Convergent processing in honeybee vision: Multiple channels for the recognition of shape

(insect vision/behavior/motion parallax/learning/memory)

S. W. Zhang*, M. V. Srinivasan*, and T. Collett[†]

*Centre for Visual Science, Research School of Biological Sciences, Australian National University, P.O. Box 475, Canberra, A.C.T. 2601, Australia; and [†]Sussex Centre for Neuroscience, School of Biological Sciences, University of Sussex, Brighton BN1 9QG, United Kingdom

ABSTRACT Advanced mammalian visual systems can recognize a familiar shape under a variety of viewing conditions. Recognition is possible whether the shape is presented in simple outline, as a random dot stereogram, or by motion contrast. We report here that bees have a similar ability: they can recognize a shape when it is learned through visual signals of one kind and subsequently viewed through another. The results reveal that (*i*) bees that have learned a shape defined in terms of luminance contrast can recognize the same shape when it is defined in terms of motion contrast, (*ii*) shapes that are delineated by motion contrast are discriminated through a channel that receives input only from the green photoreceptors, (*iii*) a shape learned through one class of signal is subsequently recognized via any of these other classes, and (*iv*) shape is memorized in a generic form regardless of whether it is initially sensed by green-contrast, blue-contrast, luminance-contrast, or motion-contrast signals.

To investigate whether bees encode shape in a generic form, regardless of input channel, we began by asking if bees that have learned a shape defined in terms of luminance contrast can recognize the same shape when it is defined in terms of motion contrast. Using a Y maze (Fig. 1*a*), we first trained bees to distinguish a ring from a disk, each presented as a black figure against a white background. These shapes are defined in terms of the luminance contrast at their boundaries. The bees learned to make this discrimination well (Fig. 1*b*). We then asked whether these trained bees can distinguish between the same shapes when they are presented as textured figures, 6 cm in front of a similarly textured background. The textured shapes can only be detected through the apparent relative motion or motion contrast between the figure and background as the bee moves relative to them. The bees trained on the "solid" shapes are, indeed, immediately able to distinguish between the textured versions of these shapes (Fig. 1*c*). Thus, bees that have learned a shape that is defined by luminance contrast will recognize the same shape when it is defined by motion contrast. Importantly, bees cannot be trained directly to distinguish between shapes that are defined purely by motion contrast: they need to be "primed" by prior training on luminance-contrast versions of the same shapes (2). After the two-stage training, on the other hand, bees can even distinguish between novel shapes that are defined purely by motion contrast. Thus, after training as in Fig. 1 *b* and *c*, the same bees can learn to distinguish between a textured pair of differently oriented oblique bars, which they had never previously encountered (Fig. 1*d*). Evidently, in transferring from the solid ring and disc to the textured versions of the same shapes, the bees learned that motion contrast carries the relevant cues for distinguishing the stimuli. They then used information transmitted through motion contrast to discriminate the novel textured shapes in Fig. 1*d*. Experiments of the kind shown in Fig. 1 *b–d* were reported in an earlier study in a different context (2) but are replicated here afresh as they form the starting point of the present study.

How do bees recognize shapes delineated by motion contrast? It is known that bees distinguish luminance-contrast shapes by their spatial properties and not by the motion signals generated as they move relative to the shapes (3, 4). Does this also apply to shapes that are defined by motion contrast, or are such shapes recognized solely by their "motion signature?" Further, what role, if any, does color play in the two situations? To answer these questions, we began by asking which of the bee's three color channels [UV, blue, and green (5)] are involved in the detection of motion contrast. We tested bees that were initially trained to distinguish between two obliquely oriented black bars (Fig. 2*a*), on similar bars that were presented using colored textures. Two kinds of textures were used, each constructed using a specific pair of colors. In one kind, termed the green-contrast texture, the colors were chosen so as to provide a strong textural contrast to the green-sensitive receptors and negligible textural contrast to the blue-sensitive receptors. In the other kind, termed the blue-contrast texture, the situation was reversed: the colors provided contrast to the blue but not to the green receptors (details in Fig. 2). Bees trained on the black bars immediately distinguished between the shapes when they were presented as green-contrast textures (Fig. 2*b*), but not at all when the same shapes were presented as blue-contrast textures (Fig. 2*c*). In the latter case, bees did not learn to choose the rewarded shape even after 3 days' training (*ca.* 100 rewards per bee). These results indicate that motion contrast is detected by a channel that receives input only from the green photoreceptors. This finding meshes well with earlier data that the detection of motion *per se* is mediated by signals derived exclusively from green receptors (7, 8).

Is the analysis of "solid" shapes also mediated by signals from a specific spectral class of photoreceptors? To investigate this, we examined whether bees could learn to distinguish between a horizontal bar and a vertical bar when the colors of the bars and the backgrounds were chosen so as to present a contrast either exclusively to the green receptors (Fig. 3*a*) or exclusively to the blue receptors (Fig. 3*c*). The bees were able to learn the task in either case. Moreover, bees that had been trained on the green-contrast bars were able to transfer shape discrimination immediately to blue-contrast bars, and vice versa ($P < 0.001$ in either case; data not illustrated). Thus, bees are able to recognize a shape even when it is signaled by a class of photoreceptors that is different from that employed to learn the shape.

We could now ask whether bees would recognize a shape that was defined by motion contrast after initial training with a blue-contrast shape that could not have supplied a motion signature. Accordingly, we compared the ability of bees to distinguish textured black-white figures on a similarly textured
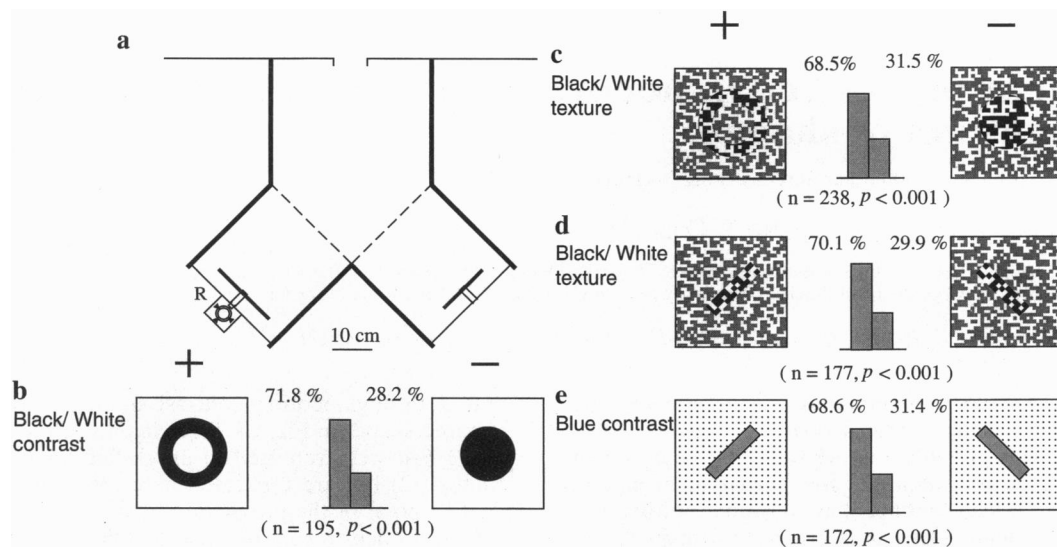
FIG. 1.   (a) Y-maze apparatus for training bees. A group of 10 freely flying bees is marked and trained to enter the apparatus, which presented two stimuli, one on the vertical end wall of each tunnel. One stimulus (termed positive, denoted by +) offers a reward of sugar water, R, placed in the box behind the wall, which the bees could reach through a tube. The other stimulus (termed negative, denoted by −) carries no reward. The positions of the positive and negative stimuli are interchanged every 10 min, and the reward is moved with the positive stimulus during the entire experiment. This prevents the bees from developing a preference for one of the tunnels and cancels the effect of any residual side preferences. The bees' discrimination performance was measured in terms of the percentage of choices that they made in favor of the two stimuli, by noting which tunnel the bee entered first when it arrived at the apparatus. The reward was always present at the stimulus labeled +, but in tests that examined the bees' preferences for stimuli other than the training stimuli, the duration of each testing session was restricted to 10 min (allowing two rewards per bee, on average). Furthermore, such tests were interspersed with long training intervals (at least 2 hr). These precautions prevented the bees from learning to distinguish the test stimuli on the basis of rewards acquired during the tests. Control experiments, using identical stimuli in both tunnels assured us that the bees' choices were not influenced by olfactory cues. For further details of the training procedure, see ref. 1. In a number of instances, discrimination performance was also measured by a different criterion, where we compared the number of landings and touches of each bee at the entrance tube associated with either stimulus, with the reward removed. These results (not shown) were fully consistent with those obtained using the criterion of tunnel entrances. Bees trained in this way learn well to distinguish between a black ring (of thickness 2.8 cm and mean radius 5.8 cm) and a black disc of the same area, of diameter 5.7 cm (b). These trained bees can immediately distinguish between the same shapes when they are presented as black-and-white textures, of pixel size 4 mm square, 6 cm in front of a similarly textured background (c). After being trained on task (c), these bees can then be further trained to distinguish between two novel textured shapes—namely, 18 cm × 4 cm bars oriented at +45° and −45° (d). Evidently, while being trained on the task of c, the bees learn that motion contrast is the relevant cue and use this cue to learn to distinguish the novel textured shapes in d. Finally, these trained bees are now immediately able to distinguish solid versions of the shapes in d, presented in blue contrast (e). These results imply that bees are able to learn a new shape that is defined purely by motion contrast and subsequently recognize this shape in a context in which it provides no motion signals. For clarity, the textured shapes are shown darker than the backgrounds in the illustrations. The histograms and percentages shown in this and following figures represent the relative frequencies of choices in favor of the positive and negative stimuli, respectively, in the learning and transfer tests. n denotes the number of choices analyzed, and p denotes the value associated with a χ^2 test for significant difference from random choice behavior.

background, when they had been pretrained on the green contrast bars (Fig. 3a) or the blue-contrast bars (Fig. 3c). The bees could distinguish between the textured shapes equally well in either case (compare Fig. 3b with Fig. 3d). Successful transfer from blue contrast to motion contrast signaled by green receptors implies that recognition is possible through input channels that were not engaged during learning. During training, the shapes were signaled exclusively by the blue-sensitive receptors, which provided no motion signatures. In the subsequent test, the same shapes were recognized in an entirely different context where they were defined exclusively by motion contrast, carried by green-contrast signals. This result implies that the bees recognize the motion-contrast pattern through its underlying shape and not just by its motion signature.

When bees learn a novel shape that is defined purely by motion contrast, as in Fig. 1d, what do they memorize about the shape: its geometry, or its motion signature? To investigate this, we examined whether the bees that had learned to distinguish between the textured, obliquely oriented bars (Fig. 1d) could distinguish the same shapes when they were subsequently presented in solid form. Accordingly, these bees were then offered a choice between solid versions of the shapes of Fig. 1d, each providing only blue contrast at the boundary (Fig. 1e). The bees immediately showed a clear preference for the bar of the correct orientation, indicating that they can, indeed,

make the transfer to solid shapes. It is significant that the solid bars in Fig. 1e presented only blue contrast because such patterns, being devoid of green contrast, carry no motion signature. Thus, bees are able to learn a novel shape that is defined purely by motion contrast and signaled exclusively by green-sensitive receptors and later recognize the same shape in a solid form that is signaled exclusively by blue-sensitive receptors without motion information. Here again, a shape learned through signals of one kind is subsequently recognized through signals of another kind and origin; but in this case, the transfer is in the opposite direction, from motion-contrast signals to solid shapes. Even if a shape is first learned through motion-contrast signals, it is memorized in terms of its geometry rather than its motion signature.

The experiments described here lead to a number of conclusions. First, although the bee possesses excellent trichromatic color vision, the perception of shape through motion contrast is mediated only by the green-sensitive receptors. Second, objects can be learned and recognized through signals from a variety of visual channels. In particular, a shape can be recognized through a channel that is different from the one through which it was originally learned. Third, shapes are memorized in terms of their intrinsic geometry, and not in terms of their motion signatures, even when motion-contrast signals are used to delineate these shapes.

Our major conclusion, that shape is analyzed through a multiplicity of visual channels, is supported by anatomical and
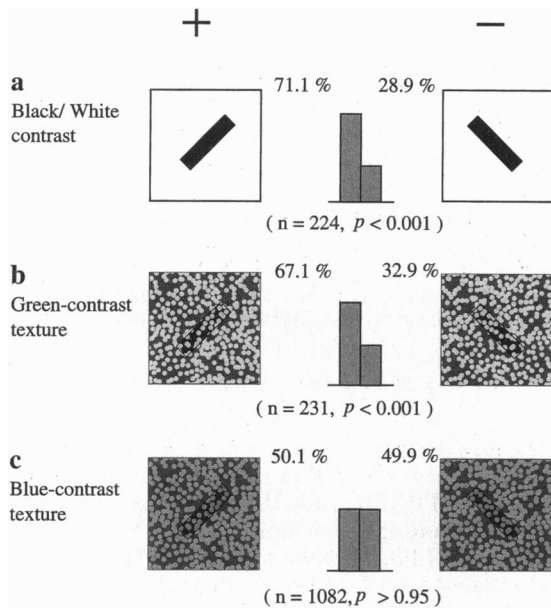
Neurobiology: Zhang *et al.*

Proc. Natl. Acad. Sci. USA 92 (1995)   3031

FIG. 2.   Bees trained initially to distinguish between two obliquely oriented, 18 cm × 4 cm black bars on a white background (*a*), can immediately distinguish between the same shapes when they are presented as green-contrast textures (*b*), but not when presented as blue-contrast textures (*c*). The green-contrast texture presents substantial contrast to the green-sensitive receptors (44%) but not to the blue-sensitive receptors (2%). The blue-contrast texture presents substantial contrast to the blue-sensitive receptors (66%) but not to the green-sensitive receptors (2%). These textures were produced by affixing a large number of 6-mm (diameter) circles of one color onto a 24-cm (diameter) background of another color. The colors were specially selected from a set of pigment papers to produce the desired contrasts in the blue and green receptors. The circles covered ≈50% of the background area and were positioned randomly within this area with the aid of a computer program. As there was negligible illumination at wavelengths below 400 nm, the UV contrast in these stimuli was not relevant (6).

physiological evidence for parallel processing of information in the insect visual pathway (9). Ethologically speaking, there are definite benefits to recognizing an object independently of the input channels that it stimulates. A flower, for example, may stimulate a bee's individual color channels differently depending upon whether it is viewed at midday or in the red-rich illumination of the late evening. Furthermore, the flower should be detectable regardless of whether it is viewed against a background of green foliage (when the primary cue would be contrast in luminance or color) or against other flowers of the same species (when the primary cue would be motion contrast). Motion contrast is also helpful in segregating objects when scenes are dappled by shadows.
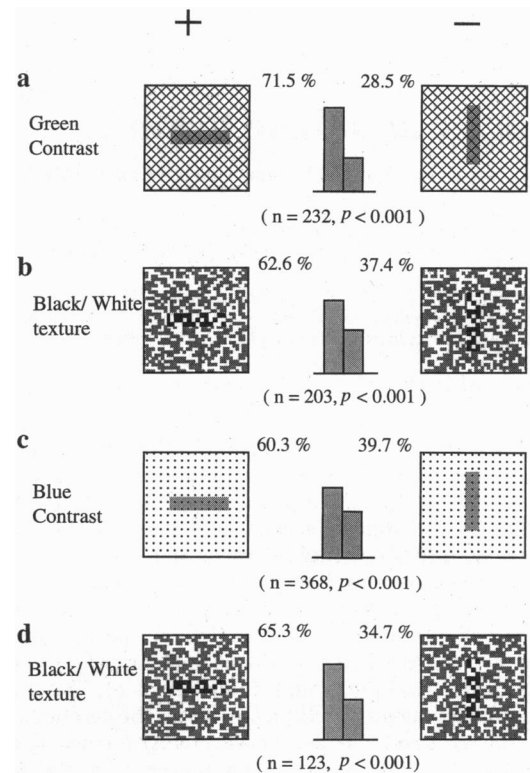

FIG. 3.   Bees that have learned to distinguish between solid, 18 cm × 4 cm horizontal and vertical bars presented in green contrast (*a*) can immediately distinguish between such bars when they are presented in blue contrast (*P* < 0.001, data not illustrated) and also when they are presented as black-and-white textures (*b*). Similarly, bees that have learned to distinguish between horizontal and vertical bars presented in blue contrast (*c*) can immediately distinguish between such bars when they are presented in green contrast (*P* < 0.001, data not illustrated) and also when they are presented as black-and-white textures (*d*). The green- and blue-contrast bars were created using the same pairs of pigment papers that were used to construct the green- and blue-contrast textures in Fig. 2 *b* and *c*.

1.   van Hateren, J. H., Srinivasan, M. V. & Wait, P. B. (1990) *J. Comp. Physiol. A* **167**, 649–654.

2.   Zhang, S. W. & Srinivasan, M. V. (1994) *Nature (London)* **368**, 330–332.
3.   Srinivasan, M. V., Zhang, S. W. & Rolfe, B. (1993) *Nature (London)* **362**, 539–540.
4.   Wehner, R. (1981) in *Handbook of Sensory Physiology*, ed. Autrum, H. (Springer, Berlin), Vol. 7/6 C, pp. 287–616.
5.   Menzel, R. (1979) in *Handbook of Sensory Physiology*, ed. Autrum, H. (Springer, Berlin), Vol. 7/6 A, pp. 503–580.
6.   Srinivasan, M. V. & Lehrer, M. (1988) *J. Comp. Physiol. A* **162**, 159–172.
7.   Kaiser, W. (1975) in *The Compound Eye and Vision of Insects*, ed. Horridge, G. A. (Clarendon, Oxford), pp. 359–377.
8.   Lehrer, M. (1991) in *The Behaviour and Physiology of Bees*, eds. Goodman, L. J. & Fisher, R. C. (CAB, Wallingford, United Kingdom), pp. 185–202.
9.   Strausfeld, N. J. & Lee, J.-K. (1991) *Visual Neurosci.* **7**, 13–33.