Can a Fly Ride a Bicycle? [and Discussion]

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Can a fly ride a bicycle?

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SUMMARY

In humans visual flow field information is available to many motor output programs enabling them to guide the whole organism. This basic organization still constitutes a major challenge for any theory of orientation. Studies of the fly *Drosophila melanogaster* during the past 10 years have shown that in the lower animals sensory-motor control has a similar degree of flexibility. In the flight simulator the tethered fly adjusts the strength of its motor commands to their efficacy. It can stabilize the panorama against rotations not only by yaw torque but also by thrust. It learns to invert its flight manoeuvres in response to positive feedback in order to stabilize a stripe in the frontal visual field.

In the present report we demonstrate that *Drosophila* is able to use the force of its legs to stabilize the panorama irrespective of the polarity of the feedback provided experimentally. All these behavioural performances have a common functional organization with the following properties: (i) the system has a desired state from which the actual state may deviate; (ii) to reach the desired state the system randomly activates a range of motor programs; (iii) the system compares efference copies of the motor programs with those sensory inputs which represent the deviation from the desired state; and (iv) if a significant correlation is detected for a certain motor program, this is used to shift the sensory input into the direction of the desired state. It is proposed that for organisms with more than one motor output this is the basic scheme of sensory-motor coordination.

1. INTRODUCTION

Insects possess powerful mechanisms of flight steering based primarily on the processing of visual cues. The investigation of some of these mechanisms has led to the assumption that straight flight is secured by a so called 'autopilot' (Rowell 1988), a hard-wired neuronal circuit correcting involuntary deviations from course. In flies, moths, bees, locusts and several other species components of this presumed circuit have been identified (Dvorak *et al.* 1975; Hausen 1981; Hengstenberg 1981; Heisenberg *et al.* 1978; Milde 1989; Rowell & Reichert 1986; Erber & Menzel 1977).

The distinction between voluntary and involuntary course deviations and the notion of an autopilot correcting the involuntary ones, raises interesting questions. To start with, let us assume that a satisfactory definition and, eventually, a functional description can be given for 'voluntary turning' (Heisenberg & Wolf 1984). How, then, can we define an insect's autopilot: a term refering to aircraft technology of the 1950s? What is the evidence that correctional steering in insects is, indeed, provided by such a rigid device of comparably low sophistication? How is the interplay between the autopilot and the general orientation system organized?

One would hardly regard the human visual guidance system as an autopilot. The high flexibility of mammalian orientation lends little plausibility to such a comparison. Consider for instance the ability to steer a vehicle. Children quickly learn to handle their first tricycle. As it seems they do not have to learn the steering at all. If guidance would be provided by an autopilot this act would be a formidable achievement. The sensory information used in locomotion naturally controls the motor programs of the legs and feet. This pathway would now be disconnected and the sensory data would instantaneously be linked to new motor programs of the hands and arms. Never in natural history have these particular motor patterns been involved in the control of locomotion. Most people can learn to steer a car with their tongue or diaphragm if the appropriate gear is provided. Apparently most motor outputs are connected to the visual (and possibly all sensory) input and any of the connections can be activated if necessary.

There is little choice as to how the activation of a particular sensory-motor connection be achieved in such a system: it must be done by trying out. The essence of trying out is the operant loop. Motor programs are endogenously activated at random and their effect on the input variable in question, in this case the flow field, is observed. If a particular motor pattern has an influence on the flow field it can be employed in the control of locomotion (Wolf & Heisenberg 1991).

Another example of the flexibility of the primate visual system is the surprising ease by which we adapt to the distortions of goggles. Recall the famous experiments of Stratton (1897), Kohler (1956), Held (1965) and others, in which it was shown that our visual system can adjust to, and even completely

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compensate for the entire or partial inversion of the visual scene. In this case active training of visuo-motor coordination for several days is necessary to achieve complete adaptation. It is important to note that training not only restores our ability to successfully operate in visual space but even in conscious perception the world returns to what it had looked before the goggles had been put on. Again, the operant loop is crucial for the reorganization of visuo-motor coordination (Held 1965).

This article is not directly concerned with the human visual system. We would like to point out though, that if insects entirely relied upon an autopilot for correctional steering, their visual system would not be able to recruit new motor outputs or to adapt to inverting goggles. We would have to concede in this case that insect and primate visual systems operate on fundamentally different principles.

Some years ago two of us described experiments with the fly *Drosophila melanogaster* somewhat reminiscent of the situation of the inverting goggles in humans (Chapter 12 of Heisenberg & Wolf (1984)). A fly in a special flight simulator with a background texture and an independently movable vertical stripe as 'foreground', is able to learn in the course of half an hour to manipulate the stripe even if it is coupled to the fly's yaw torque in a positive (i.e. inverted) feedback loop.

In the meantime we have accumulated a wealth of data on visual orientation of this species revealing surprising similarities (if not homologies!) in the basic organization of the insect and human visual systems. In this paper we first briefly summarize some of these investigations and then describe a new experiment which demonstrates that, as in humans, in *Drosophila* flow field information is readily available to motor output systems not specifically designed for this type of sensory data. We hope to convince the reader that correctional steering in insects is far more sophisticated than what the term 'autopilot' might suggest and we infer that the kind of visuo-motor coordination emerging from these studies may be universal in the animal kingdom.

2. OPEN-LOOP STEERING RESPONSES

Insects with compound eyes have the tendency to generate turning manoeuvres in response to a rotation of the visual scenery (optomotor response). The direction of the response is roughly the same as that of the stimulus. It can safely be assumed that the animal takes the stimulus as self-rotation. The optomotor response therefore operates as part of a simple negative feedback loop which keeps the animal on course by reducing self-rotation. This is the basis of the term 'autopilot'.

Directional sensitivity to motion is provided by arrays of differently oriented elementary movement detectors (EMDs) in the optic lobes (for reviews, see Buchner (1984); Heisenberg & Wolf (1984)). Their output is continuously integrated over time (Wolf & Heisenberg 1990). The integrator may be a specialty of the flight control system since the motion detector output needs to be integrated if it has to fully compensate for a constant course deviation as might be caused by an imbalance of the two flight motors. In walking, for instance, due to tarsal contact with the substrate the fly may rely less severely on visual cues for orientational stability.

At a macroscopic level optomotor responses belong to the most robust and persistent behavioural phenomena so far discovered (e.g. Götz 1975; 1983); viewed in more detail, however, they turn out to consist of small pulses of variable latency and size, occuring with a probability $p<1$. In *Drosophila*, for instance, yaw torque in stationary flight at the torque meter starts to change in response to a moving pattern as early as 50 ms after the onset of motion. In the individual traces though, latencies vary as much as 500 ms and in the case of short pulses of motion traces may show no response at all (Heisenberg & Wolf 1984, figure 87).

Furthermore, in the individual traces it becomes immediately apparent that irrespective of stimulation, endogenous yaw torque modulations must be very important. Yaw torque changes incessantly, covering a large fraction of the fly's total torque range. Inspection reveals large pulses (torque spikes; body saccades) and large, slow changes which together can be interpreted as search manoeuvres for reafferently moving visual contours. The whole torque trace is overlaid with fast fluctuations in the frequency range around $f=3.5$ Hz. The significance of this phenomenon will become apparent in the next section.

3. OPTOMOTOR BEHAVIOUR IN A MINIMAL FLIGHT SIMULATOR

In free flight the fly moves in a stable world. Inversely, in the flight simulator the fly is fixed and the visual surround moves accordingly. In this special paradigm free flight is simulated for only one degree of freedom: rotation around the vertical body axis. From the on-line signal of the torque meter the apparatus computes the angular velocity this momentum would give the fly, but instead of turning the fly it turns the panorama in opposite direction.

Using the fly's yaw torque for calculating its ensuing angular velocity should be no easy task considering that angular momentum and air friction of the fly as well as the zero setting of the apparatus are only roughly known and change from experiment to experiment. It turns out, however, that neither the coupling coefficient nor the zero setting are critical since the flies are built to cope with wing injury and can therefore adjust to these experimental parameters over a wide range (for discussion and further references see Heisenberg & Wolf (1992)).

Closing the negative feedback loop between the angular velocity of the panorama (e.g. striped drum, single vertical dark stripe in a white arena, random dot pattern, etc.) and yaw torque has the expected result. The fly instantaneously shifts its baseline of torque to the level at which the panorama is at rest (zero setting). From this level it generates occasional torque spikes and the small, fast torque fluctuations which keep the panorama in continuous motion (Wolf & Heisenberg 1990).

It is not clear how compelling for the fly the delusion of the flight simulator is. Most flight manoeuvres use more than one degree of freedom. In addition, in free flight the fly can sense its angular acceleration by its halteres and possibly other sensory organs such as wind hairs or mechanoreceptors in the joints. Yet, in closed-loop situations at the torque meter periods of uninterrupted flight are significantly longer than in open-loop optomotor experiments.

4. THE OPERANT COMPONENT IN OPTOMOTOR BEHAVIOUR

At a qualitative level the fly's behaviour in the flight simulator seems to be the same as in the open-loop situation: Motion of the visual surround causes an increased probability of torque pulses of the appropriate polarity and a slow shift of the torque baseline in the same direction. In this way the optomotor response stabilizes flight with respect to air turbulences and asymmetries in the efficacy of the two flight motors. So far the system might still be considered nothing but an autopilot if one disregards the probabilistic nature of the response and the peculiar small torque fluctuations. A quantitative comparison of open- and closed-loop responses, however, reveals that the system is of a fundamentally different nature and that the fly's behaviour immediately changes when the situation changes from open- to closed-loop or back. A cue for an understanding of this system comes from the small torque fluctuations. The fly generates them as a continuous test signal which allows it to detect the closure of the feedback loop and to calculate and to adjust the coupling coefficient. This implies that the fly generates an efference copy of the turning commands and correlates it with the visual motion input. Significant coincidences indicate that the loop is closed and allow an estimate of the efficacy of the turning commands (Wolf & Heisenberg 1990; Heisenberg & Wolf 1992). The cross-correlation can only take place between the first derivative of yaw torque (called pretorque) which is the input to the above-mentioned integrator and angular acceleration, the first derivative of the output of the movement detectors (Heisenberg & Wolf 1992).

What this shows is that correctional steering has an operant component. The fly tries out how effective its turning commands are and adjusts the response so that it compensates, in the special case tested, for at least 80% of the disturbance in about 200 ms (Wolf & Heisenberg 1990; Heisenberg & Wolf 1992). If the turning commands have no effect the initial high probability for pretorque pulses of the appropriate polarity immediately drops to small values. One explanation for this change in behaviour is that the fly tries to stop the rotation using other motor outputs such as torque spikes in the opposite direction, thrust, lift, roll or more complex motor patterns.

5. TRYING OUT

This switch can directly be demonstrated with a yaw–thrust compensator. If a negative feedback loop is set up with yaw torque the fly adjusts its baseline of torque to the level of zero net rotation of the panorama as just described. Now this loop is opened and at the same time the fly's thrust is made to control the angular velocity of the panorama. Again 'zero' is arbitrarily set to the middle of the range of thrust modulations observed and the coupling coefficient is adjusted to give about the same range of angular velocities as in the closed loop with yaw torque. If the yaw loop opens and the thrust loop closes the panorama (in this case a single vertical dark stripe) starts to rotate since thrust is not at the 'zero' level. This rotation often causes a quick directional yaw response which, of course, has no consequences since yaw is not coupled anymore to the panorama. The discovery that now thrust is in command of rotational steering takes a variable length of time and the average thrust trace reaches the baseline level of zero net rotation after about one second (Wolf & Heisenberg 1991; Heisenberg & Wolf 1992).

In this experiment the fly always shifts the stripe to that side on which thrust above the arbitrary 'zero' causes the stripe to move front-to-back suggesting some kind of forward velocity control and an elevated open-loop probability for a thrust increase in response to front-to-back motion which sometimes is, indeed, observed. Whether this is a further 'autopilot' or not, the mechanism is such that thrust quickly locks in with angular velocity and stays around 'zero' as soon as the feedback loop between the two is established. At the same time yaw torque drifts away from its former zero value which now is meaningless. If we switch back, closing the loop for yaw torque again and opening that for thrust, the arena is 'seized' by yaw torque in the course of a few hundred milliseconds and thrust starts floating freely again. Apparently, the system is faster in finding yaw torque to be the effective motor output than in discovering that thrust is. However, for both the lock-in latency is highly variable.

What this experiment tells us is that the system can instantaneously switch between different control modes, in this case yaw torque and forward thrust. Only one of them is locked in at a time and the system has to determine by trying out which one is effective. To assess the effect of the respective motor output on the situation the fly must generate an efference copy of it and search for coincidences between the efference copy and the salient sensory input, in this case angular velocity or acceleration.

Normally, the 'autopilot' against self-rotation makes it necessary to link angular velocity and yaw torque in a negative feedback loop. Positive feedback destabilizes orientation. Some time ago we observed that in a particular mutant strain (*rol sol*) with severely reduced optic lobes and, in particular, no lobula plate, the 'autopilot' is missing, i.e. no directional optomotor yaw torque response is found in open-loop. These flies still possess non-directional motion sensitivity and with it are able to compensate for a rotatory bias in closed-loop with either polarity of the feedback (Wolf & Heisenberg 1986; Heisenberg

& Wolf 1988). Again, the only way to achieve this is by continuously trying out which of the two polarities of yaw torque will diminish the amount of angular velocity.

6. THE FLY IN THE DRIVER'S SEAT

The above experiments do not prove that the fly tries many motor outputs besides yaw torque and thrust although it can not know *a priori* that we record these two. It might still be argued that the switching is only between a limited set of appropriate autopilot-type mechanisms. In contrast, we like to assume that the fly can go through a large part of its motor patterns in order to find the one which is successful (Wolf & Heisenberg 1991). If this were the basic organisation of the sensory motor interface in orientation, a fly should be able to use motor outputs for the control of the visual flow field which could not have been evolutionary disposed for this task. To put it in a different way, the fly should be able to steer a vehicle.

In the experiments to be described here flies are made to control the angular velocity of the panorama (single vertical stripe or striped drum) by their leg posture. A tethered fly is mounted in the centre of the arena on a little platform which it can push sideways with its legs against the force of a spring. The maximum displacement, as recorded by a photodiode, is about $d = 0.25$ mm to each side (figure 1). The loop between lateral displacement and angular velocity of the panorama can be closed with either polarity. Displacement of the platform to the right may lead to clockwise rotation but with a single switch, also the opposite contingency can be established (displacement to the right leading to counterclockwise rotation, displacement to the left to clockwise rotation). Irrespective of polarity, angular velocity is made proportional to the lateral displacement of the platform, the whole range of $d = \pm 0.25$ mm corresponding to $W_{\max} = \pm 254$ deg s^{-1}.

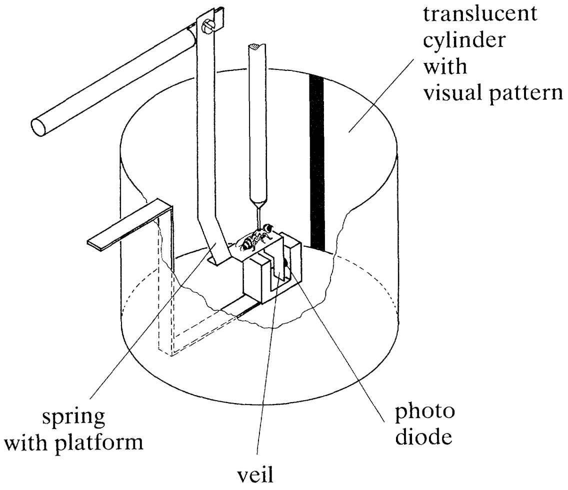

Figure 1. Modified flight simulator for closed loop with angular velocity of the panorama driven by leg posture. The fly is suspended by a rod with its head glued to the thorax. It is positioned in the center of a translucent arena, above a small platform which it can move sideways with its legs against the force of a spring. The position of the platform is monitored optoelectronically (photodiode; for a further description of this device, see Mariath (1985)). The arena either carries a single vertical black stripe (shown here; width $\delta = 10$ deg; height $h = \pm 40$ deg as seen from the position of the fly) or a periodic grating (pattern wavelength $\lambda = 18$ deg). For further details see text.

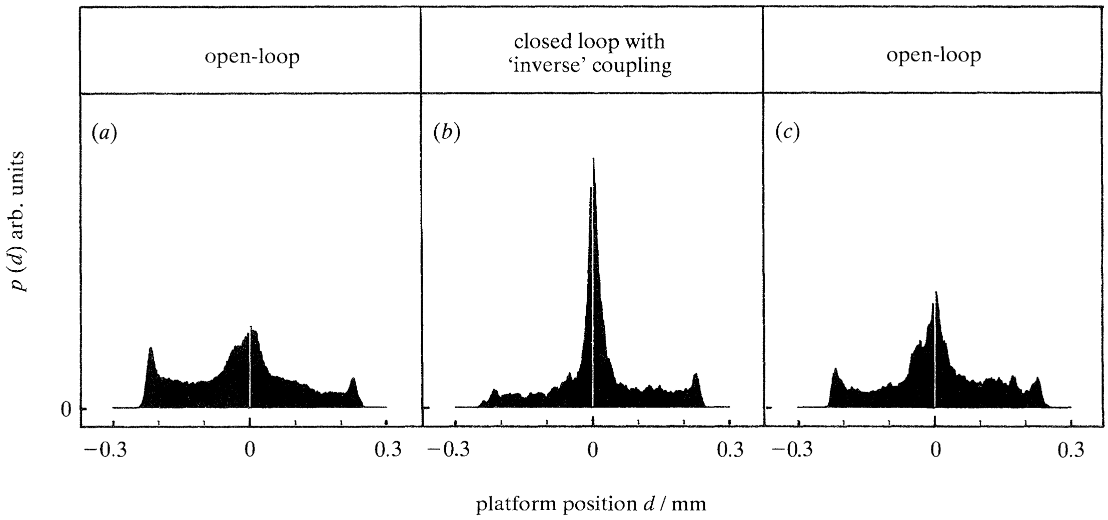

Figure 2. Platform position histograms under open- and closed-loop conditions. The arena carries a periodic grating ($\lambda = 18$ deg; height $h = \pm 40$ deg; pattern contrast $m = 0.95$). In (*a*) and (*c*) the pattern is stationary. In (*b*) the angular velocity of the arena is coupled to the position of the platform. Displacements to the right cause clockwise rotation, displacements to the left counterclockwise rotation. This is 'inverted' coupling with respect to the open-loop response shown in figures 3*a* and 4*a*. The coupling coefficient is arbitrarily set to $k = +914$ deg s^{-1} mm^{-1}. Platform position is sampled every 62.5 ms. For each fly 2 min periods are recorded at 5 min intervals for 35 min. The first five (*a*) and the last (*c*) of the seven records are in open-loop. During the sixth 5 min interval the fly is in closed-loop as indicated above (*b*). Histograms (area-normalized) are averages of four female flies of wild-type 'Berlin'. Note that the fly can push the platform slightly beyond the range of the photodiode. This causes the small peaks at the far ends of the histograms.

Contrary to the conventional flight simulator the closed loop with the platform has a resting position which is defined not only by the zero angular velocity of the panorama but also by the spring holding the platform. If the fly exerts no force or lifts its legs, the platform assumes this position and the arena is at rest. Note that the fly is severely restrained in this situation. It can not move the platform forward or backward, nor can it push it down or pull it up. The platform can only move sideways.

The fly's behaviour may be depicted as a histogram showing the probabilities for finding the platform at any of the possible positions. The fly 'explores' the whole range of positions. The distribution is flat with a somewhat higher probability for the resting position (figure 2*a*; the peaks at the far ends of the distribution are artefacts of the recording device). The fly continuously moves the platform. Apparently, it tries to free itself from its precarious situation by generating all kinds of leg and body movements. For instance, the fly may try to turn (for turning manoeuvres on the ground, see Strauß & Heisenberg (1990)) and the corresponding forces of the legs may cause the platform to move sideways. If this were the case, one should be able to measure open-loop responses to the rotation of the arena. Figure 3*a* shows that, indeed, a significant mean displacement in response to the direction of the rotation in open-loop is observed. The fly pushes the platform to the side to which the pattern moves in the frontal part of the visual field. Thus, among other motor outputs, our measuring device actually may in a complicated manner record the well known optomotor turning response (Götz & Wenking 1973).

To demonstrate that the fly uses a new motor output for the control of the flow field one has to prove that the closed-loop behaviour on the platform can not be explained by the properties of the optomotor turning response. Therefore, in the following the closed-loop behaviour is compared to the behaviour under open-loop conditions.

To start with, platform position is coupled to

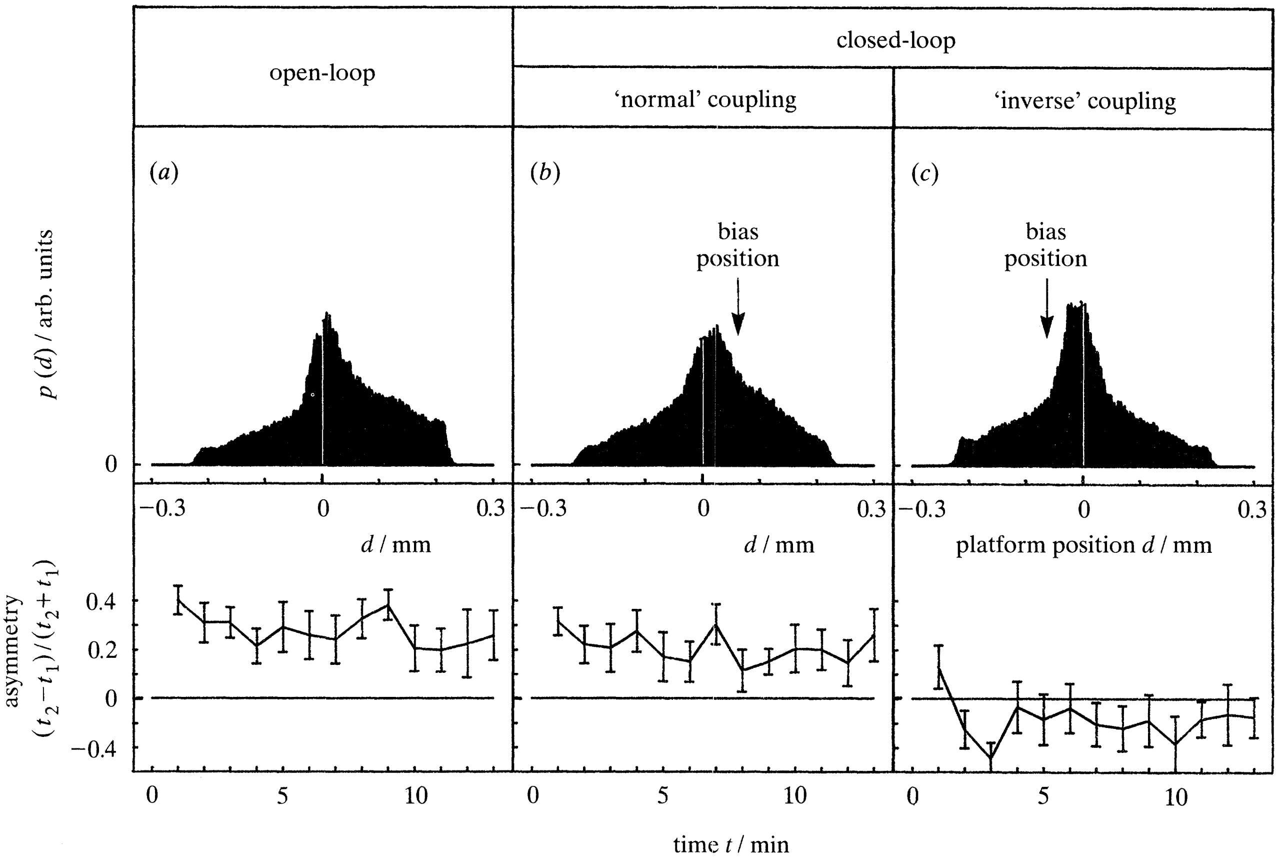

Figure 3. Rotatory bias experiments with a single vertical dark stripe ($\delta = 10$ deg; $h = \pm 40$ deg). Angular velocity of the bias is $w_b = +$ (or $-$) 58.5 deg s^{-1}. Mean position histograms (12 flies each, 13 min flight time per fly) are shown for clockwise rotation of the arena (positive bias) and include also those 50% of the experiments in which the flies had actually been stimulated with counterclockwise motion (negative bias) and had generated the mirror image of the histogram used for averaging. The lower parts of the figure show how during 1 min intervals the flies distribute their time pushing the platform to one side or the other. Vertical bars are s.e.m.s (with $n = 12$; number of flies; females of wild-type 'Berlin'). In (*a*) flies are tested in open-loop. Data indicate that the flies consistently push the platform into the same direction as that of the movement holding it there about twice as long as on the other side. In (*b*) and (*c*) closed-loop experiments are shown. Coupling coefficient is $k = +(b)$ or $-(c)$ 914 deg s^{-1} mm^{-1}. Generally flies are able to reduce the angular velocity of the bias except during the first minute with 'inverted' coupling (*c*). Note that in this and the following experiments the spring of the platform is shortened in order to adjust its displacement to the range of the photo diode.

angular velocity in a negative feedback loop with respect to the open-loop optomotor turning response described above. Because clockwise rotation in open-loop causes a displacement of the platform to the right, now a displacement of the platform to the right causes the arena to rotate counterclockwise. This should enable the fly to stabilize the panorama by means of its optomotor turning response. The effect of the closed loop on the fly's behaviour is as expected. In the probability histogram the platform positions around zero now are more probable than under open-loop conditions. The movements of the panorama which are induced by the endogenous motor activity of the fly likewise are reduced compared to what they would be without correctional steering. It seems reasonable to hold the optomotor turning response (autopilot) responsible for the reduction (data not shown).

The same interpretation, however, can not be maintained for the fly's behaviour in the following experiment. Now the feedback loop is closed with the inverse polarity, i.e. a displacement of the platform to the right now causes clockwise rotation of the arena. The result is the same as in the previous experiment: the probabilities for platform positions in the vicinity of zero are higher than in open-loop (figure 2). The opposite would have been expected on the basis of the directional optomotor turning response. In particular, one would expect the two maxima at the far ends of the distribution to increase.

It can still be argued that in the case of the positive feedback the fly is 'discouraged' and reduces the overall strength of its motor activity. This motivational change also would lead to higher probabilities for platform positions around zero. To subject the fly's steering ability on the platform to a more critical test the rotational zero of the panorama now is shifted with respect to the resting position of the platform. This situation is obtained by adding into the loop a DC voltage corresponding to a positive or negative rotatory bias of the arena. The vertical arrows in figures 3 and 4 indicate the position of the platform at which the panorama is at rest (bias position). Now the fly has to exert a permanent force against the spring to stabilize the panorama at the bias position.

This is a decisive test because to compensate for the rotatory bias in the case of inverted coupling the fly has to do the opposite of what it does during normal coupling. This can not be achieved by a predisposition for a directional response. Figure 3 shows that with both polarities of feedback the fly is able to shift the platform into the direction of bias compensation and to partly stabilize the panorama. Even if many flies do not keep the platform at the position of zero angular rotation for most of the time as they do in the flight simulator (yaw torque–angular velocity loop, figure 5*c*), flies clearly are able to keep the platform at about the bias position for extended periods of time, as individual position traces show (figure 5*a*,*b*).

Interestingly, for the polarity of coupling for which the feedback is positive with respect to the open-loop response, the fly initially does shift the platform into the wrong direction increasing the angular velocity of the arena. Thus, the directional open-loop response

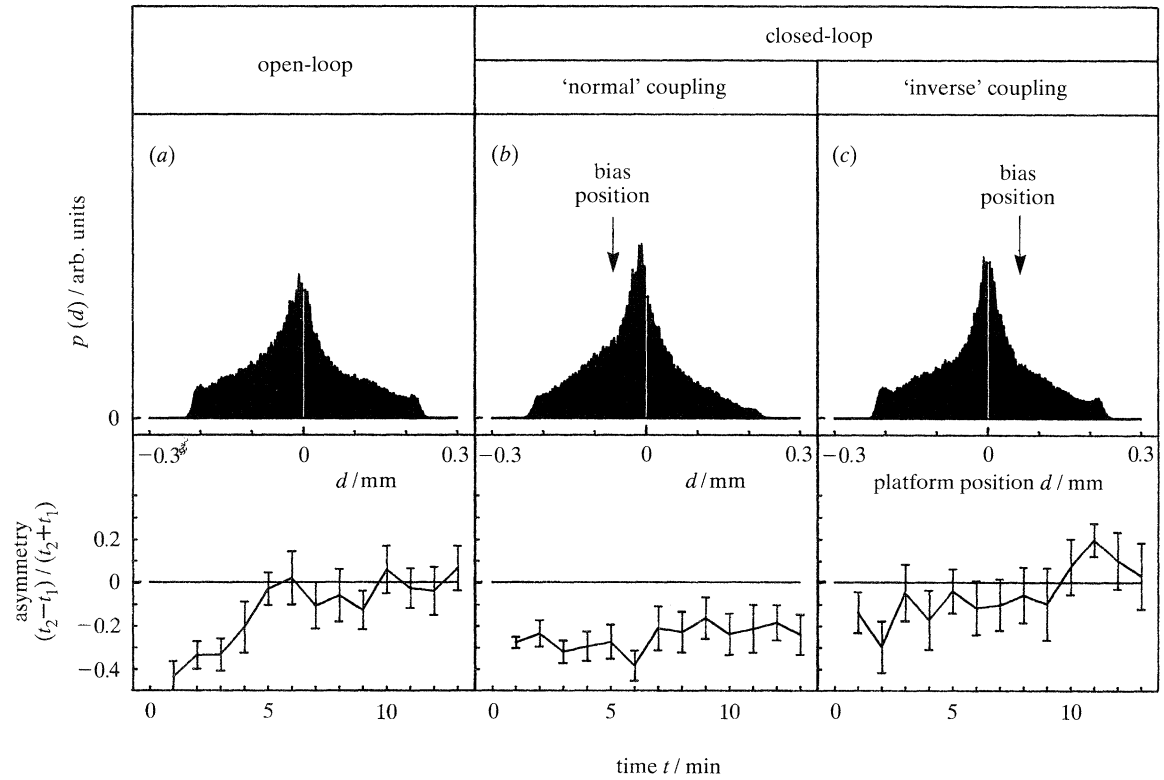

Figure 4. Each fly of the experiment shown in figure 3 is tested again 3 h later in precisely the same setting as before except that the bias direction is inverted. Between the two parts of the experiment flies are fed on sugar water. For details see legend of figure 3 and text.

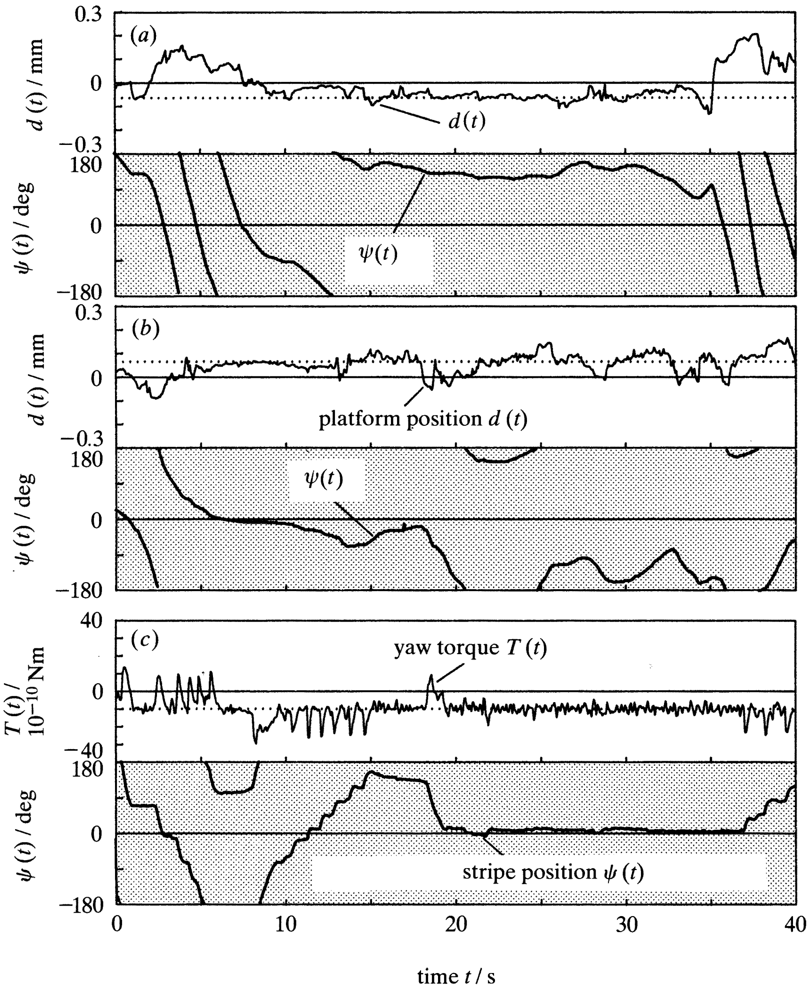

Figure 5. (*a,b*) Individual platform and stripe position traces for 'normal' (*a*) and 'inverted' (*b*) coupling showing optimal stabilization of the arena. Experimental conditions as described in the legend of figure 3. In (*c*) yaw torque and stripe position traces from a bias experiment in the flight simulator are shown for comparison. Coupling coefficient $k_T = -1.1 \times 10^{11}$ deg s^{-1} N^{-1} m^{-1}; $w_b = 110$ deg s^{-1}.

does contribute to this steering process. Flies learn to stabilize the panorama in the course of 3 min but bias compensation remains less complete than with the other polarity of feedback (figure 3*c*). If 3 h later the same flies are again tested with positive feedback but this time with the other polarity of the bias they need 10 min to adapt their behaviour (figure 4*c*). With 'normal' feedback no learning is apparent which would improve the performance. This emphasizes the problem that we do not know the true 'goal' of the fly in this situation. Note the fading out of the open-loop response in the second part of the experiment (figure 4*a*). This can hardly be fatigue as the closed-loop experiment with 'normal' coupling shows (figure 4*b*).

In the platform position traces no stable 'baseline' is found at the position of zero net angular velocity (bias position), although in some flies the bias position has the highest probability in the position histogram. This may imply that motion information is tapped before the integration stage. In the flight simulator (yaw torque–angular velocity loop) the baseline of torque is the level from which torque spikes (and possibly also the small torque pulses) are generated and which in the steady state exactly corresponds to zero net angular rotation. It represents the state of the integrator (Heisenberg & Wolf 1988; Mayer *et al.* 1988) which may be a special feature of the flight control system. As an alternative interpretation, however, it might be the motor output itself which precludes the formation of a stable baseline. This question remains to be investigated more directly.

The finding that the leg posture–angular velocity loop leads to a partial stabilization of the arena with both polarities of the feedback indicates that its main component is operant (Wolf & Heisenberg 1991). The system first cross-correlates an efference copy of its motor commands activating the legs (or proprioceptive signals from the legs) with angular velocity (or acceleration) of the arena. Second, it determines the sign of correlation and third, modifies accordingly the forces the legs exert onto the platform. This is precisely what we do when we discover how to steer a vehicle.

Humans soon after discovering a successful operant loop would establish this connection as a learned motor skill, i.e. as a new stimulus-response chain. In the present context this would mean that the fly would create a directional open-loop response (autopilot), i.e. a high *a priori* probability for a displacement of the legs to the side which in closed-loop would stabilize the panorama, whenever it would start moving. This is not what we observe. The slow reversal learning for the other bias direction after 3 h (figure 4*c*) indicates that the fly has learned a particular advantageous posture rather than the (inverted) sign of the feedback which did not change between the first and second part of the experiment. For a motor skill one would have to look for an effect of the closed-loop training on the open-loop performance. This has not yet been done.

7. CONCLUSIONS

Operant loops give flies and humans the flexibility to use a large variety of different motor outputs for visual steering. For instance, they enable humans to ride bicycles. Our ambition in showing a similar achievement for *Drosophila* does not go far enough as to include a practical test. The present experiment, however, is a further striking example of what we believe is the basic organization of sensory-motor coordination.

Trying out takes time and is a hazard. Reliable open-loop responses (autopilots) which, no doubt, exist as well, under normal circumstances make life easier, even if at the level of microbehaviour they must be understood as stimulus-related high probabilities for certain endogenous motor patterns. It is interesting to note in the present experimental example that the operant learning overrides the open-loop response (figure 3*b*,*c*). This is not always the case. For instance, so far flies have not been able to learn to stabilize the panorama in a simple flight simulator experiment with positive feedback although they are able to do so as soon as the directional response is removed, as in the double mutant *rol sol* (see above).

It is of minor importance in this context whether open-loop responses are learned motor skills or phylogenetically fixed predispositions. For instance, it is still not excluded that the normal optomotor response in open-loop is learned. We consider it more likely, however, that it has been phylogenetically fixed. Clockwise rotation of the whole panorama is an extremely reliable indicator of counterclockwise self-rotation and yaw torque in the direction of the movement will be the appropriate compensatory action. Thus, again and again the same operant loop would have been established and possibly the same stimulus-response chain learned. From this situation a directional open-loop response might easily have evolved since it would be faster (at the cost of unnecessary flexibility) and would require less neural processing. It seems reasonable to assume that originally in the evolution of brains all motor outputs were connected to all sensory inputs via operant loops and that from this situation certain sensory-motor links evolved into lastingly modifiable or even fixed ones.

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Discussion

G. D. Sullivan (*Department of Computer Science, University of Reading, U.K.*). Have the dynamic properties of the tracking responses of the 'normal' and 'reversed' flies been studied? If adaptation results from resetting a neural net, then the frequency response of the control loop should be unchanged. However, if there are significant differences in response then it would seem to imply that the fly introduces an additional mechanism.

M. Heisenberg. A careful comparison of the dynamics of platform position (or of yaw torque) during normal and inverted coupling has not been made. From casual inspection of the traces it seems that during the learning phase the dynamics are very different from what they were before the inversion of the feedback sign but that towards the end of the learning phase they normalize to a considerable degree.