
Minireview

Sensorimotor Transformation from Light Reception to Phototactic Behavior in *Drosophila* Larvae (Diptera: Drosophilidae)

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*In this paper we examine the *Drosophila melanogaster* larval response to light. We survey the morphology of the larval visual and motor systems in relation to larval locomotory behavior and phototaxis. In addition, this paper proposes a model of sensorimotor transformation and examines the reversal in taxis occurring at the *D. melanogaster* larval wandering stage.*

KEY WORDS: review; *Drosophila*; larva; phototaxis.

INTRODUCTION

The reaction of an animal to its external environment is dependent on two conditions: The animal must be sensitive to some features of the environment and the sensory receptors must be connected to the appropriate motor mechanisms. In all but the simplest reflex systems it is not adequate for the receptors to be connected directly to the motor effectors: the sensory input needs to be processed before it can provide appropriate motor control signals. The conversion of information from the format in which it is delivered by the senses to a format appropriate for the motor system is known as sensorimotor transformation. An interesting and approachable (but for the most part unstudied) example

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of a sensorimotor transformation is found in the control systems that underlie the taxis behavior of the larva of the fruit fly *Drosophila melanogaster*.

A taxis is a movement that is directed with respect to some stimulus in the environment. Examples of stimuli and their respective taxes are light (phototaxis), moisture (hydrotaxis), and gravity (geotaxis) (Wehner, 1981). During a taxic behavior the organism moves in some consistent way with respect to that stimulus. The movement might be directed toward (a positive taxis) or away from (a negative taxis) the stimulus or even at a fixed angle to it. This review concerns *Drosophila* larval phototaxis.

The *D. melanogaster* larval stage takes about 96 h at 25°C and is divided by two molts into three instars (Demerec and Kaufmann, 1940). During the first to the mid-third instar *D. melanogaster* larvae show a marked aversion to light, that is, upon exposure to light, larvae will attempt to move away from it (negative phototaxis, Grossfield, 1978). In contrast, midway through the third instar, the larva's response to light becomes a positive phototaxis (Godoy-Herrera *et al.*, 1992). This change occurs in conjunction with a series of other strain- and condition-dependent behaviors related to the selection of a suitable pupation site (see Rizki and Davis, 1953; Mishima, 1964; Kearsley and Kojima, 1967; Sameoto and Miller, 1968; Grossfield, 1978; Alvarez *et al.*, 1979; Markow, 1979; Manning and Markow, 1981; Fogelman and Markow, 1982; Sokolowski and Hansell, 1983; Wong *et al.*, 1985; Schnebel and Grossfield, 1986; Sokolowski *et al.*, 1986; Godoy-Herrera *et al.*, 1989). The model developed to describe the sensorimotor transformations involved in the production of negative phototaxis in the first to mid-third instar larvae must be flexible enough to describe the reversal in phototaxis during the third instar.

D. melanogaster is a particularly suitable species for the study of larval phototactic behavior because of our extensive knowledge of its anatomy, behavior, and genetics (Morgan, 1907; for a comprehensive review see Ashburner and Wright, 1978). In particular, the knowledge of *D. melanogaster* genetics is especially relevant since the phototactic behavior in *D. melanogaster* is simple enough for its underlying neural circuitry to be amenable to genetic and physiological manipulation.

Genes involved in the *D. melanogaster* visual system have been extensively studied. They fall into three general categories.

1. Those which appear to affect the development of adult photoreceptor cells (reviewed by Hall *et al.*, 1982).
2. Phototransduction mutations, where photoreceptor neurons necessary for receiving light signals from the physical environment and converting these signals into a form that the nervous system can interpret are disrupted (reviewed by Pak, 1979; Zuker, 1992).

3. Structural brain mutations: those with morphological abnormalities of the optic ganglia (Heisenberg and Wolf, 1984; Campos *et al.*, 1985, 1987; Steller *et al.*, 1987).

In *D. melanogaster*, it is possible to isolate genetic variants that alter behavior patterns. By comparing the behavior of mutant animals with those of normal ones, we can determine what factors and processes are necessary for the production of normal behavior patterns (Ashburner, 1989). The advantages of *D. melanogaster* for these inquiries are numerous. Once a mutant has been selected, the location of the mutant gene on the chromosome can be mapped. The gene can then be isolated by means of molecular cloning from the large proportion (90%) of the DNA in the genome that has already been assigned to certain chromosomal regions. Once the gene is cloned, the protein it encodes can be determined, as can the sites and times of its expression in the developing nervous system. The eventual participation of the protein in building the machinery of the functioning nervous system can be determined. To demonstrate that this particular gene (an actual segment of DNA) affects the behavior, a normal version of the gene can be put back (transformed) into the mutant animal to rescue or restore the normal behavior. Thus, in *D. melanogaster*, it is possible to *prove* that a given protein present in the nervous system, e.g., on a specific set or type of neuron in a restricted region of the central nervous system, is necessary for the performance of a normal behavior pattern.

Many mutations have been examined for their effects on visually related behavior in the adult fly. However, to date, few studies have concerned themselves with the larval visual system. Once a number of genes that affect the larval visual system have been identified their role in larval photobehavior during foraging and wandering can be determined. An interesting subset of these genes may affect both larval and adult photobehavior.

Here we review the following:

- (1) the *Drosophila* larval visual and locomotory systems,
- (2) mechanisms linking the *Drosophila* larval visual and locomotor systems and possible implications for phototactic behavior, and
- (3) the significance of the transition from negative to positive phototactic behavior.

We also propose a simple genetic manipulation that could provide a test between two possible methods by which a *Drosophila* larva might carry out its phototactic repertoire.

MORPHOLOGY OF THE LARVAL VISUAL SYSTEM

The anterior end of the *Drosophila* larva has similarly organized sensory systems in each of the three instars (Grossfield, 1978). The anterior segment is equipped with at least two sensory organs, a centrally positioned terminal sense

organ and a bilaterally symmetrical pair of light-receptive organs. The visual organs of *Drosophila* larvae have been localized near to the cephalopharyngeal skeleton (Steller *et al.*, 1987). The visual organ is provided with a ganglion from which nerves extend to the central nervous system below the two spheres of the brain.

The components of the larval visual system in *Drosophila* have been studied by analogy to large flies (*Musca domestica*) by Bolwig (1946) and have been found to include axons from Bolwig's organ which originate from a cluster of 12 larval photoreceptor cells near the mouth hooks above the pharyngeal sclerites of the cephalopharyngeal skeleton (Melamed and Trujillo-Cenoz, 1975; Zipursky *et al.*, 1984; Steller *et al.*, 1987) and a set of three larval neurons which establish contact with the larval optic nerve (Tix *et al.*, 1989). Additionally, there are enveloping glial cells distributed along the length of the larval optic nerve (Campos *et al.*, 1994). These neurons terminate at different sites in the developing optic lobes, most terminate superficially and a few terminate at a deeper level toward the central brain (Tix *et al.*, 1989). The light-sensitive cells are enclosed in a slit-like pockets near the mouth hooks and just above the pharyngeal sclerites of the cephalopharyngeal skeleton (Steller *et al.*, 1987). This is shown in Fig. 1. The embryonic development and morphology of the larval visual system have been described by Green *et al.* (1993) and Campos *et al.* (1994). The morphology of the visual system ensures that the larval central nervous system receives information about ambient illumination. Furthermore, it is likely that directional information about the source of the stimulus is also obtained.

MORPHOLOGY OF THE LARVAL MOTOR SYSTEM

The musculature system of the *Drosophila* larva consists of a segmented series of laterally paired hypodermal muscles, which form an almost-continuous multilayered sheet beneath the hypodermis. The larva has 28 segmentally repeated pairs of somatic hypodermal muscles in a range of orientations from longitudinal to almost circumferential.

The longitudinal and oblique muscles are attached at each intersegmental junction, except for the anterior three segments, where the longitudinal muscles are continuous. The longitudinal muscles are effective as retractors of the head and pharynx. Lengthening of the body results from the constrictive action of the oblique muscles, with the resulting increase in pressure of the blood and viscera (Ashburner and Wright, 1978).

Electromyographic readings from a copper wire inserted into abdominal segments of a freely moving *Drosophila* larva have not been done. However, recordings from the larva of the tobacco hornworm *Manduca sexta*, which has a similar anatomical organization, indicate that the neural circuitry involved in

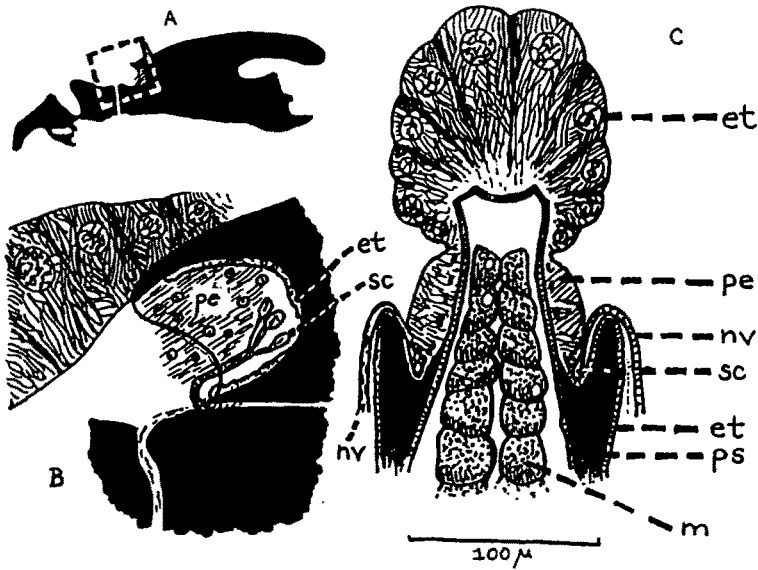


Fig. 1. The visual cells of Dipteran larvae. (A) The mouth hooks and the cephalopharyngeal skeleton of a third-instar fly larva. The shading shows the position of the light-sensitive cells. The framed area is enlarged and shown in B. The outer wall of the pocket in the skeleton has been removed, and only the outline of the pocket is shown. (C) A horizontal section through the anterior end of the pharyngeal skeleton showing the pockets with light-sensitive cells. sc, light-sensitive cells; nv, nerve; et, epithelium; pe, prismatic epithelium; ps, pharyngeal skeleton; m, muscles (redrawn from Bolwig, 1946).

each muscle segment shows a repeated pattern of innervation among the thoracic and abdominal ganglia and is normally activated by the subesophageal ganglion and the supraesophageal ganglia (brain hemispheres) (Dominick and Truman, 1986a, b).

The paired subesophageal ganglia, in the *Drosophila* larva, along with three pairs of thoracic ganglia and eight pairs of abdominal ganglia, are fused to create the ventral ganglion (Kankel *et al.*, 1978). Two large nerves are associated with each brain hemisphere, the antennal nerve and Bolwig's nerve (White and Kankel, 1978). Two maxillary nerves connect the sense organs of the head and the muscles with the most anterior portions of the subesophageal ganglion. A nerve is associated with each of the thoracic and abdominal ganglia and connects their respective body segments with these ganglia and the sense organs and associated musculature (Bodenstein, 1950).

Thus the musculature of the *Drosophila* larva is suitable for generating the basic motor patterns of extension and contraction. Much of the innervation is controlled locally, which means that fairly high-level commands, such as "lean

left," could be sent from the supraesophageal ganglia without needing to specify the activity of all 28 muscles in each segment. High-level instructions could, in principle, be executed by the local circuits. The innervation of each muscle seems to be sufficiently discrete to allow controlled turning or swaying in response to commands from the central nervous system. We now need to describe orientation behavior as well as the various relevant behaviors of *Drosophila* before speculating on the various processes that might take place between visual information arriving at the brain and such high-level motor commands leaving.

LOCOMOTORY BEHAVIOR IN THE *Drosophila* LARVA

Since the maggot has no legs to direct its motions, it must accomplish all of its actions by movements of its body, but, so well developed to this end are the muscles of the body wall, that no act of shortening or lengthening, no contortionistic twist or turn is impossible to it (Snodgrass, 1924, p. 19)

Drosophila larvae, like most insect larvae, move by a cyclical, muscular peristalsis. This results in discrete steps of movement that, because of the oblique arrangement of the main anteroposterior muscles, shows a distinctive left/right alternation. In the absence of any particular stimulus conditions, the left and right steps are about equal, resulting in, on average, straight progress across the substrate.

Locomotion is achieved by a wave of extension running anteriorly from the posterior segments to the head, which throws the mouth hooks forward like a grappling iron where they can dig into the substrate. The larva then bends toward the substrate so that the terminal sense organ, which is on the most anterior segment, is pressed firmly against the surface. The anterior segments of the body behind the anchored front end then lifted, contracted, which moves them forward, and pressed down again against the substrate. The rest of the body then follows the advanced and anchored front segments by means of anteriorly directed, peristaltic contraction of each segment in turn commencing with the posterior segments. Once the larva is fully contracted, the next movement begins with a renewed thrust of the anterior segments, and so it continues moving its anterior end alternately forward to the right and left. This is shown in the first part of Fig. 2, which shows the movement of a larva before a light is turned on. Now we are in a position to see how locomotion might be affected by changes in the environment, in particular, the direction of ambient light.

NEGATIVE PHOTOTAXIS

Upon sudden exposure to light a *Drosophila* larva that has not yet reached the second half of the third instar usually stops moving and begins to swing its anterior end in all directions (Jennings, 1904; Mast, 1911, 1938; Grossfield,

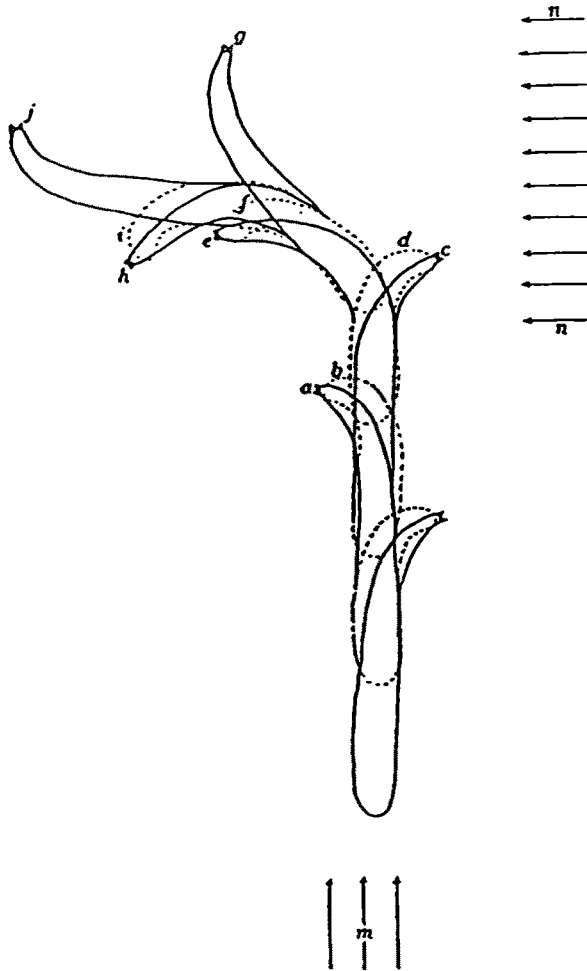


Fig. 2. Reorientation in *Drosophila* larvae. The larva expands to a, contracts to b, expands to c, etc., with the light m on. At d, m is put out and n put on. The lateral movement to e is somewhat larger than a; the next one (g) increases the light falling on the receptors and is corrected by a swing over to h (from Mast, 1911, pp. 61-62).

1978). Swings away from the light are generally larger and so the larva rapidly orients itself to be pointing away from the light source (Mast, 1911). An example of this behavior is shown in Fig. 2. Bolwig (1946) observed similar behavior in the larva of the house fly, *Musca domestica*.

By observing the response to light shone from various directions, Mast

(1911) concluded that it was the amount of light falling on the larva's anterior end which influenced the behavior, that is, the larva sought positions in which the anterior end was exposed to the least amount of light. Ellsworth (1933) demonstrated that the cephalic lobes were involved in some way in the phototactic control of the behavior of the larva of the fleshfly, *Lucilia sericata*, whose behavior is similar to that of *Drosophila*. He severed the lobes and found that locomotion was no longer responsive to light.

Negative phototaxis is seen for most of the larval life of *D. melanogaster*. This is consistent with the lifestyle of the larva in this stage. It burrows into the nutritive substrate, e.g., fruit. Negative phototaxis likely helps direct the larva into a food source. This occurs in concert with other relevant sensory information such as the presence of certain chemicals and moisture concentrations (Lilly and Carlson, 1990). Near the end of the third and final instar the larva's behavior undergoes a dramatic change. In preparation for pupation it starts to seek dry surfaces, rather than the moist depths of fruit. Its previous negative phototaxis changes to positive phototaxis.

POSITIVE PHOTOTAXIS

As mentioned above, in the late third instar, a general change occurs in the behavior of *D. melanogaster* larvae: They cease foraging and commence what has been called "wandering behavior" (Sokolowski *et al.*, 1984). This behavior precedes pupation and presumably has the effect of optimizing the choice of pupation site. One feature of wandering behavior is positive phototaxis (Godoy-Herrera *et al.*, 1992). An example of positive phototaxis is shown in Fig. 3. The data illustrated here were obtained in our laboratory and are presented in a format that allows comparison with the data presented in Fig. 2, which date from 1911. There are no obvious gross anatomical changes which occur at the time of the emergence of wandering behavior (A. R. Campos, unpublished results). The existing sensorimotor apparatus must be used but in a different, and in the case of phototaxis, opposite way.

The reversal of phototaxis provides an exciting opportunity to relate motor behavior to sensory input. Premorphogenic behavior is highly stereotyped in *Drosophila* and occurs at a specific developmental stage, thereby allowing a detailed analysis of the roles of internal factors, e.g., hormones such as ecdysone and juvenile hormone, as well as external factors, e.g., photoperiods, which may influence this behavior (Dominick and Truman, 1984, 1985).

SENSORIMOTOR TRANSFORMATIONS IN LARVAL PHOTOTAXIS

Phototactic behavior thus forms an interesting challenge to explain in terms of the sensorimotor transformations involved. Any model must be flexible enough to explain the reversal in phototaxis found in the third instar but must also be constrained to use the neural machinery available.

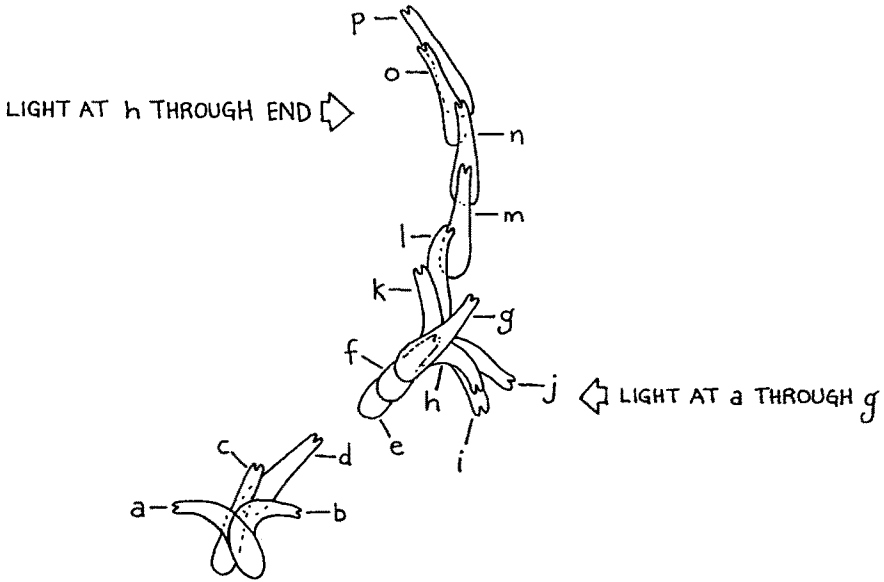


Fig. 3. Positive phototaxis in a wandering *D. melanogaster* larva. The larva expands (a) and swings its anterior laterally, in response to onset of light right, then expands (c) and moves toward the light stimuli (d-f). Right light is put out and left light is put on. Larva swings laterally (h-m), contracts, and moves toward light (n-p).

Phototaxis involves both the neural assimilation of sensory information and the modulation of motor responses. What processes might take place between these parts? Broadly there are two ways of achieving phototaxis. The larva needs to ascertain which areas of the world are darker (or lighter) than others. It is necessary to compare samples of sensory information to make this decision, but the comparison can be made in space or time. Fraenkel and Gunn (1961) have used the terms klinotaxis and tropotaxis to describe these strategies. Klinotaxis is their term for comparison of stimulus intensity at successive movements in time; tropotaxis refers to a spatial comparison. The two possibilities are illustrated in Fig. 4.

A temporally based decision (klinotaxis) involves comparing the outputs of the sense organs at different times. This is illustrated in Fig. 4A. The method involves some kind of "memory," since each sample of sensory input needs to be compared to a previous set. An example is provided by the negative phototaxis of the blowfly larva *Calliphora* (Fraenkel and Gunn, 1961). The larva crawls away from light by turning its head alternately to the left and right and swinging its body away from the side to which the head is turned when a stronger light is received. It is *when* the light falls, rather than *where* the light falls, that matters. So if a light directly overhead is switched on only when the blowfly

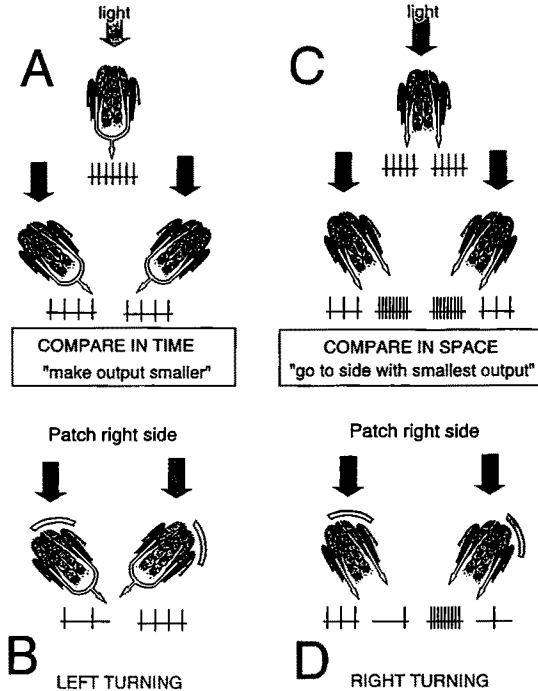


Fig. 4. Turning experiment in *Drosophila*. Diagrammatic representation of two possible mechanisms for negative phototaxis in the *Drosophila* larva. The larva is shown as in Fig. 1 but with the translucent epithelium removed. Arrows indicate output from the photoreceptors located in shielded pockets beneath the condyle spine (see Fig. 1). Underneath each arrow, the expected neural activity is indicated by the thick gray arrow. (A, B) The outputs are summed, making the animal like a photocell. By comparing the output at different times and applying a simple rule ("make output smaller"), the animal will move away from the light. (C, D) An alternative mechanism in which the outputs of the two sides are compared. Again, by applying a simple rule ("go to side with smallest output"), negative phototaxis can be achieved. The two possibilities can be distinguished by patching one side. This will result in turning (see text) away from the patched side (to the left in the case of right patching; B) if the outputs are summed but toward the patched side (D) if the outputs are compared.

larva turns its head toward the right, it crawls continuously toward the left (negative klinotaxis).

It is not necessary that the visual organs of larval Diptera are directional for klinotaxis. If there are darker or lighter areas available, the organism will

eventually find the desired level by chance. Perhaps this is what Holmes (1905) had in mind when he talked about a "trial-and-error" mechanism.

A spatially based decision system (tropotaxis) compares the information coming from the different parts of space. This is illustrated in Fig. 4C. Tropotaxis requires that the visual organs are directional and that they sample different areas of space. Choosing to move in the direction sampled by the organ with the lowest activity leads to negative phototaxis. *Daphnia*, *Armadillidium*, and *Planaria* exhibit this sort of tropotaxis (Fraenkel and Gunn, 1961) and can move directly toward or away from a source of stimuli without turning alternately toward the left or right. A refinement is to compare different parts of the image of a single visual organ, as animals with optically focused eyes can do.

Which system does the *Drosophila* larva use? The swinging of the head when a light is turned on is suggestive of klinotaxis. On the other hand, the anatomical structure of the visual organs at the bottom of little pockets suggests that they are directional, which is compatible with tropotaxis.

Figure 4 illustrates a simple test that could be performed on *D. melanogaster* to distinguish between the two possible mechanisms. Removing the input from one eye makes opposite predictions for the two mechanisms. Both predict that turning should occur, but the two mechanisms predict turning in the opposite directions. The input from one visual organ could be removed by painting it over, patching it, removing it surgically, or, most elegantly, performing genetic manipulation (see below). Consider a negatively phototactic larva with a patch painted over the right visual organ and a constant source of light placed directly in front of the larva (Fig. 4). A temporally based direction (klinotaxis) results in turning away from the patched side (Fig. 4B). A spatially based decision mechanism (tropotaxis), however, predicts turning toward the side with the patch (Fig. 4D).

Whichever sensory strategy (klinotaxis or tropotaxis) is used, the output of the sensory decision rule ("move to side with the smallest output" or "make output smallest") needs to be converted to a batch of signals in the appropriate form to the appropriate muscles. What pattern of signals should leave the central nervous system to cause appropriate body movements is not known. At first glance it would seem that, at the time of reversal, either the rule could be reversed or simply the output signal (from negative to positive phototaxis) could be redirected. This is not the case, however, since if the muscle arrangement was switched but the rule was kept the same, the system would be in open-loop, that is, the behavior would no longer tend toward canceling the sensory input and an unstable situation would result.

CONCLUSIONS

The change from negative to positive phototaxis is reminiscent of reversals in other parts of the animal kingdom that occur as the development phase of an animal puts opposing demands on the nervous system. The development of the

flatfish is a well-documented example. In this species, the eyes migrate from lateral positions in the larvae to both being on the same side as an adult (Graf and Baker, 1983, 1990). Minimal anatomical rearrangement occurs in the central nervous system of a metamorphosing flatfish and an essentially identical nervous system has to control the oppositely directed eye movements of the adult for a given sensory input. This is achieved by altering synaptic weightings, a system that might also be employed by the *Drosophila* larva.

Of considerable interest is the possibility of external stimuli reconfiguring the neural circuitry at a critical time in the alteration of physiological development such as the onset of larval wandering in the late third instar. The *Drosophila* larva can be at least as useful as the leech for investigating the ways that simple neural nets can carry out complex conversions of sensory to motor information and maintain flexibility (Churchland and Sejnowski, 1987; Keshishian and Chibe, 1993; Lockery and Sejnowski, 1993). What it loses by its inconvenient size compared to the leech, it gains by the immense power opened up by our superior genetic understanding of *D. melanogaster* and the possibility of directly exploring the genetic basis of behavior. The *glass* mutation, in which these mutants appear to be missing the larval visual organ, provides us with a genetic tool to test the model described above. This can be done by generating larvae that are mosaic (chimeras) for normal and mutant (in this case *glass*) tissues (Hall, 1978). In this way a larva can be constructed that is missing part of (e.g., the left or right side) its visual system. One can think of it as a way to "patch" different parts of the visual system genetically with mutant *glass* tissue. The data collected on the phototactic behavior of mosaic larvae will provide a test for the model presented in Fig. 4.

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