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Short report

Conditioning pigeons to discriminate naturally lit insect specimens

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Abstract

Pigeons (*Columba livia*) were trained on a visual discrimination task using a novel apparatus which enabled pinned specimens of insects, illuminated by natural daylight, to be presented under a pecking key transparent to ultraviolet light. Three birds showed evidence of learning to discriminate between sets of wasp and fly specimens. This response transferred to specimens of four hoverfly species, the strength of the response varying between the different hoverfly species. This conditioning technique offers a promising means of analysing mechanisms of visual processing in birds that are relevant to theories of the evolution of camouflage and mimicry. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

In order to build models of the evolution of camouflage or mimetic resemblance in prey populations, it is essential to understand the mechanisms of sensory processing and learning that operate in predators. Discriminative operant conditioning techniques are a powerful means of investigating these mechanisms, and have been used by Dittrich et al. (1993) to investigate the phenomenon of 'imperfect mimicry' (Lindström et al. 1997). Examples of 'imperfect' mimics are hoverfly species (Diptera, Syrphidae) that possess yellow and black abdominal bands yet have little resemblance to wasps or bees in their body shape. One possible explanation for this apparent paradox is that birds may not perceive the same relative similarities between stinging insects and the hoverfly species concerned as humans do. To test this hypothesis, Dittrich et al. trained pigeons to discriminate between photographic images of wasps and of non-mimetic flies, and then measured the strength of their responses to images of different hoverfly species. The pigeons' behaviour showed a consistent ranking of hoverflies in their similarity to wasps that was similar to the rank ordering made by human observers, except that two 'imperfect' mimic species were treated by the birds as closely similar to wasps.

Two problems have been identified in using colour photographs or video images as stimuli in the analysis of pattern discrimination by predators (Delius, 1992; Cuthill and Bennett, 1993; D'Eath, 1998). Photographic and video imaging systems are designed so that, ideally, a human observer cannot distinguish the colour of a region of the image from that of the original surface. Differences between avian and human colour vision imply that the same will usually not be true for birds, and, therefore, that measurements of birds' ability to discriminate colour images of objects may not provide accurate information about their ability to discriminate the original objects under natural illumination. Also, fewer cues to the shape of a solid object are available in an image than in a natural scene and, again, results obtained from photographs may not generalise to natural objects. Delius (1992) has described a technique that addresses this problem, training birds on a discrimination task using solid objects as stimuli. Here, we describe the successful use of a method suited to the investigation of birds' perception of the colour patterns of insects, in which pinned insect specimens are presented to pigeons under natural daylight.

2. Materials and methods

2.1. Housing

The birds used in the experiment were drawn from an established colony of domestic pigeons (*Columba livia*) of both sexes and from 1 year upwards in age. The colony was housed in a loft of floor area 4.5 m^2, with access to an outdoor aviary adjoining a laboratory building.

2.2. Apparatus

The conditioning apparatus was mounted in a south-facing window in one wall of the aviary, and protruded into it, so that the birds could fly freely to the platform (Fig. 1). A 4 cm square

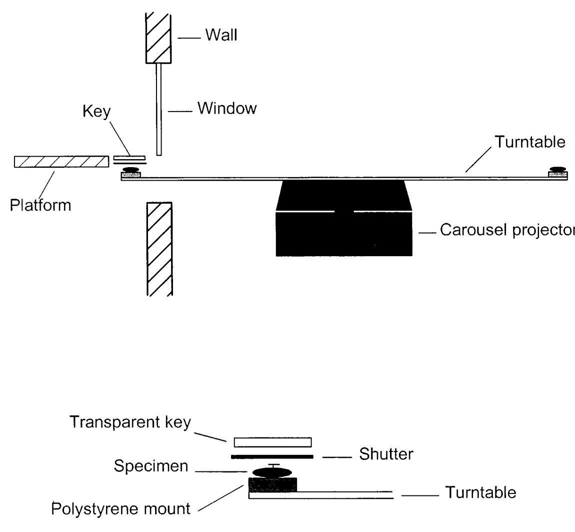

Fig. 1. Apparatus used to train pigeons to discriminate insect specimens (top). The platform and key are outdoors, under natural daylight. Magnified view of the arrangement of the pecking key, shutter and specimen (bottom).

transparent pecking key was set in the platform, hinged so that a peck of approximately 10 g force would close a microswitch. A solenoid-operated hopper was used to release single pieces of corn, measuring approximately 5×3 mm, into a small dish alongside the key. Insect specimens were presented to the birds by means of a circular turntable, 90 cm in diameter, mounted on a carousel projector. A strip of white polystyrene was glued around the edge of the turntable, and divided into 80 sectors of equal size by vertical strips of card. Pinned specimens could be inserted into these sectors, and so each operation to advance the projector brought a new specimen into view, underneath the centre of the pecking key and with its top surface 1 cm below the key. The vertical separators were high enough to ensure that only one specimen was visible through the key at a time. A solenoid-operated shutter placed just under the key was used to block the bird's view of the turntable between trials. The hopper, shutter and projector were controlled by a PC, which also recorded closures of the microswitch when the pecking key was depressed.

The design of the apparatus ensured that the spectral composition of light reflected from the insect specimens and reaching a pigeon's eye was exactly the same as if the bird viewed them under natural conditions. The specimens were illuminated by natural daylight, and the pecking key was made of fused silica, which is transparent to all wavelengths of light visible to humans, and to ultraviolet wavelengths down to 235 nm. Since the lower limit of pigeons' sensitivity to ultraviolet light is 310 nm (Emmerton, 1983), the key was transparent to all wavelengths of light visible to the birds.

The specimens were: (1) A set of 40 wasps (*Vespula vulgaris*), of approximately equal size. (2) A set of 40 non-mimetic flies (*Calliphora* and *Sarcophaga* spp.), of varying sizes. The wasp and non-mimetic fly specimens were mounted on pins through the thorax, with the wings folded and the head of the pin visible from above in both sets. (3) Four sets, of 10 specimens each, of different hoverfly species (*Scaeva pyrastri*, *Myiatropa florea*, *Sericomyia silentis*, *Chrysotoxum arcuatum*). All the hoverfly specimens had been pinned with the wings extended and the head of the pin invisible from above. All specimens were mounted on the turntable with their heads facing its centre (and therefore facing away from the pigeon).

2.3. Procedure

The birds were deprived of food except for a 2 h period each day, when they were given weighed amounts of food in individual cages. This period followed the experimental sessions, which were conducted between 10:00 and 15:00. The amounts of food were adjusted so as to maintain their weights between 85 and 90% of the baseline weight before the experiment began. Once the deprivation schedule was established, the birds were released individually into the aviary for pre-training sessions. They were first encouraged to visit the platform by scattering food on it, and then to take pieces of food from the dish when the hopper operated. Once this behaviour was established, they were shaped to peck at the key. During this stage, no specimens were present and only the white polystyrene backing was visible through the key. The birds that succeeded in learning to peck were then habituated to the operation of the shutter and the rotation of the turntable (still with no specimens present). They were then transferred to a reinforcement schedule in which every fourth peck at the key caused the shutter to close and the food hopper to operate.

Five birds successfully passed through all the stages of pre-training, and were used in the discrimination training sessions, run at 1- or 2-day intervals. In each session, 40 wasp and 40 fly specimens were mounted on the turntable, in a semi-random sequence in which no more than three consecutive specimens were the same. The sequence of specimens changed from one session to the next, and corresponding sequences were stored on disc so that the reward contingency could be controlled automatically by the PC. Pecks at wasp specimens were rewarded for three birds, and pecks at fly specimens for two. On trials where a rewarded specimen (S+) was presented, the bird was allowed 20 s in which to make 4 pecks. If it did so, a piece of corn was delivered and the trial ended immediately. On trials where a non-rewarded specimen (S −) appeared, it remained visible for 20 s before the trial ended. At the end of a trial, the shutter closed for 2 s while the turntable advanced. Sessions consisted of a maximum of 80 trials, although in some cases there were fewer, when the birds left the platform for short periods. An observer noted such trials, which amounted to 26% of the maximum possible number, and data recorded on the PC during them was excluded from analysis.

Three birds (two wasp + , one fly +) showed evidence of learning to discriminate between wasps and flies, and were given discrimination sessions that included transfer trials in which hoverfly specimens were presented. In each of these sessions, the hoverfly specimens were placed in 20 of the 80 sectors of the turntable, while the remaining sectors were divided equally between wasps and flies. The 20 hoverfly specimens consisted of five from each of the four species sets, chosen at random and inserted into the sequence at random points. The specimens used, and their positions in the sequence, changed from one session to the next. The S + contingency applied during half the transfer trials in which each hoverfly species was presented, and the S − contingency during the other half. Reward contingencies during wasp and fly trials continued unchanged from the earlier discrimination sessions.

During discrimination sessions, the latency from the start of each S + trial to the fourth peck (when a reward was delivered) was recorded. If no reward was obtained on an S + trial, a latency value of 20 s was recorded. On S − trials, the latency to the first peck and the number of pecks made in 20 s were recorded.

3. Results

Discrimination performance was measured as the percentage of correct trials in each session, excluding any transfer trials. An S + trial was counted as correct if the bird pecked and obtained a reward before the end of the trial and an S − trial was counted as correct if the bird made no pecks during the trial. Fig. 2 shows this measure for the three birds that achieved 75% or more

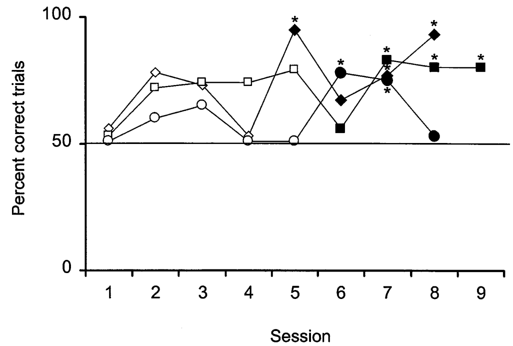

Fig. 2. Percentage of correct trials in each session of discrimination training for three birds (squares, diamonds: wasp + ; circles: fly +). Filled symbols denote sessions that included transfer trials, and asterisks denote sessions from which transfer data were used.

correct trials in at least two consecutive sessions. These birds were given transfer trials with hoverfly specimens during their last three or four sessions, but transfer data from only those sessions in which wasp–fly discrimination was 75% or more correct were used in further analysis (Fig. 2).

The latencies recorded in transfer trials were used to calculate the mean latency for the trials in which specimens of each hoverfly species were presented. These are shown in Fig. 3 for each bird separately, together with the mean latencies to respond to fly and to wasp specimens in the

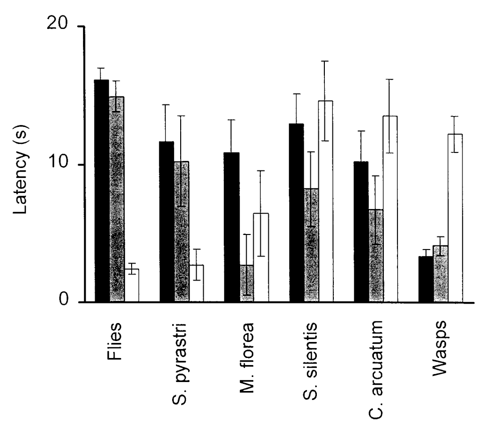

Fig. 3. Mean latencies to peck at each set of insect specimens recorded from individual birds (filled or hatched bars: wasp + ; open bars: fly +). Vertical bars show S.E.s.

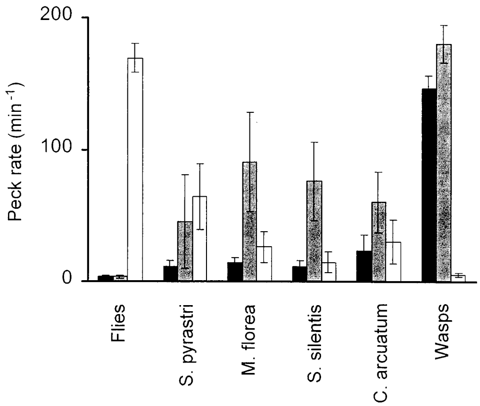

Fig. 4. Mean peck rates to each set of insect specimens recorded from individual birds (filled or hatched bars: wasp +; open bars: fly +). Vertical bars show S.E.s.

remaining trials of the same sessions. Because of the way in which the software recorded the latencies, the values for wasp and for fly trials are not strictly comparable, as they represent the time elapsing before the fourth or the first peck on a trial, respectively. However, this recording method tends to reduce any difference in responses to the two kinds of insect specimen, and therefore the actual differences in latency to the first peck at wasps and at flies are slightly greater than Fig. 3 shows. Since the mean latencies for each hoverfly species are all based on equal numbers of trials on which S + and S − contingencies were operating, the recording method allows direct comparisons between latencies of response to different species. In most cases, mean latencies to respond to hoverfly specimens fell between the values recorded for wasps and flies (Fig. 3). The rankings of mean latency to respond to the six different insect species were consistent across the three birds, after reversing the ranks of the bird trained with fly + (Kendall's coefficient of concordance $W = 0.68$, $k = 3$, $N = 6$, $P < 0.05$).

The pecking rates during individual transfer trials were used to calculate the mean peck rate to each of the four hoverfly species. These are shown in Fig. 4 for each bird, together with the rates during the wasp and fly trials of the same sessions. All birds responded to all hoverfly species at a mean peck rate lying between those to flies and to wasps. The rankings of the mean peck rates to the six different insect species were consistent across the three birds, after reversing the ranks of the bird trained with fly + (Kendall's coefficient of concordance $W = 0.9$, $k = 3$, $N = 6$, $P < 0.05$).

4. Discussion

The results from training indicate that pigeons can learn to discriminate between two sets of insect specimens presented under natural illumination. Of the five birds shaped, three performed at a level of 75% or more correct choices during at least two sessions. The method of mounting the two kinds of specimen was identical, and did not provide any cues to discriminate between them. The set of fly specimens was deliberately chosen to vary in size, across a range spanning that of the wasps, and so specimen size was not a valid cue to distinguish the groups. Other features of the procedure were the same as in the experiments of Dittrich et al. (1993), and so the evidence is equally strong in both cases that the birds learned to discriminate on the basis of a set of visual features differing between wasps and flies.

On both the latency and peck rate measures, the responses to hoverfly specimens during transfer tests generally fell between the values for wasps and flies, indicating that the birds perceived them as having some similarity to wasps. The variations in response strength observed to the different hoverfly species further suggest that the birds perceived them as having different similarities to wasps. These variations cannot be explained in terms of the different method of pinning the specimens from that used with the wasps and flies, as the method was identical across all the hoverfly specimens. As in the results of Dittrich et al. (1993), *Scaeva pyrastri* was consistently ranked as least similar to wasps, indicating a degree of similarity in the pigeons' perception of insect specimens and of photographs of them.

The responses of the birds to hoverflies observed in this experiment indicate that the conditioning method has the potential, when more data are available, to yield precise values for the similarities perceived by birds between insect species and so to contribute to the explanation of 'imperfect' mimicry.

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