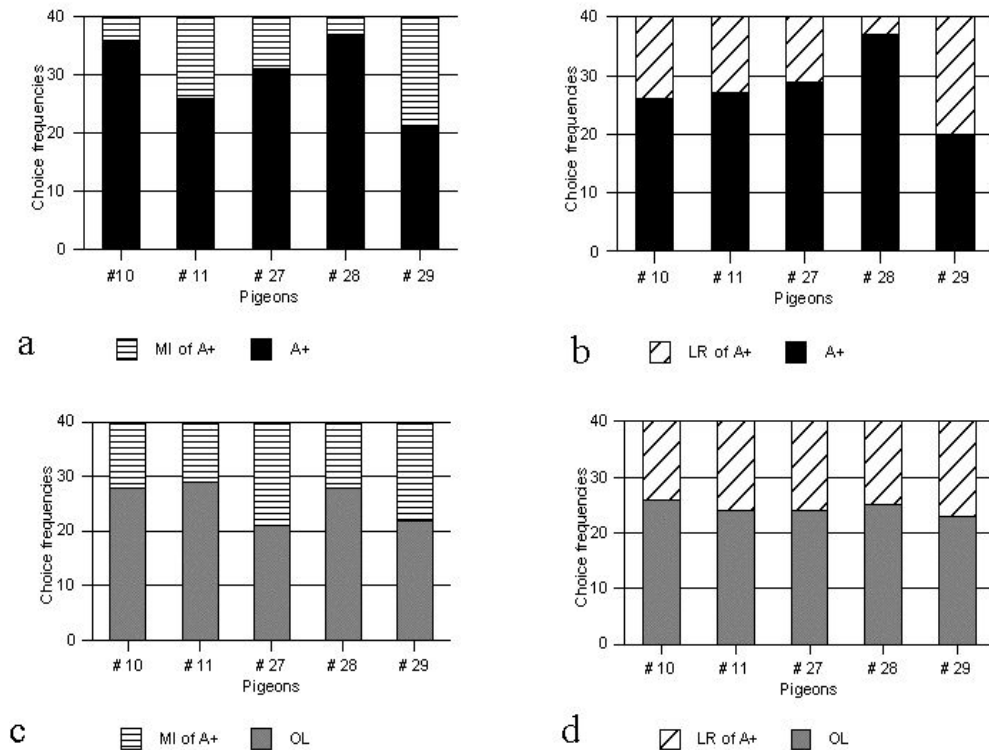


Figure 2. Choice frequencies out of $n = 40$ for the four experimental conditions for each pigeon.

Because the data were binary choice frequencies and because we had repeated measures, a replicated goodness-of-fit test (G statistic) was used (Sokal & Rohlf, 1981). Two G values for each condition are reported in Table 1 and they are compared to χ^2 values in the tests of significance: (1) G_p (P for Pooled), which compares group choice proportions to a chance level of 50:50; (2) G_H (H for Heterogeneity), which tests for individual variation. A significant G_H means that an individual choice proportion differed significantly from that of the group.

The results of the first two conditions show that the pigeons clearly differentiated A+ from its MI (Figure 2a) and from its LR reversal (Figure 2b). The choice proportions in these two conditions were significantly different from chance

$G_p(1) = 54.54, p < 0.001$ for A+ vs. MI and $G_p(1) = 31.24, p < 0.001$ for A+ vs. LR. These results rule out any absolute ambiguity. In the last two conditions, the MI and the LR reversal were not chosen more often than 50% of the time, showing an absence of facultative ambiguity (Figures 2c and 2d, respectively). In other words, the birds did not prefer the MI or the LR reversal when the A+ was absent. Surprisingly, there was a preference for the OL stimuli: MI and LR were both chosen significantly less often than chance $G_p(1) = 15.89, p < 0.001$ for MI vs. OL and $G_p(1) = 9.76, p < 0.005$ for LR vs. OL.

Not enough data for individual OL were available to test for any differences. Nonetheless, the OL which was chosen most frequently over the MI (91%) had two components in the same position as in the A+ (top left and bottom right components). In contrast, the OL which was chosen least frequently over the MI (18%) had two components in the same position as in the B- (bottom left and bottom right). It seems then, that the concordance of the position of components in the A+, the B-, and the OL might have been an important element on which pigeons based their choices.

For the first two conditions, the G_H was significant, meaning that individual choice proportions are heterogeneous $G_H(4) = 25.60, p < 0.001$ for A+ vs. MI and $G_H(4) = 19.96, p < 0.001$ for A+ vs. LR. The heterogeneity reflected individual differences in the magnitude of the choice frequencies but not in the direction. In other words, if a group choice frequency showed that the pigeons preferred a stimulus, they all did so to a greater or lesser degree. One exception is Pigeon 29, which failed to discriminate between the two test stimuli in all conditions. For the last two conditions, the ones with the OL stimuli, the results are homogenous: No individual differences were detected $G_H(4) = 6.17, p > 0.05$ for MI vs. OL and $G_H(4) = 0.54, p > 0.05$ for LR vs. OL.

Discussion

The birds in this experiment discriminated (i.e., perceived as different) the MI from the original image, as in previous work by Cerella (1990) and Hollard and Delius (1982). Hence, an absolute confusion, in which the image and its MI are undistinguishable to the birds, is ruled out by the data. The same can be said for the Left-Right transposition of the A+. Moreover, the pigeons did not prefer either the MI or the LR to other layouts (OL) of the same pattern components: A facultative confusion where the MI or the LR would be preferred to OL was also ruled out.

Not only were the MI and the LR chosen less frequently than the OL, but the reverse was true: We found a significant preference for the OL over the MI and over the LR. These results are in line with our predictions. Because pigeons strongly weight the position of pattern components in the recognition process (Biederman, 1987; Landry & Plowright, 2001; Wasserman et al., 1993), they view the MI and the LR as different from the A+. In support of this view, the OL pattern that was chosen most frequently had two pattern components in the same position as in the A+ and the OL pattern that was chosen most infrequently had two components in the same position as B-. This analysis raises the question of whether spatial relations of the symbols in the A+ were encoded. Perhaps pigeons attended to only one pattern component (such as “c” in the bottom left) and made the discrimination on that basis. Which element controlled the behaviour might also have

varied across birds (Spetch & Mondloch, 1993). The “aversion” to the LR might possibly be explained by its having “c” at the bottom-right, as did the B-, but this could not explain the “aversion” to the MI which did not have bottom-right “c”. Given that our experiment included 10 different OL patterns, the overall preference for the OL cannot have been due to one particular element in one particular position. More likely the pigeons encoded the positions of more than one symbol and perhaps even the spatial relations among them.

The preference for the OL patterns over the LR stands in marked contrast with our results on bumblebees, with the same patterns and same procedure, showing the reverse: A preference for the LR over OL (Plowright, 1997). Species differences in behaviour are fraught with difficulties in interpretation. They might reflect differences in attention, response tendencies or motivation. Certainly it would be premature to speculate whether different mechanisms underlie the recognition of visual patterns in different species. One functional explanation for the results on bees is that a LR transposition of a floral pattern would enable foraging bees to recognize vertically symmetrical flowers that were partially occluded at the time of learning (Gould, 1988). This kind of functional explanation could not apply to pigeons.

Two aspects of our procedure might account for the strong discriminations observed. The first has to do with training: The original discrimination (A+ vs. B-) required extensive training (about 90 sessions of 40 trials) even though learning might have been accelerated if correction trials had been used earlier. It also necessitated a particular attention by the birds to the spatial positions of the pattern components and possibly even their spatial relations. Perhaps by forcing attention to spatial relations, the procedure predisposed the pigeons not to be confused by patterns with the same components arranged differently. In other situations, in which the positions of the components are not important in resolving the learning task, there may well be spontaneous confusion, as in the study on learning of natural scenes by humans followed by mirror image confusion of the scenes (Standing et al., 1970). This possibility needs to be assessed with pigeons.

The second aspect of the procedure that might have triggered the strong discrimination is the choice of stimuli. When the A+ was transformed, both symbols from the left side were moved to the right side of the pattern and vice versa. In most of the studies on MI confusion (e.g., Todrin & Blough, 1983), however, there is only one stimulus component (one figure or symbol in the center of the key). Consequently, when the MI is introduced, the pattern appears at essentially the same position (for instance, the MI of “<” in the center of a key is “>” also in the center of a key-the patterns occupy virtually the same space). The marked change of position of the components might, in the present experiment, have been an important factor. In studies where no MI confusion was obtained (e.g., Delius & Hollard, 1995), the stimuli were branched, and so the MI clearly had figure-parts in new spatial areas, which might have enhanced the stimulus discriminability. Viewed in this way, there is nothing special about MI confusion or discrimination. It simply reflects the way in which pigeons use spatial information to judge the similarity of newly encountered patterns with memories of old patterns. Future research on the treatment of MI might profitably take into account the change in position of stimulus components as an important variable.

References

- Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. *Psychological Review*, **94**, 115-147.
- Cerella, J. (1990). Pigeon pattern perception, limits on perspective invariance. *Perception*, **19**, 141-159.
- Corballis, M. C., & Beale, I. L. (Eds.). (1976). *The psychology of left and right*. Hillsdale: Erlbaum.
- Corballis, M. C., & Cullen, S. (1986). Decisions about the axes of disoriented shapes. *Memory and Cognition*, **14**, 27-28.
- Delius, J. D., & Hollard, V. D. (1995). Orientation invariant pattern recognition by pigeons (*Columba livia*) and humans (*Homo sapiens*). *Journal of Comparative Psychology*, **109**, 278-290.
- Gould, J. L. (1988). A mirror-image "ambiguity" in honey bee pattern matching. *Animal Behaviour*, **36**, 487-492.
- Hollard, V. D., & Delius, J. D. (1982). Rotational Invariances in Visual Pattern Recognition by Pigeons and Humans. *Science*, **218**, 804-806.
- Kinsbourne, M. (1967). Sameness-difference judgments and the discrimination of oblique in the rat. *Psychonomic Science*, **7**, 183-189.
- Kinsbourne, M. (1971). Discrimination of orientation by rats. *Psychonomic Science*, **22**, 50.
- Korneluk Y.G., & Plowright, C. M. S. (1995). Mirror image pattern matching by bumble bees. *Behaviour*, **132**, 87-93.
- Landry, F., & Plowright, C. M. S. (2001). Use of spatial dimensions in pattern discrimination and similarity judgments by pigeons. *International Journal of Comparative Psychology*, **14**, 76-89.
- Lashley, K. S. (1938). The mechanism of vision, XV. Preliminary studies of the rat's capacity for detailed vision. *Journal of General Psychology*, **18**, 123-193
- Mackintosh, J., & Sutherland, N. S. (1963). Visual discrimination by the goldfish: The orientation of rectangles. *Animal Behaviour*, **11**, 135-141.
- Parriss, J. R. (1964) A technique for testing cat's discrimination of differently oriented rectangles. *Nature*, **202**, 771-773.
- Pavlov, I. P. (1927) *Conditioned reflexes*. London and New-York: Oxford University Press.
- Plowright, C. M. S. (1997). Function and mechanism of mirror-image ambiguity in bumblebees. *Animal Behaviour*, **53**, 1295-1303.
- Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, **171**, 701-703.
- Sokal, R. R., & Rohlf, F. J. (1981). *Biometry*. San Francisco: Freeman.
- Spetch, M. L., & Mondloch, M. V. (1993). Control of pigeons' spatial search by graphic landmarks in a touch-screen task. *Journal of Experimental Psychology: Animal Behavior Processes*, **19**, 353-372.
- Stack S., & Giurfa, M. (2001). How honeybees generalize visual patterns to their mirror image and left-right transformations. *Animal Behaviour*, **62**, 981-991.
- Standing, L., Conezio, J., & Haber, R. N. (1970). Perception and memory for pictures: single-trial learning of 2500 visual stimuli. *Psychonomic Science*, **19**, 73-74.
- Sutherland, N. S. (1960). Visual discrimination of orientation by octopus: Mirror images. *British Journal of Psychology*, **51**, 9-18.
- Sutherland, N. S. (1963). Cat's ability to discriminate oblique rectangles. *Science*, **139**, 209-210.
- Tatham, T. A., & Zurn, K. R. (1989). The MED PC experimental apparatus programming system. *Behavior Methods, Instruments and Computers*, **21**, 294-302.
- Todrin, D. C., & Blough, S. D. (1983). The discrimination of mirror-image forms by pigeons. *Perception and Psychophysics*, **34**, 397-402.
- Van Hof, M. W. (1966). Discrimination between striated patterns of different orientation in the rabbit. *Vision Research*, **6**, 89-94.
- Van Hof, M.W. (1970). Mechanisms of orientation discrimination in the rabbit. *Experimental Neurology*, **28**, 494-500.

Wasserman, E. A., Kirkpatrick-Steger, K., Van Hamme, L. J., & Biederman, I. (1993). Pigeons are sensitive to the spatial organization of complex visual stimuli. *Psychological Science*, **4**, 336-341.

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