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Visual pattern memory without shape recognition

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SUMMARY

Visual pattern memory of *Drosophila melanogaster* at the torque meter is investigated by a new learning paradigm called novelty choice. In this procedure the fly is first exposed to four identical patterns presented at the wall of the cylinder surrounding it. In the test it has the choice between two pairs of patterns, a new one and one the same as the training pattern. Flies show a lasting preference for the new figure. Figures presented during training are not recognized as familiar in the test, if displayed (i) at a different height, (ii) at a different size, (iii) rotated or (iv) after contrast reversal. No special invariance mechanisms are found. A pixel-by-pixel matching process is sufficient to explain the observed data. Minor transfer effects can be explained if a graded similarity function is assumed. Recognition depends upon the overlap between the stored template and the actual image. The similarity function is best described by the ratio of the area of overlap to the area of the actual image. The similarity function is independent of the geometrical properties of the employed figures. Visual pattern memory at this basic level does not require the analysis of shape.

INTRODUCTION

Humans and probably animals can store new visual images throughout life. The excessive abundance of visual data must be processed in an efficient and economical way. Images, as they reach the retina, are not simply memorized point by point, but are analysed by a plethora of invariance mechanisms that enable the organism to recognize the same object under different conditions, e.g. under dimmer or brighter illumination, at a larger or shorter distance, when rotated or partially occluded (Sutherland 1968, 1969; Shephard & Metzler 1971; Bundesen & Larsen 1975; Ingle 1978; Holland & Delius 1983; Schwartz *et al.* 1983; Perrett *et al.* 1985; Rolls & Baylis 1986; Cerella 1990; Sary *et al.* 1993). These invariance mechanisms providing form constancy require generalizations across broad ranges of parameter values. They must have been added and perfected step by step during phylogeny. Some basic properties, however, of insect and mammalian pattern vision are very similar (O'Carroll 1993; Srinivasan *et al.* 1993, 1994). By studying visual perception in lower animals, it may be easier to separate fundamental mechanisms from the more advanced processes generating invariances. The investigation of small visual systems can teach us new algorithms of visual processing and their possible implementation in both nature and machines. Moreover, they provide insight into the ecological requirements of visual functions.

Several aspects of the insect visual system are understood to some extent, e.g. movement perception (Hassenstein & Reichardt 1956; Buchner 1984; Egelhaaf & Borst 1993), figure–ground discrimination (Egelhaaf 1985) and visual course control (Götz 1980; Wolf & Heisenberg 1990; Heisenberg & Wolf 1984, 1988, 1993). While most of these studies have been in flies, visual pattern recognition, in contrast, has been a domain of honeybees (for reviews see: Wehner 1981; Gould 1990). Only a few investigations on Diptera are available in the literature: Mimura (1982) reported specific preferences for differently oriented bars and star-like patterns in *Drosophila* and found that photoreceptor cells R1–R6 are major contributors to this performance. With *Musca* at the torque compensator Reichardt & Guo (1986) proposed a network explaining most of their data on spontaneous pattern preferences. These as well as other studies (Reichardt 1972; Wehner 1972*a*; Pick 1976; Horn 1978) did not deal with visual memory. Until recently the major obstacle for research on pattern vision in Diptera was the lack of appropriate learning experiments. The discovery of pattern avoidance conditioning at the torque meter (Wolf & Heisenberg 1991) focused our interest on the storage and recognition of images.

We first concentrated on the question of position invariance (Dill *et al.* 1993), a problem especially adequate for investigations at the torque meter because the spatial relations between the tethered fly and its visual surround are under complete experimental control. It was shown that flies remember the position of stimuli in the visual field and are able to distinguish two identical patterns by their coordinates in space. Displacement experiments revealed that position information is not only sufficient but also necessary for recognition of a learned pattern, since stimuli learned at one height during the avoidance training are not distinguished any longer at a new height. This lack of

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positional transfer represents compelling evidence for the retinotopic organization of visual memory in insects as already inferred from the study of free-flying honeybees and homing ants (Cartwright & Collett 1982, 1987; Collett 1992; Wehner 1981; Wehner & Müller 1985; Antonsen & Wehner 1994). The present study further characterizes visual pattern memory in *Drosophila* and proposes a graded similarity function for what may be pattern recognition in its simplest form.

MATERIAL AND METHODS

Two to six day old female *Drosophila* flies are reared on standard medium under a 16 h–8 h light–dark cycle in an environmental room (25 °C, 60% humidity). One day before experiments a silver wire (50 μm in diameter) is fixed between thorax and head by a UV-sensitive glue (Loctite). Until the beginning of the experiment, animals are kept separate on a wet filter in little tubes in the environmental room.

Flies are attached to a torque meter by the silver wire (Götz 1964; Heisenberg & Wolf 1984, 1988). Intended turning manoeuvres can be measured on-line and are used to steer the rotations of a surrounding arena in a negative feedback loop simulating free flight in a horizontal plane (flight simulator; Reichardt & Wenking 1969; Heisenberg & Wolf 1979, 1993). The arena is illuminated homogeneously from behind with a mean luminance of $I = 10$ cd m^{-2}.

Visual patterns are cut from a self-adhesive foil (Alcor black for 98%, Letraton LT286 for 70% contrast) and are attached to a flexible plastic sheet. Patterns for the experiments in figure 5*b* are designed by a graphics program (Harvard Graphics) and printed on overhead transparencies by a laser printer HP Laserjet 4L. Pattern and background show 40 and 70% transmittance, respectively, leading to a contrast of about 40%. (Contrasts are verified by a Beckman DU-40 spectrophotometer.) All triangles are equilateral and measure 40°, 30°: (figure 6) or 20° (figure 7) in height. In figure 8 edges of squares measure 20° in length.

Two conditioning paradigms at the torque meter are available for studying pattern vision. They differ only in the training procedure. The first, using heat as reinforcer (figure 1), has been described in detail (Wolf & Heisenberg 1991; Dill *et al.* 1993). The fly flies in the flight simulator mode. The arena carries two pairs of patterns, with identical patterns in opposite quadrants. Heat is switched on by the computer whenever one pattern is in the frontal quadrant of the fly's visual field, and is switched off when the other pattern moves into that region. After 4 min of training the heat source is switched off to test the fly's pattern preference. Flight traces are stored in a computer and used later to calculate learning success as a performance index $PI_A = (t_1 - t_2)/(t_1 + t_2)$, representing the relative times spent in quadrants previously associated with the presence (t_2) or absence (t_1) of heat. Repeat of the training-test sequence normally leads to an increase of the performance index (Wolf & Heisenberg 1991; Dill *et al.* 1993). At the beginning of every test period the arena is randomized by a 1 s rotation at a random velocity greater than 128 deg s^{-1}. Six minutes of unreinforced flight precedes the first training in experiments in figure 5*a*, *b* to control for spontaneous pattern preferences and to familiarize the flies with the artificial flight situation.

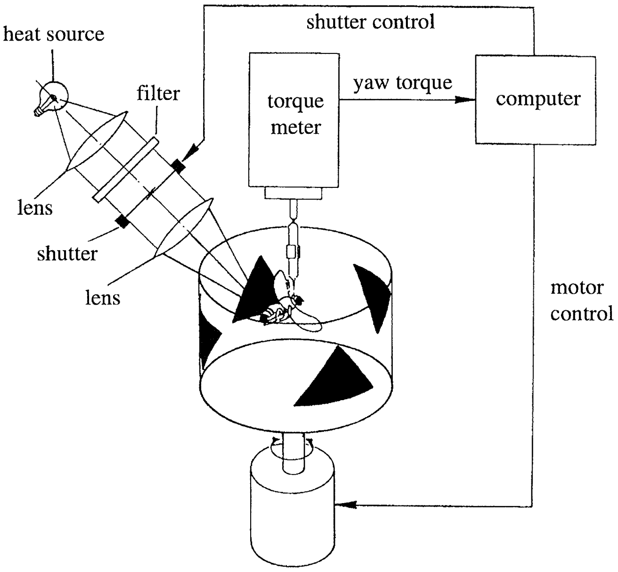

Figure 1. Avoidance conditioning set-up. The fly is tethered to a torque meter transducing the animal's yaw torque into a direct current voltage which can be used to control the angular velocity of a surrounding arena (coupling coefficient $k = 11$ deg (s 10^{-10} N m)$^{-1}$). The wall of the cylinder can be covered by arbitrary figures, in this case two pairs of triangles in different orientations, with identical figures in opposing quadrants. As negative reinforcer the light of a microscope lamp (Zeiss, 6 V, 15 W) is focused on the fly by a lens system unless intercepted by a computer-controlled shutter. Visible wavelengths of the spectrum are removed by an infrared filter (Schott RG780, 3 mm). During training the shutter is open, i.e. the fly is heated, as long as one pattern type is in the frontal quadrant of the visual field. It is closed, however, as soon as the other pattern type enters the frontal quadrant. For further details see Wolf & Heisenberg (1991), Dill *et al.* (1993) and Materials and methods.

In the second paradigm the fly's preference for a novel pattern as compared with one just seen is exploited (figure 2). The fly again is flying in the flight simulator, this time without any obvious reinforcement. Training lasts 1 or 10 min in the experiments of figures 2, 3 and 8, and 18 min in the experiments of figures 4, 6 and 7. The arena displays four identical patterns. For the subsequent test two (or all four) of the training patterns are exchanged manually for new ones. While the patterns are exchanged, which takes about 45 s, the fly remains in the arena with homogeneous background illumination. The arena then is randomized as above and the fly is tested for 2 min for its preferences for the new or previously seen patterns. The PI_N (calculated as above, but with t_1 the time in front of the novel pattern and t_2 the time in front of the known pattern) in this experiment reaches positive values if the novel patterns are preferred. In all experiments (except for the experiments shown in figures 7*a*–*d* and 8, where training has only been done with large triangles) data for both transfer directions (e.g. large to small and small to large) and both triangle orientations are pooled. Unless stated otherwise, the subgroups were not different from each other.

For replay experiments a first animal is tested in the flight simulator as described above. Its flight trace is recorded by a computer and stored on hard disk. For a second animal the positional data of this master file is used as a reference for computer-controlled rotations of the arena. Thereby the flight of the master fly is played back at the replay fly that itself is not able to control the movements of the arena by its own yaw torque manoeuvres (for details of replay experiments see also Heisenberg & Wolf (1988) and Wolf & Heisenberg (1991)).

Bars in figures 2–8 represent the mean performance indices and standard errors during 2 min intervals of flight of *n* flies. Data are evaluated by either of two statistical methods. To test for significant differences from zero individual indices are transformed (arcsine) to normality and subsequently subjected to a two-tailed *t*-test. A comparison between two experimental groups, e.g. transfer and control animals, is achieved by a *u*-test from Wilcoxon, Mann and Whitney (Sachs 1974). Correlations are determined by calculating a correlation coefficient according to Pearson (Sachs 1974).

RESULTS

(*a*) *Novelty choice, a new visual learning paradigm*

In avoidance conditioning (Wolf & Heisenberg 1991; Dill *et al.* 1993) the heat can be detrimental for poorly avoiding flies. Therefore, a new learning procedure without heat has been developed that relies on the fly's preference for new patterns to previously viewed ones. After a short exposure to four identical geometrical figures in the flight simulator the transparency in the arena is exchanged for one with two alternating pattern types of which one is new and the other is identical to the conditioning figure. In the subsequent choice test *Drosophila* shows a preference for the new pattern (figure 2).

Novelty choice is pronounced after 10 min of training with a preference index PI_N comparable in height with that obtained in avoidance conditioning. A significant although somewhat smaller preference index is already obtained after a 1 min exposure to the conditioning figure (figure 3*a*). A control with four identical new patterns in the test shows the absence of any artificial effects independent of the patterns (figure 3*b*). Interestingly, novelty choice is also observed after *replay* training (figure 3*c*). In this experiment the yaw torque manoeuvres of a different fly in the flight simulator are recorded and are subsequently displayed to the experimental animal under open-loop conditions. The fly has no control of the pattern movements. In other words, novelty choice is not an operant learning paradigm. This distinguishes it from avoidance conditioning which has clearly been shown to depend on the fly's own control of pattern motion during the training (Wolf & Heisenberg 1991; Dill *et al.* 1992). The exact movements and positions of the patterns during training seem to be of minor importance as shown by the comparison of individual pairs of master and replay animals. Although both flies receive the same visual input, their preference indices are not correlated ($r = 0.01, p > 0.2$). Central processes or predispositions seem to dominate individual performance.

(*b*) *No position invariance in pattern memory*

Obviously, the fly has to recognize the previously viewed pattern to distinguish it from the new one if it is to display novelty choice. Moreover, for the recognition process it needs a memory template. In the following, novelty choice is used to study pattern memory. The first problem to be addressed is that of position invariance.

Retinal transfer in visual pattern memory has frequently been studied (see, for example: Myers 1955; Muntz 1963; Cronley-Dillon *et al.* 1966; Cerella 1990; Nazir & O'Regen 1990; Biederman & Cooper 1991; for insects, Wehner 1972*b*). In most experiments with freely moving animals, however, it is difficult to decide whether a pattern memorized with one part of the retina can be recognized by a different one. Owing to

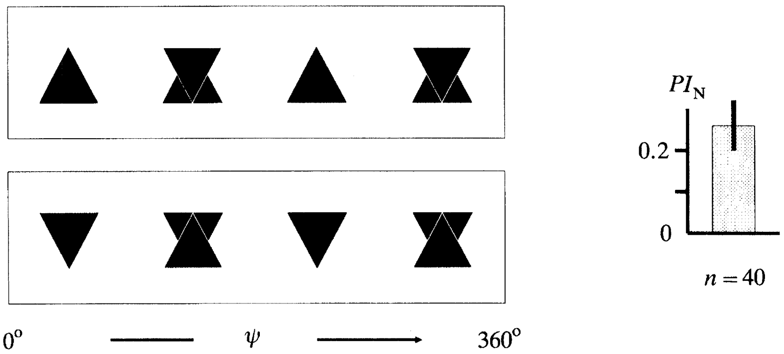

Figure 2. Novelty choice. The same apparatus is used as in avoidance conditioning except that no reinforcement is given. During 10 min of training four identical black triangles, centred in the four quadrants of the arena, are presented to the fly. During the subsequent test two opposing triangles are exchanged by identical figures in a new orientation. The new patterns are significantly preferred ($t = 4.02$, $p < 0.001$). In this and all following experiments half of the flies are trained with triangles oriented base down (upper panel), the other half with triangles rotated by 60° (base up, lower panel). In most figures only one quadrant and one orientation of training and test patterns are shown.

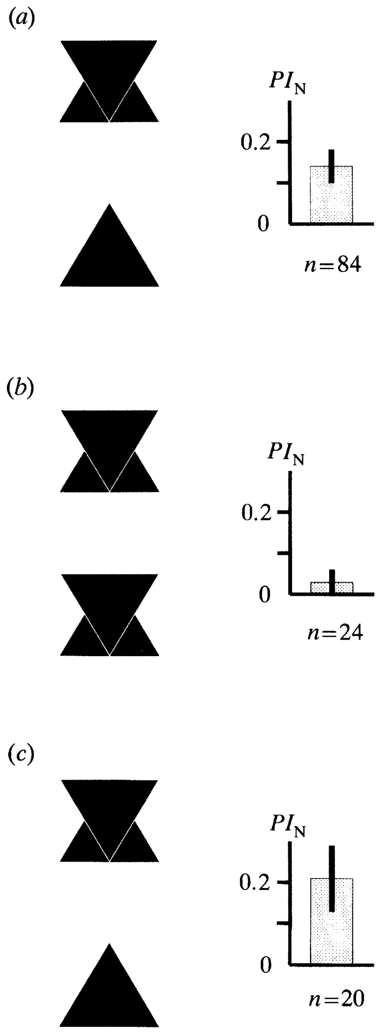

Figure 3. Control experiments. (*a*) Same experiment as in figure 2 except for shorter (1 min) training period ($t = 3.85$, $p < 0.001$). (*b*) Four identical new patterns do not lead to a significant preference index (training period 1 min, $t = 0.91$, $p > 0.1$). (*c*) The training periods of 20 animals from the experiment of figure 2 are played back after 10 min with the identical sequence of relative pattern positions to 20 naive flies in open loop (see Material and methods). The bar shows the preference index during a subsequent choice test in closed loop ($t = 2.60$, $p < 0.05$).

the special situation of tethered flight at the torque meter, position invariance can be rigorously tested in *Drosophila*. The animal is fixed in space; its head is glued to the thorax and, hence, also immobilized. In the flight simulator the patterns in the arena can be moved by the fly to the left or to the right, but not vertically. Every pattern, therefore, can only stimulate a subset of visual elements oriented towards the corresponding heights in the arena.

Using avoidance conditioning we recently demonstrated that training at one height and displacement of the patterns to a new height in the test does not lead to a significant transfer effect, even for displacements as small as 9° (Dill *et al.* 1993). To ensure that this finding is not specific to heat avoidance conditioning but reflects a general property of *Drosophila* pattern memory we did a similar displacement experiment using novelty choice. Flies are trained for 18 min to four identical triangles in the flight simulator. Subsequently a new pattern transparency is inserted showing two triangles of the already known type and two in a new orientation. For one group of animals all four patterns are displaced vertically by 10°, while a second group views the test patterns at the same height as during training. Half the animals are trained with either of the two orientations and either of the two heights. Thus, a total of eight groups of animals is formed, ruling out pattern preferences and height-specific effects. The results are the same as in the corresponding heat conditioning experiment. Whereas the control flies viewing the test patterns at the same height as during training display novelty choice at a similar level as in the standard experiment (figure 2), animals seem not to recognize the training figure if during the test the patterns are presented at a new vertical position (figure 4). Thus, like in avoidance conditioning flies give no indication of position invariance of their pattern memory.

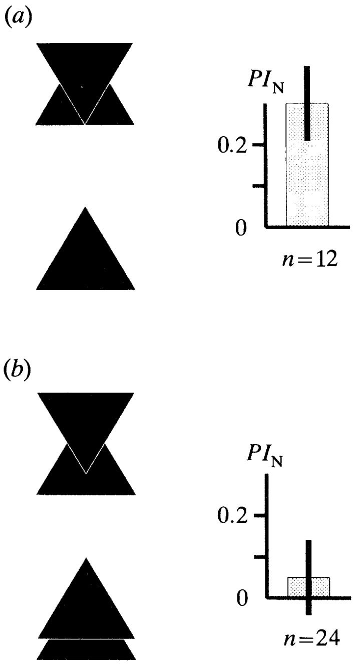

Figure 4. Displacement experiment. Half the animals are trained with the four identical triangles centred at the equator, the second half with the triangles centred at 10° above the equator. For half the animals in each group (*b*) the four types of patterns (training triangle base down or base up; at or above equator) are displaced between training and test to the other respective height. The other half of the flies in each group serves as a control (*a*). For them the four types of patterns are presented at the same height during training and test. While the control group is significantly different from zero ($t = 2.94$, $p < 0.05$), displacement animals do not show a reliable mean after-effect ($t = 0.50$, $p > 0.2$). The four subgroups (upward and downward displacement, training triangle base down or base up) show distinguishable, though not yet statistically significant, performance indices ($n = 6$ for each of the four groups) which are in qualitative accordance with retinotopic template matching (see Discussion and figure 9).

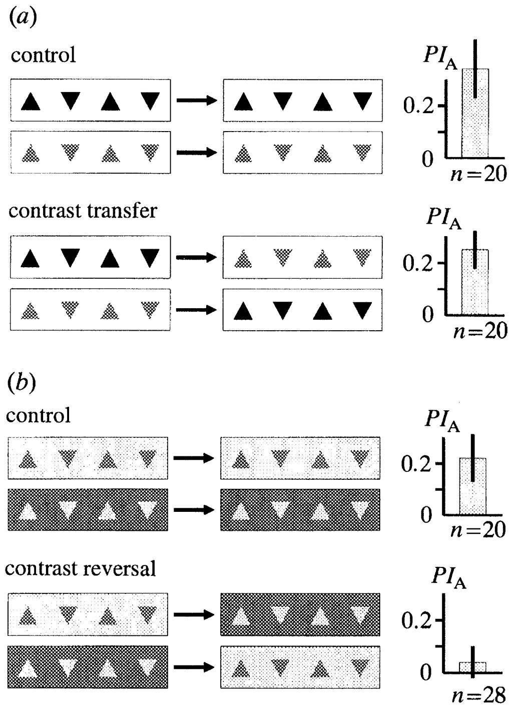

Figure 5. Contrast transfer experiments. (*a*) Flies are trained in the avoidance conditioning paradigm as described in Material and methods. Only the results of the 2 min test periods are shown. Both performance indices are significantly different from zero (control $t = 3.17$, $p < 0.01$; transfer $t = 3.09$, $p < 0.01$). (*b*) After contrast reversal the performance index is significantly different from controls ($u = 97, p < 0.05$). In both experiments the avoidance scores during training of control and transfer groups are not distinguishable.

(*c*) ***Partial contrast invariance***

If trained in the avoidance paradigm with black triangles (98 % contrast) and tested with grey patterns of 70 % contrast (or vice versa), flies still distinguish heat-associated and 'safe' orientations with respect to the triangles (figure 5*a*). The PI_A in the transfer test is not significantly different from that obtained without a change in contrast between training and test. In the novelty choice paradigm the PI_N after a change in contrast is clearly reduced as compared with the controls (data not shown), but still significant ($PI_N = 0.13 \pm 0.05$, $n = 20$, $t = 2.35$, $p < 0.05$).

Interestingly, there seems to be no transfer if a 40 % contrast is completely reversed (figure 5*b*). The internal representation of the triangles, therefore, is not independent of brightness levels as would be expected if shapes were predominantly defined by their contours. On the contrary, the contrast transfer observed in figure 5*a* and in the corresponding novelty choice experiment may simply reflect a graded similarity function (see below) rather than a special mechanism transforming figures into contour line images.

(*d*) ***Partial size invariance***

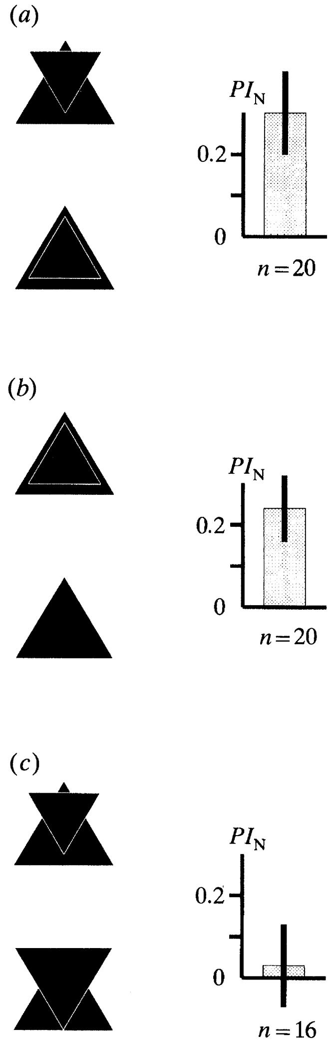

Figure 6. Limited size transfer in the novelty choice experiment. (*a*) Reduction/enlargement of the triangles between training and test. Transfer is significant ($t = 2.89$, $p < 0.01$). (*b*) Training as in (*a*), but in the test triangles of the same orientation and differing in size are presented. Flies show a significant preference for the new size ($t = 2.79$, $p < 0.05$). (*c*) The size novelty effect is not obtained after rotation by 60° ($t = 0.26, p > 0.1$). In experiments (*b*) and (*c*) the performance index shows a bias for larger patterns. In (*b*) this is superimposed by the novelty effect.

Landmarks used for orientation appear smaller on the retina of the fly when seen at a larger distance and increase in size during the approach. To identify these sites independently of distance *Drosophila*, like honeybees (Horridge *et al.* 1992*a*), might be expected to possess mechanisms generating size invariance. Indeed, limited size invariance can be observed at the torque meter.

After being trained in the novelty choice paradigm with triangles of a certain size and orientation, flies in the subsequent test with triangles in two orientations prefer the new patterns to the ones already seen, even if both patterns, the new and the old, differ in size from the training figure (figure 6*a*). The transfer is nearly perfect, although the area of the small shapes comprises only 56 % of the large triangles. The PI_N is about the same for both transfer directions.

This result would be trivial if the sizes were too similar to be discriminated or to be stored differentially. That this is not the case can be shown by training the flies as above and testing them with patterns of the

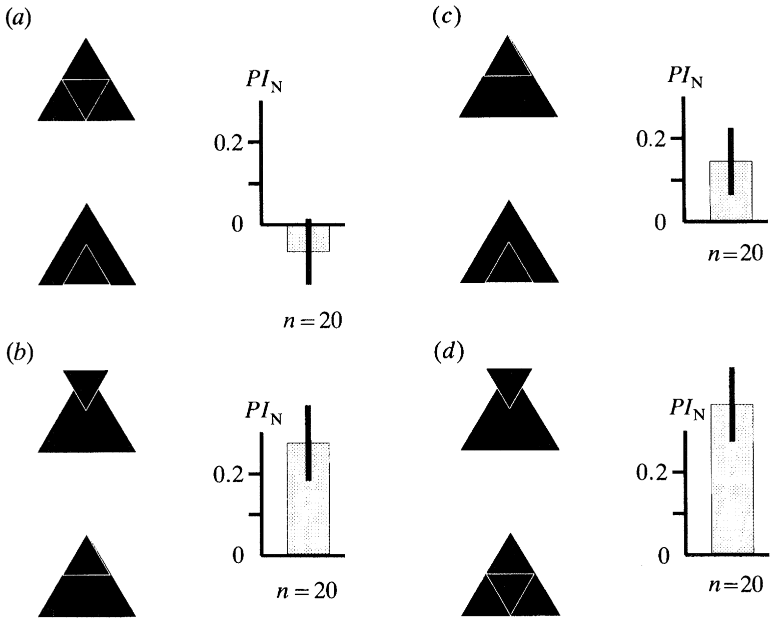

Figure 7. No evaluation of shape. (*a*) No preference is observed for the small triangle in the new orientation ($t = 0.84$, $p > 0.1$) as long as both test patterns fit completely into the training triangle. (*b*) In contrast, the small test triangle in the new orientation is preferred if it is presented at a height at which it protrudes from the template under conditions of optimal fit ($t = 3.05$, $p < 0.01$). (*c*, *d*) The same rule applies for test triangles that have the same orientation but are presented at different heights ((*c*) $t = 1.80, p < 0.1$; (*d*) $t = 4.02, p < 0.001$). The slight preference in (*c*) might depend on spontaneous preferences in one experimental group.

same orientations as used in the training, but differing in size. Under these conditions flies prefer the new size to the old one, which indicates that the difference is big enough to be recognized and memorized (figure 6*b*). Note that the same pattern is judged either familiar or unfamiliar after identical training, depending on pattern context (see for example figure 6*a*, *b*). Thus, pattern similarity is not an all-or-none function. Moreover, the PI_N is a nonlinear representation of the internal similarity function.

It can be argued that in the experiment of figure 6*b* absolute sizes might be evaluated without any reference to patterns. This hypothesis is tested in an additional control experiment. The same training procedure and the same test patterns (triangles) are used as before but now the patterns are rotated by 60° before the test. No preference for the new size can be detected (figure 6*c*). This result not only disproves that it is absolute size that is remembered; it excludes at the same time substantial rotational transfer. If *Drosophila* pattern memory was invariant for pattern rotations of as much as 60° the fly would still be able to recognize by its size the pattern seen before and show a preference for the less familiar size.

To probe the limits of the observed size transfer we choose even smaller triangles in the test. Now the triangles measure only a quarter of the area of the training figure and, what is most important, are presented at two different heights. At one height both orientations can be fitted equally well into the training patterns. Under these conditions no novelty effect is obtained (figure 7*a*). At a different height, however, at which one of the patterns cannot fully be fitted into the template, this triangle is regarded as novel and is clearly preferred (figure 7*b*). Even more surprising, a similar effect is obtained with small triangles of identical size, shape and orientation, but presented at different heights. Triangles that under conditions of optimal fit still protrude from the putative memory template are preferred to triangles that completely fit into the template (figure 7*d*). Again, if both triangles fit (figure 7*c*), there is only a small and hardly significant aftereffect, which might be explained by a spontaneous pattern preference in one of the two experimental groups.

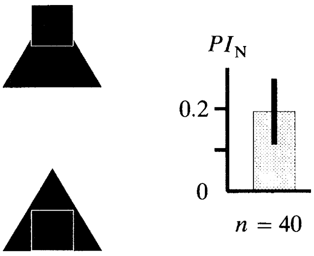

Figure 8. Transfer from triangle to square. Flies are trained with a large triangle but tested with two identical squares presented at different heights. They significantly prefer the squares protruding from the triangular template ($t = 2.49$, $p < 0.05$).

The familiarity of some of the small triangles in the experiments of figure 7 cannot be explained by a special size invariance mechanism but seems to be related to the degree of overlap between the test figure and the putative memory template under conditions of optimal fit. The orientation of the triangles seems to be of little relevance for the familiarity or novelty as long as both test figures are completely covered by the training figure under optimal fit conditions. If this conclusion is correct it should not even matter whether triangles or other shapes are used as test patterns. In the experiment of figure 8 flies are trained for 1 min with four identical large triangles. For the test the transparency is exchanged for one displaying four small squares at two different heights. The square at one height fits completely into the triangular template, at the other it protrudes from it by about 40%. Flies show a clear preference for the protruding square. The novelty of the geometrical shape in the non-protruding square seems to interfere little if at all with its familiarity.

DISCUSSION

We have used avoidance conditioning and the newly developed novelty choice paradigm in *Drosophila* to study one particular aspect of visual pattern memory: the similarity of patterns. The flight simulator is particularly well suited to investigate this question since it provides complete control of the visual stimuli as they reach the eyes of the fly. Before turning to the problem of similarity of patterns we shall briefly discuss the new learning paradigm, novelty choice, by which we study it.

(*a*) *Novelty choice, a new learning paradigm*

The observed preference of new to familiar patterns (novelty choice) can be classified by analogy to humans as incidental learning (Catania 1992). It is formally comparable to similar learning performances in vertebrates (Thinus-Blanc & Foreman 1993; Wilson & Rolls 1993) and newborn infants (see, for example, Peterzell 1993). It differs from avoidance conditioning in that no apparent reinforcer is required.

On the other hand, this may be a superficial distinction. We cannot exclude that the artificial experimental conditions in the flight simulator constitute a sufficiently negative reinforcement to give the training pattern a disadvantage in the subsequent choice test. After all, being tethered deprives flies of much of the regular sensory and proprioceptive input which must be an alarming experience. Moreover, the flight simulator provides imperfect and unnatural visual feedback conditions (Heisenberg & Wolf 1993) and it is known that open-loop pattern motion, indeed, can act as a strong negative reinforcer (R. Wolf, personal communication). Finally, in the flight simulator the flies never reach the patterns they try to approach. This again may lead to stress and frustration. Whether flies do display some sort of curiosity or whether they associate the training pattern with a negative experience remains to be investigated. Alternatively, non-associative learning (habituation; Thompson & Spencer 1966) would explain the effect as well.

For various reasons novelty choice is not attributable to fatigue or sensory adaptation at the level of the eye or lamina. A peripheral adaptation process could hardly be specific for one particular pattern. The unfamiliar pattern is still significantly preferred 5 min after a 1 min training (data not shown). In the zone of the visual field in which the patterns move, local brightness levels continually switch between black and white. The shapes of the figures at this level lead to particular phase relations between the changes in the receptors and do not affect their mean level of adaptation.

A further result emphasizing the importance of central processes (as opposed to peripheral adaptation) is the observation that the correlation between the learning success of master and replay flies is very low. Although the two flies of a pair receive identical visual inputs and although both groups show similar mean learning scores, the master and respective replay flies are entirely independent in their test preferences. Internal states must be more important for the individual test performances than the temporal sequence of the visual input to the photoreceptors.

(*b*) *No special invariance mechanisms in novelty choice*

To summarize the visual pattern recognition results, we observe no special pattern invariance mechanisms in this test situation. Variations of retinal position, contrast, size and orientation (rotation) abolish recognition. This also applies to the heat avoidance paradigm for changing position and reversing contrast. Thus, under the conditions of novelty choice, visual pattern recognition seems to be a simple process. First, the system has to optimize the fit between the memory template and the actual image by moving and turning in space. Once the optimal fit is found a similarity value is calculated. This may be, for instance, the relative degree of overlap of the actual image with the template (figure 9). In novelty choice, the pattern giving the lower similarity value is preferred.

The reader surely has noticed that small variations of contrast, size and retinal position (Dill *et al.* 1993) are tolerated by the recognition process. Although they are large enough to be detectable for the fly, this limited transfer can be explained without recourse to special invariance mechanisms if one assumes that matching between memory template and actual image is not an all-or-none process but is graded implying that the similarity does not drop to zero at the slightest detectable difference between the template and the actual image. 'To recognize' in common language is used as a qualitative term. Someone or something is recognized, or it is not. In template matching as described here a step function for similarity would be of limited use because it would make retrieval exceedingly difficult.

Quantitative descriptions of the similarity function (*sf*) have been proposed more than 20 years ago (Cruse 1972, 1974; Anderson 1977) and other variants can easily be designed (figure 9). Although so far we have not made a systematic attempt to measure the function it is obvious from our few data that most of these equations do not even qualitatively account for them. As an arbitrary example, in figure 9*d* (left panel) the observed performance indices (PI_N) are compared with ones (PI_T) calculated on the base of a similarity function that is the ratio of overlap to the memory template ($sf = Q/(Q+T)$). No significant correlation is observed.

To our surprise, a similarity function proportional to

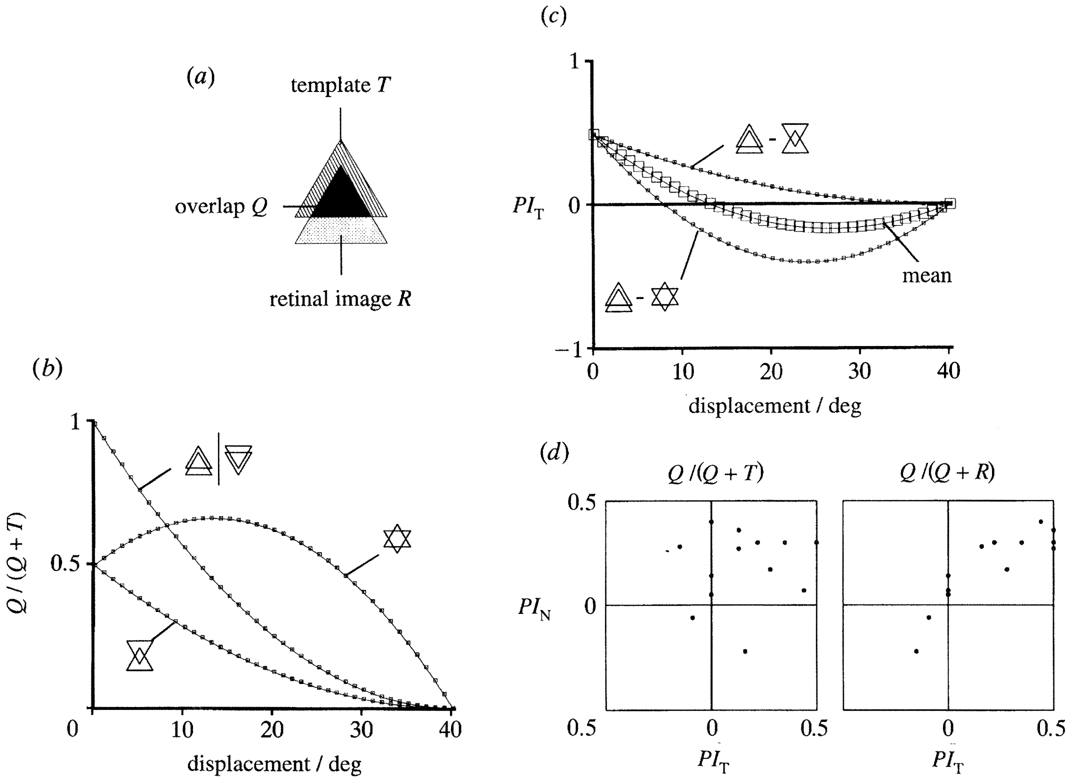

Figure 9. Similarity functions. (*a*) Definition of terms. Schematic drawing of overlapping area Q and the remaining parts R and T of retinal image $(R+Q)$ and memory template $(T+Q)$, respectively. (*b*) Area of overlap relative to area of figure ($Q/(Q+T)$ or $Q/(Q+R)$) for vertical displacement. The four possible permutations for relative pattern orientations and directions of displacement (o–d variants) yield three different overlap functions. (*c*) Since in each test the fly has to choose between two similarity values, the theoretical preference index PI_T for each displacement is obtained by subtracting the two respective overlap values. The four o–d variants thus lead to two partial PI_T functions (⊡). The final PI_T function (□) represents the theoretical mean for the two subgroups. (*d*) Comparison of theoretical and experimental preference indices. All novelty choice data with 18 min training are included (figures 4, 6 and 7). Every point represents the mean of 8–20 animals (total $n = 172$). Individual performance indices PI_N correlate well with PI_T for $sf = Q/(Q+R)$ (right panel, $r = 0.34$, $p < 0.001$), but not, however, for $sf = Q/(Q+T)$ (left panel, $r = 0.08$, $p > 0.2$).

the ratio of the area of overlap to the area of the actual retinal image ($sf = Q/(Q+R)$; figure 9*d*, right panel) provides a highly significant correlation between the observed and calculated performance indices in novelty choice. Comparison of the part of the retinal image that had been stimulated before with the retinal image itself may be the simplest possible way to judge the novelty of a figure.

However, as figure 9*d* (right panel) shows, even the equation $sf = Q/(Q+R)$ does not predict novelty preferences quantitatively. One difficulty is that in the choice test we can observe only the difference between two similarity values. Interactions between the two test patterns might distort the similarity function. Alternatively, behavioural processes like selective attention could amplify small differences between similarity values. Additionally, test indices higher than 0.4 have hardly ever been observed in this paradigm, suggesting some kind of clipping effect. The performance in heat avoidance learning, finally, may even be explained by a different similarity function.

The complete absence of special invariance mechanisms in the novelty choice paradigm comes as a surprise. The usefulness of visual pattern recognition for orientation in free flight should critically depend upon such mechanisms. The relative contrast of objects changes with varying conditions of illumination such as the moving sun and clouds. The retinal size of objects varies with distance; their orientation on the retina rotates during banking turns and precise retinal position in the real world is difficult to match. To a limited extent the graded similarity function makes up for this total lack of invariance mechanisms. It must reduce but certainly does not solve the matching problem in free flight.

As it seems, insects have evolved elaborate behavioural strategies to cope with the difficulty of finding the match. At their first departure from the hive bees must turn around and take a close look at the hive from the position of an arriving bee in order to later recognize the entrance upon return (Lehrer 1993). Recently Collett & Baron (1994) have observed that their Sussex bees, which are trained to locate a food source by a nearby landmark, approach the foraging site always facing south. Evidently, behavioural strategies like this one can immensely facilitate the matching process.

Our contrast reversal data indicate that the memory template must represent the relative brightness values of pattern and background in the memorized image (template). This implies that patterns are not stored as 'line drawings', as has been suggested on the basis of the transfer properties of lamina monopolar neurons in large flies (Laughlin 1987). Training honeybees with random gratings van Hateren *et al.* (1990) have shown that bees can transfer 'orientation of edges' to patterns of completely different brightness distribution. O'Carroll (1993, 1994) has recorded cells in the lobula of dragonflies and recently Diptera showing specific sensitivity for the orientation of edges. It has not yet been shown whether these cells are, indeed, involved in pattern recognition, but what is clear is that with respect to invariance mechanisms other insects seem to be doing better than *Drosophila*. Is the visual system of *Drosophila* more primitive than that of other insects?

Perhaps the missing invariances are not a species property of the fly but a consequence of the restricted behavioural situation in the flight simulator where only a single degree of freedom, turning around the vertical body axis, is provided artifically. Successful transfer tests with insects have been obtained with freely moving animals and extensive training (see, for example: Wehner 1972*b*; Ronacher 1979; Horridge *et al.* 1992*a*, *b*). Insects might be able to generalize a certain pattern property only by comparing several related memory templates in which this property varies. Our experiments were not designed to detect such generalizations.

(*c*) *Concluding remarks*

Retinotopic template matching as revealed by *Drosophila* at the torque meter is a close approximation to the minimal model of visual pattern recognition. (The only further reduction would be a replacement of the graded similarity function by a step function.) Even the minimal model as described here poses formidable problems concerning its realization in the fly. How is the template inscribed? Is it a static 'snapshot' like a photograph? Or is it the output of an array of local movement detectors during a special turning movement? In flight the visual scenery never stands still. Is the whole visual field stored or only a small fraction of it? Which mechanism selects time and space for the snapshot? How many images can a fly store? Does it extract invariances from a comparison of several templates? Does it take several snapshots with different spatial frequency filters of the same scenery (Cartwright & Collett 1987; Collet & Kelber 1988)? Finally, where in the brain are these templates stored? This list could easily be extended. Additional problems regarding the matching process have been mentioned above.

If retinotopic template matching is the minimal model of visual pattern recognition, as we do believe, it is tempting to speculate that it is also the phylogenetically oldest one. Given the severe limitations of such a system more complex systems must have gradually evolved by adding better invariance mechanisms and improving the storage economy. Functional dissection of complex visual systems should pursue the evolutionary route.

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