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Prior experience enhances pattern discrimination in insect vision

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It is well known that prior knowledge or experience aids us tremendously in uncovering objects that are poorly visible, partially hidden or camouflaged^{1–3}. Is such enhancement in performance unique to higher animals? Here we find that bees cannot be trained directly to distinguish between differently shaped, camouflaged figures. They can, however, learn to break the camouflage and make the discrimination if they are trained initially on a simpler task that exposes them to shapes that are presented later in camouflage. Evidently, even organisms with relatively simple nervous systems can use prior experience to advantage in processing visual images.

Few who view the scene in Fig. 1 for the first time would see a familiar object, especially if they were unaware of the picture's content. Once the camouflaged object has been discovered, however, it is detected and recognized readily every time the picture is re-encountered. Evidently, prior experience or knowledge aids the visual system significantly in the task of uncovering objects^{1–3}. Is the ability to enhance processing in this way restricted to highly developed visual systems, such as those of humans and higher mammals? Here we investigate whether bees are able to use prior experience to advantage in detecting objects and discriminating their shapes.

Using a Y-maze (Fig. 2a), we attempted to train bees to distinguish between two shapes—a ring and a disc—when each shape was presented in a camouflaged fashion as a textured figure 6 cm in front of a similarly textured background (Fig. 2b). We found that bees were unable to learn to make this discrimination, despite lengthy training incorporating over 100 rewards per bee (Fig. 3).

Next, we examined whether bees could learn to distinguish the camouflaged stimuli if they were first trained on a related, but simpler discrimination. To this end, we trained a fresh group of bees to distinguish between a black ring and a black circle, each presented 6 cm in front of a white background. The ring and the circle were of the same size and shape as their textured counterparts, and their spatial configuration in relation to the background was identical to that in the previous experiment. The bees were able to learn this new task: the average choice frequency in favour of the rewarded stimulus (ring) was 63.1%, and this was significantly different from random choice ($P < 0.005$, χ^2 test; Figs 3a, 4a). Then the black figures were replaced by textured figures and the white backgrounds by similarly textured backgrounds, so that the new pair of stimuli was identical to that used in the first experiment (Fig. 2b). The bees now showed a clear ability to distinguish between the camouflaged stimuli (Figs 3b, 4b). The bees that were pre-trained on the black figures performed significantly better than those that were trained directly on the camouflaged stimuli (compare with Fig. 2b).

Similar results were obtained when we used a different pair of camouflaged shapes—textured horizontal and vertical bars—presented 6 cm in front of a similarly textured background. Bees were unable to learn to distinguish between the camouflaged stimuli when they were trained directly on them (Fig. 2c). But they were able to learn to do so when they were pre-trained on black bars presented in front of a white background, using a procedure analogous to that described for Fig. 4a, b. At the end of the pre-training phase, the bees displayed a choice frequency of 73.6% for the correct stimulus (black horizontal bar; $n = 811$, $P < 0.001$; data not shown). At the end of the subsequent training on the textured bars, they displayed a choice frequency of 65.1% for the correct stimulus (textured horizontal bar; $n = 189$, $P < 0.001$; data not shown).

Distinguishing the stimuli in Fig. 2b (or Fig. 2c) is a relatively complex task. It is very unlikely that the bees use stereoscopic vision to detect the camouflaged figures, given their relatively small interocular separation, poor visual acuity⁴ and the small disparity between figure and background. Rather, it appears that they use relative motion cues generated by their own motion in flight to detect the camouflaged figures and discriminate their shapes⁵. The boundary of each figure is signalled by the difference in apparent motion (motion parallax) between the figure and its immediate background. There is good evidence that bees can detect such boundaries by using motion parallax as a cue⁵,



FIG. 1 A familiar, but camouflaged object (readers experiencing difficulty in recognizing the Dalmatian dog may wish to view the picture upside-down). Photo courtesy R. C. James. Reprinted from Lindsay and Norman¹, with permission of authors and publishers.

but until now it has been impossible to train bees to discriminate the shapes of figures whose boundaries are defined solely by motion parallax⁵. Evidently, bees are unable to learn to make this complex discrimination in a single step. However, our results show that bees can learn such a task if they are pre-trained on

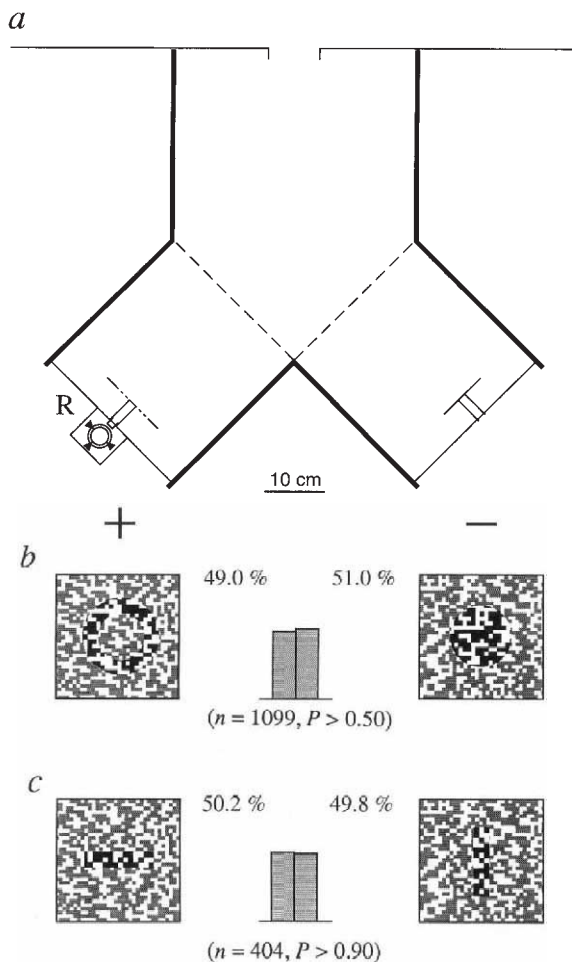


FIG. 2 *a*, Y-maze apparatus for training bees. A group of 10 freely flying bees was marked and trained to enter the apparatus which presented two stimuli, one on the vertical end wall of each tunnel. One stimulus (termed positive, and denoted by +) offered a reward of sugar water, R, placed in the box behind the wall, which the bees could reach through a tube. The other stimulus (termed negative, and denoted by -) carried no reward. The positions of the positive and negative stimuli were interchanged every 10 minutes, and the reward was moved with the positive stimulus during the entire experiment. This prevented the bees from developing a preference for one of the tunnels, and cancelled the effect of any residual side preferences when learning performance was assessed. The bees' learning performance was measured in terms of the percentage of choices that they made in favour of the two stimuli, and statistical tests for significant differences from random choice. A bee's choice was determined by noting which tunnel the bee entered first, when it arrived at the apparatus. Control experiments, using identical stimuli in both tunnels assured us that the bee's choices were not influenced by olfactory cues. For details of the training procedure, see ref. 9. Bees trained in this way were unable to distinguish between *b*, a textured ring and a textured circle, or *c*, between textured horizontal and vertical bars when these figures were presented 6 cm in front of similarly textured backgrounds. For clarity, the textured figures are shown darker than the backgrounds in the illustrations. The percentage figures and the bars depict the relative frequencies of choices in favour of the positive and negative stimuli respectively, as measured during the end of each training phase. *n*, Number of choices analysed; *P*, value associated with a χ^2 test for significant differences from random-choice behaviour.

a related but simpler discrimination that gives them a 'hint' as to what is expected of them ultimately.

What is the nature of the information that the bees acquire from the step-by-step training? Do they merely acquire information pertaining to the shapes of the figures that are to be discriminated, or do they learn something more general, such as the ability to distinguish between any shapes that are defined solely by motion-parallax cues? To investigate this question, we examined whether the group of bees trained to distinguish between the camouflaged ring and disc (using the step-by-step training procedure shown in Fig. 4*a, b*) could next be trained to distinguish between a different pair of camouflaged stimuli, namely, textured horizontal and vertical bars. We found that the bees were able to learn to make this discrimination (Fig. 4*c*)—albeit after a brief dip in the step-by-step learning curve at the start of training phase *c* in Fig. 3, when they evidently noticed that the camouflaged shapes had changed, and were learning to discriminate the new shapes. This is in contrast to the bees that were trained directly on the textured bars: they could never learn the task (Fig. 2*c*). Thus, the step-by-step training procedure that we have adopted here teaches the bees more than just the specific shapes of the figures to be distinguished; it teaches them to use motion parallax cues to extract the shapes of camouflaged figures in a more general sense. Furthermore, the dip and subsequent recovery in the learning curve when the stimuli are changed from textured ring and circle to textured bars (the transition from phase *b* to phase *c* in Fig. 3) indicate that the bees do not abandon motion parallax as a potential cue during the brief period of 'confusion' (about 10 rewards per bee, or 1 hour).

Is the facility that the bees acquire from the two-step training genuinely a consequence of acquiring relevant prior experience during the first step, or is it merely a nonspecific enhancement of performance produced by pre-training? To examine this question, we investigated whether a group of bees trained to distinguish the black-and-white stimuli of Fig. 4*a* (ring versus disc)

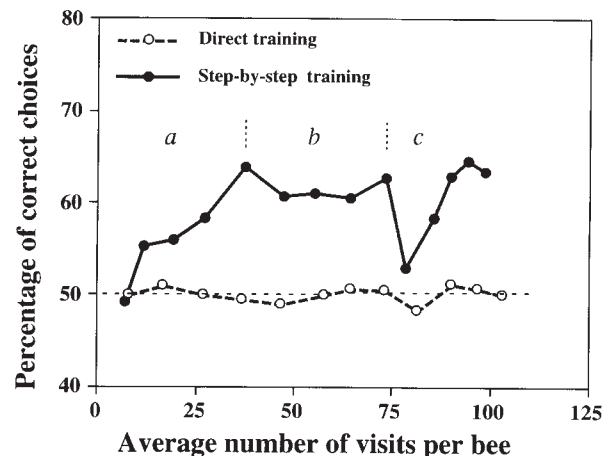


FIG. 3 Learning curves corresponding to the training experiments illustrated in Figs 2*b* and 4. The bees were unable to learn to distinguish the stimuli of Fig. 2*b* when trained directly on them, even after each bee had received over 100 rewards, on average, as illustrated by the dashed curve in the present figure. However, bees were able to learn the same task when they were trained in a step-by-step fashion, as described in Fig. 4 and illustrated by the solid curve here. (The segments labelled *a*, *b* and *c* on the step-by-step training curve correspond to training phases using the stimuli illustrated in Fig. 4*a-c* respectively.) Furthermore, bees trained in this way were also able to learn to distinguish between novel camouflaged shapes, such as textured horizontal and vertical bars (segment *c* on the step-by-step training curve). Each data point on the learning curves depicts the choice frequency in favour of the positive stimulus, as measured by analysing all of the choices made since the previous point.

could learn directly to distinguish the differently shaped, camouflaged stimuli of Fig. 4c (horizontal versus vertical textured bar). In this two-step training, the cues that are germane to the first task are irrelevant to the second. We found that although these bees learned the first task (as before), they were unable to learn the second (choice frequency for correct stimulus, 49.3%; $n = 369$; $P > 0.85$). Thus, pre-training enhances the bees' subsequent performance only when it contains cues that are relevant to the subsequent task. Furthermore, the finding that bees are able to learn to transfer discrimination from the camouflaged ring and disc (Fig. 4b) to the camouflaged horizontal and vertical bar (Fig. 4c) but not from the black/white ring and disc (Fig. 3a) to the camouflaged horizontal and vertical bar (as described above) suggests that the enhancement in discrimination performance is not merely the result of learning to distinguish motion signals of different magnitudes that would arise from scanning the patterns in the horizontal and vertical directions. Rather, it appears that the bees are learning to use motion-parallax cues to extract information on shape.

Our findings do not reveal precisely in what way the pre-training modifies processing of information in the visual pathway. At one extreme, the pre-training could generate an abstract, high-level representation of the objects to be discriminated. This representation could facilitate detection and discrimination of the same objects when they are camouflaged, partially occluded, poorly visible or viewed under different conditions. Such schemes are envisaged in current models of 'top-down' processing in human cognition and computer vision^{1-3,6-8,10}. At the other extreme, the pretraining could simply promote extraction of a number of related, low-level visual cues that are potentially use-

ful to the discrimination, by sensitizing the appropriate visual interneurons. These interneurons could be situated in a pathway that is associated with perception, or in a pathway that simply mediates a behavioural reflex which guides the bee toward the correct stimulus.

Irrespective of these unresolved questions, our results demonstrate clearly that the ability to use prior experience to enhance visual performance is not a faculty that is restricted to primates or higher mammals; it is possessed even by creatures with brains that weigh less than a milligram and carry <0.01% as many neurons as we do. The neural basis of this phenomenon is largely unknown, although it is currently the subject of much interest, speculation and modelling⁶⁻⁸. The relatively simple nervous system of the bee offers a promising substrate in which to explore the underlying mechanisms. □

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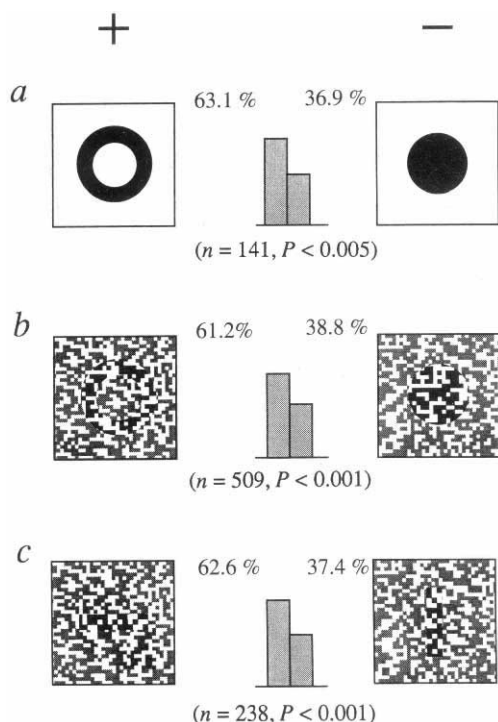


FIG. 4 a, b, Results of a separate experiment, using a fresh group of bees that were trained ultimately to distinguish between the stimuli shown in Fig. 2b, but in two steps. First, the bees were trained to distinguish between a black ring and a black disc, each presented in front of a white background. They learned this task well (a). The same bees were then trained with the textured shapes presented in front of the textured background. These bees learned to discriminate the camouflaged shapes well (b), in contrast to the bees that were trained directly on the camouflaged shapes (compare with Fig. 2b). Furthermore, the group of bees trained in the step-by-step fashion could also learn to discriminate other camouflaged shapes (c).

Unusual permeability properties of gastric gland cells

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PHYSIOLOGISTS have long pondered the riddle of why the stomach is itself not digested by the very juice it secretes. One explanation is that a mucus-bicarbonate barrier, coating the stomach lumen as well as superficial portions of gastric glands, prevents autodigestion¹. However, this leaves unanswered the question of what protects cells deeper in the glands, which seem to lack a mucus barrier². These are the parietal and chief cells, which secrete acid and pepsin. Using perfused single gastric glands from rabbit, we recently found that intracellular pH is uniquely resistant to extreme degrees of luminal acidification², suggesting that the apical (luminal) barrier might also exclude ammonia and carbon dioxide, to which cell membranes are generally highly permeable^{3,4}. We now show that this is indeed the case. There are three reports of membranes with very low permeabilities to NH₃ (refs 5-7), and none of membranes impermeable to CO₂.

We used intracellular pH (pH_i) changes to assess the permeability of apical and basolateral membranes of parietal cells and chief cells to NH₃ and CO₂. Perfusing single gastric glands, we loaded cells with the pH-sensitive dye BCECF, determining the pH_i of many individual cells using digital processing of fluorescent images². We found that the apical barriers of both parietal and chief cells are impermeable to NH₃ and CO₂, as well as to NH₄⁺ and HCO₃⁻.