

In summary, the oenocytes of the adult foraging honey bee form an innervated sheet of tissue around each abdominal segment. Each cell of the sheet contains many electron-opaque iron-containing granules in the cytoplasm.

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## A Specific and Enduring Improvement in Visual Motion Discrimination

**Abstract.** *Training improves the ability of human observers to discriminate between two similar directions of motion. This gradual improvement is specific to the direction on which an observer is trained, and it endures for several months. Improvement does not affect motion perception generally, nor does it depend on recognition of details of the movement.*

Practice can improve ability to discriminate among objects. This perceptual learning often simply reflects improved ability to pick out features distinguishing one visual target from another (1, 2). Other times, perceptual learning requires a change in the observer's use of verbal labels to describe his experience (3) or heightened attention or arousal (4). We report an enduring alteration in vision that is specific to the stimulus on which an observer is trained. Rather than resulting from an increased ability to pick out some critical feature of the stimulus, this form of perceptual learning may be related to changes in the selectivity of elements in the visual system.

Since previous work suggested that motion perception is plastic (5, 6), we set out to train an observer's discrimination of the direction of moving targets. Before training, we measured how well observers discriminated small differ-

ences in direction of motion. Discrimination was assessed around eight different directions: 0° (rightward), 45°, 90° (upward), 135°, 180°, 225°, 270°, and 315°. Hereafter, we refer to directions 0°, 90°, 180°, and 270° as principal directions and 45°, 135°, 225°, and 315° as oblique directions. Eight observers were tested: one was K.B. and six were naïve about our purposes.

Stimuli were bright, spatially random dots moving along parallel paths over the face of a cathode ray tube at 10° per second. At any one time, about 400 dots were visible within an 8° circular aperture. The dots, and their movement, were highly visible: the luminance of the dots was approximately 50 times that required for them to be just seen against a constant veiling luminance of 2 cd/m<sup>2</sup>. Opposite ends of the display were linked electronically so that dots disappearing at one side wrapped around, to reappear at the opposite side. Full details of the

display are given elsewhere (6). Observers viewed the displays binocularly, fixating a dark, stationary, central point. To guard against the possibility that observers might learn to identify details of our display, a new array of spatially random dots was used every 50 trials (7).

Each trial consisted of two 500-msec intervals. This pair of intervals was separated by a 200-msec period during which only the uniformly illuminated cathode-ray tube was visible. Two equiprobable types of trials, "same" and "different," were randomly ordered. On "same" trials, motion took the same direction during both intervals; on "different" trials, motion in one interval was in a direction differing by 3° from that of the other interval. The observer viewed both intervals and judged the two directions "same" or "different."

A block of 50 trials was characterized by one standard direction. This direction appeared in both intervals of "same" trials and in one interval of "different" trials. In the remaining interval of "different" trials, a random choice was made to present motion 3° either clockwise or counterclockwise of the standard direction. Whether the first or second interval contained the standard direction on "different" trials was also randomly determined. A tone after each correct judgment gave immediate knowledge of results.

The main experiment required seven sessions over 10 to 12 days. In sessions 1, 4, and 7, discrimination performance was measured for all eight directions. The order of testing was separately randomized for each session and observer. In sessions 2, 3, 5, and 6, an observer trained on just one of the eight directions, principal and oblique. At the start of the experiment, a different training direction was assigned each observer, who retained that assignment throughout the experiment. During a training session, an observer made 500 "same-different" judgments (ten blocks of 50 trials) with the assigned direction. For both training and test sessions, observers were rewarded with 2 cents for each correct response; 1 cent was deducted for each incorrect response.

Responses in a block of trials were reduced to a pair of proportions: the proportion of "different" trials correctly identified as such (hits), and the proportion of "same" trials misidentified as "different" (false alarms). These proportions were converted into *d'*, a measure of discrimination performance (8). This measure granted immunity to spurious performance changes that would follow

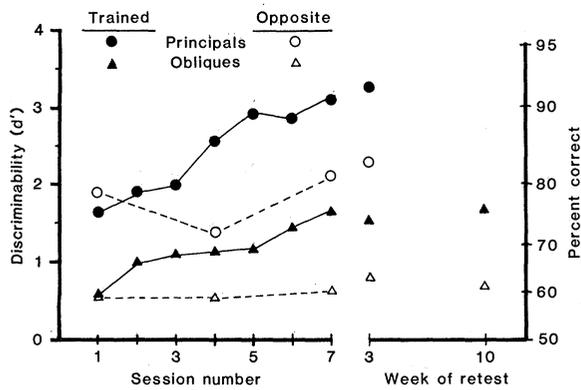


Fig. 1. Discriminability ( $d'$ ) of a motion's direction as a function of session number and at retest, 3 and 10 weeks after the end of training. Percentages (right ordinate) were calculated under the assumption that observers would have an equal bias for responding "same" or "different" (8). Data are averages across observers.

systematic shifts in the observers' use of the two response categories.

Performances before and during training were compared by analysis of variance. Generally, discrimination was better for the principal directions (up, down, left, or right) than for the oblique directions, confirming earlier work (9). Our experimental design estimated discrimination for an observer's training direction in all seven experimental sessions, but estimated performance with other directions only in sessions 1, 4, and 7. Several findings are of particular importance. (i) With the training direction, performance improved linearly across the seven sessions [ $F(1, 6) = 151.31$ ,  $P < .01$ ]. This gradual, steady improvement, which was seen for all observers, suggests an underlying process different from the sudden improvement produced when observers learn to pick out the distinctive, spatial features of a stimulus pair (1). (ii) Training was not effective for the three directions most different from the training direction, including the direction opposite the training direction [ $F(3, 17) = 65.74$ ,  $P < .01$ ]. Improvement with the trained direction did not come at the expense of diminished performance with the opposite direction, however (Fig. 1). (iii) Training with oblique or principal directions produced comparable improvements [ $F(6, 36) = 1.81$ ,  $P = .12$ ]. One result is not illustrated in Fig. 1. Although discrimination improved at either direction  $45^\circ$  from the trained direction, the improvement was significantly less than that at the trained direction itself [ $F(2, 12) = 65.74$ ,  $P < .01$ ].

This enhancement of discrimination endured in the absence of more training. Two retests were made after training, at 3 and 10 weeks. Six of our original eight observers were available for the first retest, and four were available for the second. Virtually all of the original improvement was retained (Fig. 1). Moreover, the improvement continued to be

sharply restricted: the difference between trained direction and the direction opposite was just as large as it had been at the end of training.

To test whether improved discrimination would also alter other aspects of motion perception we determined the minimum dot luminance necessary for them to be just barely visible (that is, their detection threshold). Thresholds were measured with the dots moving at  $10^\circ$  per second, the training speed. Three directions were tested: the training direction, the direction opposite, or a direction  $45^\circ$  from the training direction. Luminance thresholds were determined with a two-alternative forced-choice method (8). On each trial, moving dots were presented in one of two 500-msec intervals; only the uniformly lit display was visible during the other interval. The observer had to identify the interval during which dots had been presented. A tracking procedure located the threshold luminance, the luminance enabling correct identification on 75 percent of the trials. Thresholds were determined in our second group of eight observers on the day after each one's seventh experimental session. The earlier observation that training persisted for many weeks, made us confident that these observers were being tested at a time when they still retained the effects of training.

There were no reliable differences among the contrasts required to see movement in the training direction versus those needed to see motion in either of the other two directions (12.5 percent versus 12.5 and 13.1 percent,  $P > .50$ ). Apparently, training can improve discrimination of direction without affecting detection.

We wondered whether the improvement in discrimination performance might have arisen from an improvement in the accuracy of tracking eye movements. This possibility was examined by recording eye movements while two observers made direction discriminations.

Using an infrared corneal-reflection technique to measure eye movements, we found that with steady fixation verified, observers performed at the same levels as they had during the actual experiments. Since tracking eye movements are not necessary for direction discrimination, it is unlikely that changes in such eye movements play a role in the performance changes with practice (10).

Many aspects of our results require additional work, for example, the role played by immediate knowledge of results (11). Although it is premature to speculate about their precise explanation, our results show that under proper conditions, the mature human visual system exhibits a remarkable degree of plasticity (12). In fact, training regimens such as ours may provide a useful, noninvasive tool for examining neural plasticity generally (13).

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