Behavioral Analysis of *Drosophila* Landmark Learning in the Flight Simulator

Marcus Dill, Reinhard Wolf, and Martin Heisenberg¹

Theodor-Boveri-Institut für Biowissenschaften
Lehrstuhl für Genetik
Am Hubland
D-97074 Würzburg, Germany

Abstract

***Drosophila* flies can be trained in the flight simulator to operantly avoid heat by choosing certain orientations relative to landmarks. Flies primarily store pattern orientations associated with the absence of heat. They readily escape from heat-associated orientations under the direct influence of the reinforcer but not in the subsequent memory tests. The flies tend to keep the largest possible distance from the "hot" or potentially "hot" regions, that is, they head toward the center of the "cold" sector. The results are discussed in the light of the retinotopic matching model explaining visual memory in flies by the superposition of a retinotopically stored template with the actual retinal image. Window experiments confining visual feedback to two 90° sectors indicate that the memory template covers most of the visible space.**

Introduction

In most conditioning paradigms with freely moving animals, defining the relevant behavior involves long series of experiments (for review, see e.g., Rescorla and Holland 1982; Catania 1992). To partially overcome this problem it is necessary to restrict the animal's behavioral options and precisely register its actions and reactions. A paradigm that nicely fits these requirements of being both complex and controllable is the visual avoidance conditioning of individual tethered *Droso-*

phila flies in the flight simulator (Wolf and Heisenberg 1991). The yaw torque of a fly is monitored on-line and is made to control the angular velocity of a surrounding arena, thus leading to the simulation of the animal's turning movements around its vertical body axis. In this simulation *Drosophila* can choose between different flight directions relative to visual stimuli displayed at the arena wall. As a reinforcement the fly is irradiated by infrared light whenever it is heading toward one of two pattern types. After a few minutes of training the animals strongly avoid those flight directions relative to the patterns that are associated with heat. The effect has been shown to be operant (Wolf and Heisenberg 1991), although flies with training experience can also be conditioned classically (Dill et al. 1993a).

The controllability and complete record of both the sensory input and the flight traces make this paradigm especially valuable for detailed investigations of the interplay between sensory and motor processes in visual pattern recognition. In this and a related learning paradigm, depending on a preference for novel stimuli (Dill and Heisenberg 1995), it has been shown that landmark memory relies on retinotopic matching (Dill et al. 1993b; Dill and Heisenberg 1995). For recognition flies seem not to use any special invariance mechanisms of position, contrast, size, or rotation but, instead, measure similarities between a stored template and the retinal image by comparing their overlapping and total areas (Dill and Heisenberg 1995).

In the retinotopic matching model, formation and recognition of the template places high demands on flight strategies. This is most notable in free flight (Collett and Cartwright 1983), but even in the flight simulator with only one degree of freedom of motion, understanding the processes of storage and retrieval requires a detailed characterization of the underlying microbehavior. In the

¹Corresponding author.

present study we further specify what the fly learns and remembers in visual avoidance conditioning. We show that (1) it remembers only non-reinforced pattern orientations, (2) it prefers flight directions that are the farthest away from the heated zones, and (3) its memory templates comprise most of the visual field.

Material and Methods

EXPERIMENTAL PROCEDURES

Drosophila melanogaster flies are reared on standard cornmeal-molasses medium under a 16 hr light/8 hr dark cycle in an environmental room (25°C, 60% humidity). For experiments female flies are prepared at the age of 2–4 days. A triangle-shaped silver wire (diam. 50 μm) is attached to their head and thorax by a UV-sensitive glue. Until the beginning of the experiment, at least 4 hr later, individual animals are kept on wet filter paper in little chambers with a few grains of sugar.

For recording, the fly is connected by the silver wire to a torque meter (Götz 1964; Heisenberg and Wolf 1984) measuring intended turning maneuvers of the fly (yaw torque T). The animal is positioned in the center of a vertical cylinder illuminated from behind ($I = 10 \text{ cd/m}^2$). In the flight simulator mode (Reichardt and Wenking 1969; Heisenberg and Wolf 1979) the angular velocity of the cylinder is made proportional to the fly's yaw torque in a negative feedback loop. The fly establishes optomotor balance and can choose between different orientations relative to the visual patterns on the wall of the cylinder. Patterns typically are two pairs of equally spaced geometrical figures cut from black, self-adhesive foil (Wolf and Heisenberg 1991; Dill et al. 1993b; Dill and Heisenberg 1995; see also inset of Fig. 1) or, alternatively of quadrant-filling matrices of random black-and-white squares (angular size at equator, $12.9^\circ \times 12.9^\circ$; Fig. 2a; cf. Dill et al. 1993b) printed on overhead transparencies.

Negative reinforcement is provided by a beam of infrared light heating the fly whenever it is heading toward one quadrant type. The beam is intercepted by a computer-controlled shutter when the fly is oriented toward the alternative quadrants. The experiment consists of 4 min of operant training followed by 2 min of testing. This sequence is repeated at least once. At the beginning of each test period the orientation of the

arena is turned at high velocity to an arbitrary angular position.

EVALUATION OF DATA

Flight traces are stored in a computer, and the performance index for avoidance conditioning of individual flies is calculated as $PI_A = (t_1 - t_2) / (t_1 + t_2)$, with t_1 and t_2 being the total time spent in "cold" (t_1) and "hot" (t_2) quadrants during a 2-min period. Bars in Figures 2 and 3 represent mean and S.E.M. of n flies tested. The data were statistically tested against zero by t -tests (after arc-sine transformation, two independent groups are compared by u -tests).

For dwelling time distributions (Figs. 1 and 4a,c) the individual time periods a fly stays in a particular quadrant (dwelling times) are first sorted by type of quadrant and then by their duration. They are displayed as cumulative log-log plots (cf. Shimada et al. 1993). Every point $P_{(t,y)}$ indicates that $y\%$ of all dwelling events in that quadrant type was longer than t sec. Curves lying on the right represent longer, and those on the left shorter, dwelling times. Events shorter than 1 sec are strongly influenced by flight dynamics (Heisenberg and Wolf 1984; Wolf and Heisenberg 1988) and, therefore, are not included in the evaluation. Distributions are compared statistically by Kolmogoroff–Smirnov tests. The alternative representation of the data (Fig. 4b) is the mean of individual medians of dwelling times, and is evaluated by Wilcoxon (paired) or u -tests (unpaired). Further details and explanations of other analytic procedures are in the text and figure legends.

Results

FLIES AVOID DANGEROUS FLIGHT DIRECTIONS IN AN ARTIFICIAL SURROUNDING

For operant conditioning in the flight simulator the fly is heated whenever it is heading toward one of two pattern types on the wall of the surrounding arena (Fig. 5). After a few minutes of training the animal acquires a strong preference for the pattern type not associated with heat, even after discontinuing reinforcement. Immediate repetition of the training leads to an even stronger and highly significant aftereffect, showing that flies

Figure 1: Dwelling time distributions for experiments with geometric figures. (a) Upright and inverted black Ts (height and width 40°, stem width 10°); (b) upright and inverted solid triangles (40° height); (c) lightly and darkly shaded triangles (40° height). Data have been presented previously, where more detailed information on these experiments is given (Dill et al. 1993; Dill and Heisenberg 1995). Only the test results are shown. For half the animals (solid symbols) the stimuli were changed after training and presented during test either at a new vertical position (a, 30°, and b, 9°) or at a reversed contrast (c). Controls received the same visual input as in training (open symbols). Both manipulations prevent recognition of the learned figure. In all three experiments there are no significant differences ($P > 0.2$) between control and transfer groups with respect of the dwelling time

distributions for heat-associated figures (triangles), whereas transfer animals show largely reduced dwelling times in cold quadrants (circles) as compared to controls. This difference is, however, significant only in b ($D_{\max} = 0.16$; $P < 0.01$) and c ($D_{\max} = 0.13$; $P < 0.05$).

in the flight simulator can remember flight directions in relation to landmarks.

This experiment has been performed with four evenly spaced geometric figures (Wolf and Heisenberg 1991; Dill et al. 1993b; Dill and Heisenberg 1995) and with random matrices of the types shown in Figure 2a covering the whole wall of the arena (Dill et al. 1993b). Even the flies surrounded by random squares are able to effectively avoid heat and to distinguish (previously) hot and cold pattern orientations in subsequent tests without reinforcement (Fig. 2b).

TWO BEHAVIORAL STRATEGIES IN CONDITIONED PATTERN AVOIDANCE

In the experiment of Figure 2b, training and test are repeated four times. The performance index during training starts at $PI_A = 0.5$ and goes up

to $PI_A = 0.75$, whereas the learning score reaches a plateau slightly above $PI_A = 0.3$. To understand this discrepancy between nearly complete heat avoidance and moderate pattern preference, we analyzed the flight traces in more detail. They were segmented into so-called dwelling events, that is, the time that flies spent in a particular quadrant. All dwelling events of the 32 flies of Figure 2b in each quadrant type were pooled and sorted according to their duration. Cumulative dwelling time distributions are plotted in Figure 4a. In addition, the same calculation was performed for the control experiment without reinforcement. During these control flights flies are highly active and on average stay in a quadrant for only a few seconds. During training periods, dwelling times are further diminished in the hot sectors, whereas in cold sectors they are increased as indicated by the displacement of the corresponding curves in Figure 4a (shorter dwelling times, displacement to

Figure 2: Pattern avoidance conditioning with random-square textures. (a) Eight textures used in *b*, and Figs. 3 and 6. Textures cover the whole inner wall of the arena (angular position ψ from 0° to 360°). The second half (180° to 360°) of each transparency is an exact copy of the first half (0° to 180°). The width of each field is 12.9° ; in two transparencies squares are separated by 1° blanks. (b) Repeated conditioning with random patterns. Half of the 64 flies are trained in the pattern avoidance paradigm (patterned bars), the second group (open bars) is tested for spontaneous behavior without heat. Subgroups of four animals each are conditioned with one of the eight transparencies shown in *a*. For two flies of the conditioned group, the first quadrant is heat-associated; for the other two, the second is heat-associated. Even after short training (shaded bar) the heat-associated flight directions are clearly avoided. During test (hatched bar), flies show a highly significant preference for the patterns not associated previously with heat (*t*-test for the individual means of all four tests, $t = 4.55$; $P < 0.001$). This preference cannot be explained by spontaneous behavior (*u*-test: $u = 189$; $P < 0.001$) but does not reach the training level (Wilcoxon: $R = 10.5$; $P < 0.001$).

the left; longer dwelling times, displacement to the right). This cannot only be seen at the level of the dwelling time distributions of the whole experimental group but also for the medians of individual animals (Fig. 4b). Obviously, two effects contribute to the high training performance. To avoid being heated, flies leave the hot quadrants early and stay longer in the cold ones.

To our surprise, in the test periods no escape behavior from the quadrants previously associated with heat was observed. Dwelling times immediately relax to those of untrained flies. On the other hand, the increased attraction to the previously cold quadrants is maintained at the final training level. Of the two behavioral strategies, “Get out of the heat!” and “Stay if it is not hot!,” only the latter is maintained beyond the reinforcement phase of the experiment. The former is a more acute, temporary maneuver. This point is underscored by comparing the dwelling time distributions for the four training blocks (Fig. 4c). The distributions for the hot sectors are indistinguishable from each other, indicating that the strategy *Get out of the heat!* in the first 4 min of training is as good as in the final training block. The improvement in the

Figure 3: Experiments with white screens occluding parts of the visual field. Flies were trained with the complete panorama (a), screens occluding the lateral quadrants (b), or screens preventing frontal and backward vision (c). The learning success (bars) is significant for a ($t = 2.99$; $P < 0.05$) and c ($t = 2.48$; $P < 0.05$), not however for b ($t = 0.44$; $P > 0.3$). The training scores (not shown) cannot be distinguished statistically.

Figure 4: (a) Dwelling time distributions for the data of Fig. 2b. Flight traces are segmented into periods of staying in one quadrant (dwelling times). Dwelling time distributions (see Material and Methods and text for more detail) of all flies are calculated for spontaneous controls and separately for punished and unpunished quadrants during training and test. ($\square$) Training cold; ($\circ$) test cold; (∇) training hot; (Δ) test previously hot; ($\blacksquare$) spontaneous control. Training and test distributions for cold quadrants show only slight differences (Kolmogoroff–Smirnov, $D_{\max} = 0.047$; $P < 0.1$), dwelling times in heat-associated quadrants during test are not significantly different from

spontaneous behavior (Kolmogoroff–Smirnov, $D_{\max} = 0.034$; $P > 0.2$). All other comparisons led to significance levels of $P < 0.001$. (b) Mean and S.E.M. of individual medians of dwelling times for the 32 flies of each group of Fig. 2b. Statistical analysis leads to results similar to whole distributions (training–test cold, $P > 0.2$; test in previously hot sector vs. control, $P > 0.2$. All other differences are highly reliable at $P < 0.001$). (c) Dwelling time distributions for cold (curves on the right) and hot (curves on the left) sectors during the four training periods. ($\blacksquare$) Block 1; ($\square$) block 2; ($\circ$) block 3; (∇) block 4).

training scores is entirely attributable to increasing dwelling times in the cold sectors.

To ensure that this is not a special effect of the random-dot patterns employed here, we evaluated earlier experiments with geometric figures. In every data set the attractiveness of unpunished flight directions increases upon conditioning. Differences in dwelling times between training and test are only detected for heat-associated orientations, whereas in cold sectors after switching off the reinforcement, dwelling times stay at the high level acquired during training. Especially telling are three studies (Fig. 1), where in one group, animals received normal training and test in the second group, the patterns were either displaced from their vertical position (Dill et al. 1993b; Fig. 1a,b) or inverted (Dill and Heisenberg 1995; Fig. 1c) after training. Both stimulus manipulations prevent recognition completely. Dwelling time distributions for normal and transfer tests show no significant differences for sectors associated with heat during the preceding training. The time spent in these orientations, therefore, is not influenced by the manipulation of the stimuli. However,

Figure 5: Flight simulator and setup of conditioning experiments. Detailed descriptions are contained in earlier publications (Wolf and Heisenberg 1991; Dill et al. 1993) and in the text. (TM) Torque meter; (S) computer-controlled shutter; (F) infrared filter; (L) lens; (M) motor; (C) computer.

dwelling times in cold quadrants that had increased during training (not shown) are reduced by pattern manipulations to the level of the dwelling times in the previously hot sectors (i.e., those of untrained flies). These data show that the only lasting behavioral changes in these conditioning experiments with distinct geometric figures, as with random-dot patterns, concern flight directions associated with the absence of heat.

PATTERN AVOIDANCE LEARNING REQUIRES LARGE PARTS OF THE VISUAL FIELD

The compound eyes of *Drosophila* cover ~85% of the visual sphere, omitting a vertical stripe of ~40° width in the back. There is no behavioral or physiological evidence for a fovea with increased angular resolution (for review, see Heisenberg and Wolf 1984). Although the fly might have a functional fovea necessary and sufficient for learning performance, it may also require information in wider sectors of the visual field. Finding that a certain flight direction is stored by the fly, therefore, does not tell which regions of the visual field contribute to the increase in dwelling times while the fly is in the cold orientation.

Experiments with additional screens occluding the patterns in parts of the visual field reveal that large parts of the panorama have to be visible for *Drosophila* to show a full-sized conditioning response (Fig. 3). If the fly has a 90° window in front, and a second one in the back, its learning score is not different from zero. If the two windows are positioned laterally, the animal shows a weak but significant learning performance. Training scores of the three groups are not significantly different from each other (not shown). These results make a functional fovea in the frontal part of the visual field (e.g., in the region of overlap of the two eyes) very unlikely. To the contrary, the results show that lateral parts of the visual field are sufficient for some residual pattern recognition. A wide distribution of landmarks in the visual field may actually be advantageous.

FLIES PREFER FLIGHT DIRECTIONS IN THE MIDDLE OF THE COLD QUADRANT

As shown above, despite the aversive character of conditioned pattern avoidance flies do not remember the flight directions associated with heat. Instead, the growing and lasting increase of

the dwelling times in the cold sectors strongly suggests that the flies select one or a few permissive flight directions and stay with those. The gradual stabilization of preferred orientations of individual animals reported earlier (Dill et al. 1993b) is in line with this conclusion. What the dwelling time distributions do not tell is whether flies choose any arbitrary directions in the cold sectors or whether they form some kind of spatial representation of the hot and cold regions of the panorama, and orient accordingly.

To get a first answer to this question we calculated orientation distributions from the flight traces that yielded the performance indices of Figure 2b. As these data were obtained from experiments with eight different random-dot textures (Fig. 2a) the pooled distributions do not reveal orientation preferences with respect to any features of the panorama. They do show, however, that the most attractive part of a cold sector is its center, where the animals spend more than twice as much time than near the borders to the hot areas (Fig. 6a).

To quantify the avoidance of the borders, orientation distributions are plotted relative to the side of entry into the quadrant (Fig. 6b,c). Spontaneous flight behavior leads to a function that decreases monotonously and can be simulated (not shown) with a few simple assumptions on dynamics of yaw torque (Heisenberg and Wolf 1988, 1993). During training, flies spend significantly less time in a 30° sector next to the border of entry than the untrained animals of the control group ($u = 229$; $P < 0.01$). Instead, they focus on the central part of the quadrant ($u = 250$; $P < 0.001$). Orientations close to the far border again have probabilities slightly below spontaneous. This alone indicates that the flies are not simply repelled by the heat but recognize the central part of the cold sectors. Even when heat is permanently switched off flies still avoid regions close to the previously hot sectors and prefer the center of the cold quadrant. Note the remarkable similarity of the functions for training and test. As shown above for the dwelling time distributions, here again the behavior in the cold regions does not change much after training ceases.

As demonstrated earlier, *Drosophila* relies on reafferent control of yaw torque in the flight simulator to arrive at a spatial concept of its visual surround (Heisenberg and Wolf 1984). Knowing the efficacy of its yaw torque enables the fly, for instance, to perform a 360° loop in a striped drum.

Figure 6: Orientation preferences in pattern avoidance conditioning. (a) Orientation distributions for training (□), test (○), and spontaneous controls (■) of Fig. 2. Because of the mirror symmetry of the arena, the distributions are plotted for 180° only. (b) Positional distribution relative to the side of entry into the cold quadrant. The curves are normalized to the amount of time spent in these sectors. (c) Distributions for training and test after subtracting the curve for spontaneous flight.

To find the center of the cold sector the fly seems to transform the temporal sequence of heat/no-heat periods during training into a spatial concept of hot and cold regions in the panorama. The changes in heat coincide with certain flight directions in a systematic way. This does not necessarily require pattern recognition. The fly may find the center of the cold sector also by turn integration. In the test, however, temporal information about the heat/no-heat border is no longer available. The animal, therefore, does need landmark information to retrieve “safe” flight directions.

Discussion

BE POSITIVE!

The present study is a telling example why an analysis of the behavioral performance in condi-

tioning may be important. The interpretation of what is happening in the animal is often misled by the apparent design of the experiment. Our pattern avoidance paradigm uses a strong aversive reinforcer. One might expect, therefore, that the fly improves its heat avoidance by recognizing and escaping heat-associated flight orientations. Analysis of the dwelling times shows, however, that the escape from the hot sector is a temporary response and not a lasting behavioral modification. The dwelling time distributions in the hot sector for each of the four conditioning blocks are very similar (Fig. 4c), indicating that this behavioral component does not improve in the course of the training. As quickly as it develops during heat exposure, it vanishes during test periods without heat (Fig. 4a). The difference between the dwelling time distribution during the test in the previously heat-associated sector and that of the naive

control animals is not significant. There is no indication that the flies use landmark recognition at all while being heated.

It is tempting to consider the escape from the hot sector a hard-wired response. Heat-triggered vigorous turning and thrust maneuvers might be a reliable strategy in free flight to get out of a narrow plume of hot air. Independent studies have shown, however, that in the flight simulator the fly is able to compare its actively generated behaviors with the resulting outcome and can thus try out which of the motor patterns is successful (Wolf and Heisenberg 1991). Therefore, this behavioral component may be an operant activity as well.

For the behavior in the cold sector the situation is quite different. Dwelling times increase in the course of the conditioning period and stay at the final level even after reinforcement is stopped (Figs. 1 and 4). What was designed as an aversive paradigm turns out to generate an appetitive behavior. In retrospect, this result should have been predicted: It makes no sense for the fly to memorize heat-associated pattern orientations. The fly would expose itself to the heat in each recognition process. Avoiding the punishment completely by orienting to safe quadrants is certainly more effective than just escaping from ongoing reinforcement. Moreover, because of the retinotopic organization of the landmark memory it would have to store many memory templates for all the orientations associated with heat. It is less demanding on storage capacity to store memory templates of only one or a few safe pattern orientations and stick to them once they have been retrieved. This is what we find. The fly selects certain flight directions in the cold sector and deviates from them less and less often (Dill et al. 1993b and dwelling time distribution in Fig. 4). To minimize the heat *Drosophila* is likely to maintain this strategy beyond the reinforcement period because it can only find out whether the danger is over by risking the heat.

The behavior in this paradigm has many parallels in avoidance conditioning of vertebrates (for review, see Mackintosh 1983; Catania 1992). Both the fly in the flight simulator and a rat pressing a lever to avoid shock have to correlate their behavior with nonreinforcement. A stimulus signalling nonreinforcement might elicit a motivational state—sometimes referred to as “relief”—sufficient to reinforce the avoidance response (here, the longer dwelling times in the cold sectors). In the formal description of associative learning of

Rescorla and Wagner (1972) the nonappearance of an anticipated punishment adds a negative associative value to the avoidance response. The expectation of reinforcement implied in this model can be provided, as in Pavlovian conditioned inhibition, by the concurrent presentation of a stimulus that, by itself, signals punishment (CS^+). Alternatively and similarly effective, associating the experimental context with punishment can set the ground for the expectation of reinforcement. The latter would be the case at the flight simulator.

THE FLY OPTIMIZES ITS ORIENTATION IN THE COLD SECTOR

The behavior during avoidance conditioning can thus be summarized by two simple and obviously useful rules: (1) “If it is hot, get out of the heat!” and (2) “If not, keep the orientation you have!” But the flight simulator has further interesting details to offer about the fly’s behavior in the cold sector. Under training as well as under test conditions the fly avoids the regions next to the borders. More than that, in the random-dot panorama the animal tends to hold the maximum distance to the quadrant borders. These findings seem to imply that flies have a spatial concept of the hot and cold areas in the panorama, but the present data leave open alternative interpretations. For instance, the flies may arrive at the center of the cold quadrant just by measuring directly the probability of encountering heat when generating course perturbations. Further evidence for a spatial concept of the quadrant borders will be provided elsewhere (R. Wolf and M. Heisenberg, in prep.).

To better understand the fly’s behavior we need to know more about the memory template. By impeding the fly’s view in frontal or lateral sectors, we have shown that the template probably covers a large part, maybe even all, of the visual field. This finding is in line with earlier observations on freely moving insects (Tinbergen and Kruyt 1938; Anderson 1977; Wehner and Rber 1979; Cartwright and Collett 1982; Gould 1987; Lehrer 1990). A full-sized template is useful in landmark orientation in which the animal has to find by retinotopic matching the orientation during which the template was inscribed. The larger the area compared, the smaller is the probability of misleading chance similarities.

Because it is negative, the result in Figure 3 has to be qualified, as we cannot exclude causes other than template size as being responsible for the suppression of the learning performance. It will be most important to find out whether the template is a static image or a "motion signature," whether it is retinotopically fixed in the horizontal as it is in the vertical, how many templates a fly in the flight simulator stores, how these are related, and how templates are improved. Answers to some of these questions will probably lead us much further into the interactions between motor programs and visual processing in pattern recognition.

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