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## On Head and Body Movements of Flying Flies

G. Geiger\* and T. Poggio

Max-Planck-Institut für biologische Kybernetik, Tübingen, FRG

**Abstract.** Head and body movements of flies (*Musca domestica* and *Calliphora erythrocephala*) have been studied during sustained flight. Two main points emerge from the analysis: a) Changes in body direction and head direction occur simultaneously in almost all cases. b) During visually guided flight active neck movements are initiated together and in the same direction of body movements. This does not hold in absence of a visual pattern ("search"). Implications of these findings with respect to the organization of the control system underlying head-body coordination in flies are briefly discussed.

In a simplistic view on vertebrate eye movements one recognizes a few types of movement patterns: rapid saccadic movements, drift and high frequency tremor. The main criterion for this distinction relies on their widely different time courses. In a typical record of eye movements during fixation of a target, saccades appear like sudden discrete "jumps", while "intersaccadic" drifts are smooth and slow<sup>1</sup>. The existence of widely separated time scales occur in other contexts too: human head movements during tracking of moving objects are typically much slower than eye movements (Bizzi et al., 1972).

While much is known about eye movements and head-eye coordination in vertebrates, similar information about arthropods is rather scarce. Here we describe head- (and therefore, in flies, eye-movements) and body-movements made by flies during sustained flight. We show that different time scales are not clearly separable neither in the head movements nor in the combined head-body movements.

Flies (*Musca domestica* and *Calliphora erythrocephala*) were suspended from above on a needle pivot supported on conical microbearing (Franceschini, 1976), which allowed them to rotate freely. The pivot was nearly frictionless and inertialess (about 10% of the *Musca* inertia and 3% of *Calliphora* inertia). Flying flies were placed at the center of a 5.6 cm diameter translucent white drum containing a black pattern, lit homogeneously from outside with an average brightness of about 378 cd/m<sup>2</sup>. The flies were viewed with a videocamera from above through an operation microscope; the camera was connected to a time lapse video-recorder (50 pictures per second).

The records were analysed frame by frame to obtain the angular position in the horizontal plane of the head ( $\alpha_h$ ) and of the body ( $\alpha_b$ ). The data were digitized and stored for further processing<sup>2</sup>.

In a stationary drum *Musca* flies flew most of the time towards a vertically oriented black stripe (fixation): Figure 1a shows a sample of head ( $\alpha_h$ ), body ( $\alpha_b$ ) and neck ( $\alpha_h - \alpha_b$ ) angular movements during part of a long fixation period. Figure 1b gives a similar record in the case of a white panorama without any pattern.

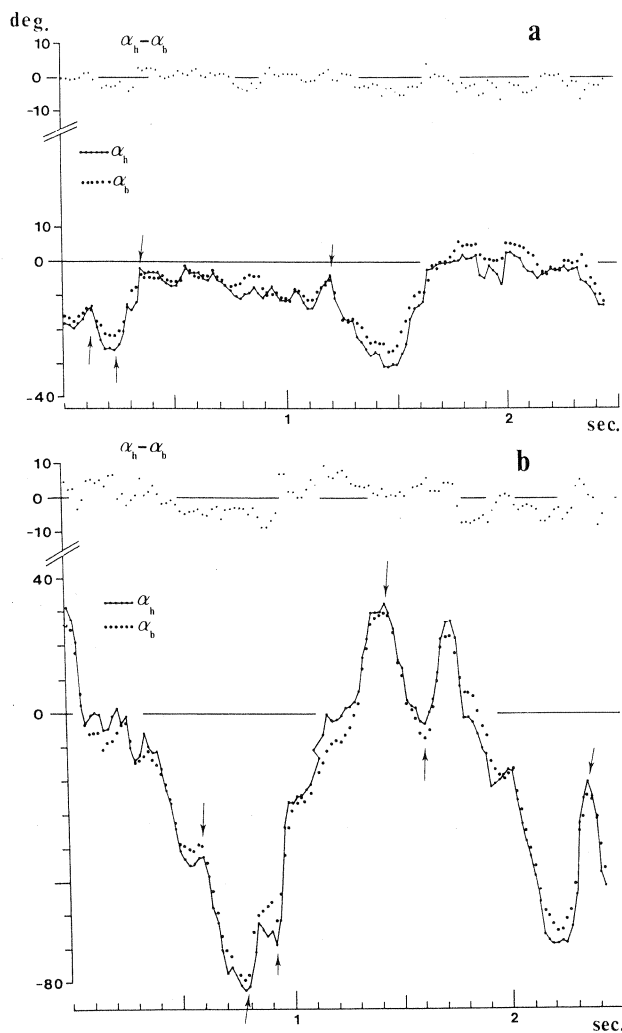
We were unable in these and various other similar records to recognize clearly two or more widely separated time scales in either head or body movements. No clear-cut saccadic flicks can be consistently separated from smooth drift, although more rapid movements are seen from time to time.

Table 1 summarizes some statistical information about longer records both in the fixation and in the no-pattern case. Histograms of the neck angle ( $\alpha_h - \alpha_b$ ) are shown in Figure 2, together with histograms of the angular variations from one frame to the next one,

\* Present Address: EMBL, Heidelberg, FRG

<sup>1</sup> The importance of saccades for the maintenance of fixation has been recently questioned by R. Steinmann et al. (1973). They maintain that microsaccades are an "overlearned motor habit". Smooth drift seems sufficient for fixation

<sup>2</sup> Angles were estimated with a maximum error of  $\pm 1^\circ$  for the body,  $\pm 2.5^\circ$  for the head and  $\pm 1.5^\circ$  for the neck. Controls were performed by independent double evaluation of the same records. It seems rather difficult to obtain a better accuracy



**Fig. 1a and b.** **a** Two sample records of the head ( $\alpha_h$ ), body ( $\alpha_b$ ) and neck ( $\alpha_h - \alpha_b$ ) movements of a fly (female *Musca domestica*) during fixation of a black vertical stripe ( $4^\circ$  wide and extending on the vertical from  $-50^\circ$  to  $+45^\circ$  with respect to the eye's equator). The sample rate is 1 point each 20 ms. The arrows show changes of directions that occur simultaneously for head and body. Other examples can be easily found in the records. Male flies show similar head and body movements. **b** Sample records of head and body movements of the same fly in absence of any contrasted pattern. The body performs a kind of "random walk", pointing with equal average frequency in all angular directions. The short samples shown here again demonstrate the same kind of head-body movements as in **a**. The neck does not apparently play a consistently active role in the initiation of direction changes

which represent an approximation of the neck angular velocity. Three points emerge from these studies

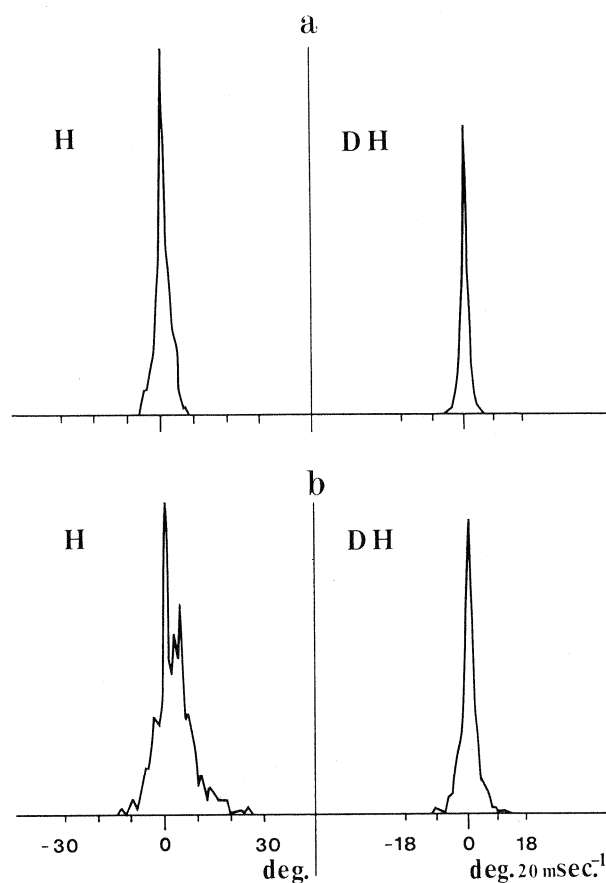
a) Changes in body direction ( $\alpha_b$ ) and head direction ( $\alpha_h$ ) occur simultaneously in almost all cases<sup>3</sup>.

b) During fixation of one stripe active neck movements coherent with body movements can be observed

<sup>3</sup> Even if the temporal resolution of the videocamera is only 20 ms, the very high percentage of "simultaneous" head and body jumps observed in the same frame implies that our actual resolution is much better

**Table 1.** Direction changes of either head or body larger than  $5^\circ$  (and therefore significantly above the noise level) were counted from several records like Figure 1a and b for a total of 24 s (fixation) and 12 s (no pattern). In the limits of our temporal resolution almost all these head- and body-"jumps" occurred simultaneously in both the fixation case (97%) and the no-pattern situation (99%). In the fixation case, after initiation of a jump, the head was mostly moving faster than the body, implying an active coherent role of the neck. When no visual stimulus is present neck movements are apparently more independent from body movements. Results consistent with Table 1 were also obtained with other criteria, for instance involving "course changes" in either body or head. The two populations—fixation and no fixation—are significantly distinct

	Fixation [%]	No fixation (no pattern) [%]
Simultaneous jumps	97	99
From these: head faster	53	27
body faster	13	14
equally fast	34	59



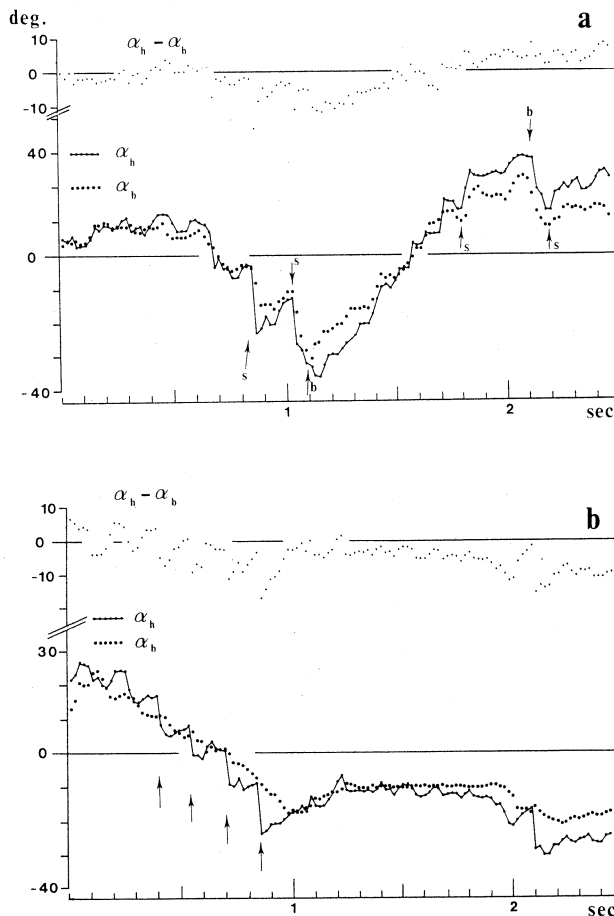
**Fig. 2a and b.** Histograms of the neck angle (H) and of its angular displacement from one frame to the next one (DH) in **a** the fixation (compare Fig. 1a) and **b** in the no pattern case (compare Fig. 1b). The records evaluated in this way total 24 s in both cases. The histograms are not normalized. The distribution of the angle between body and head (neck angle) seem to depend on the presence of the visual input

in a significant number of jumps. As a consequence head jumps are faster than body jumps, although both are simultaneously initiated. In the case of no pattern (random search by the fly) head movements are less coherent with body movements. The distribution of neck movements is different in the two cases; the velocity distribution remains more similar (Fig. 2).

c) Under our experimental conditions, neck movements seem to play no discernible role for stabilizing the head. In particular the head does not seem more stable on target than the body.

These results are in conflict with recent observations made on *Calliphora erythrocephala* by M. Land (1973), who consistently observed rapid saccades of the head followed by slow<sup>4</sup> movements of the body and active neck compensatory movements in the opposite direction to the body movements. One of the possible explanations for this discrepancy is the comparatively large inertial load of Land's pivot, which we have estimated in the order of 6 times the inertia of *Calliphora*. Therefore, we compared *Musca* and *Calliphora* head and body movements during fixation, with and without an additional inertial load added to the pivot of our system. Figure 3a shows fixation of a black vertical stripe (4° wide) in the case of *Calliphora*. In the experiment shown in Figure 3b the same fly fixated the same pattern with an additional inertial load of about 10 times its own (and no significant increase in friction). Figure 3b is again a sample of a long record and reveals, in contrast with Figure 3a (and 1a, b) a pattern of head-body movements similar to the one described by Land. Thus, Land's data are probably affected by the too large inertia of its device<sup>5</sup>. Other experiments without additional inertia but more "structured" patterns (i.e. (a) 8 equidistant stripes, each 4° wide; (b) 4 equidistant stripes, each 20° wide; (c) a vertical stripe in the lower half of the drum with visual noise in the upper half; (d) a rotating stripe) do not reveal head-body movements of the "Land-type".

In conclusion, our results are consistent with the view that body and head initiate independently and simultaneously changes in their direction, under common visual control. Peripheral feedback loops may successively provide a finer coordination of head and body movements. For instance, sensory mechano-

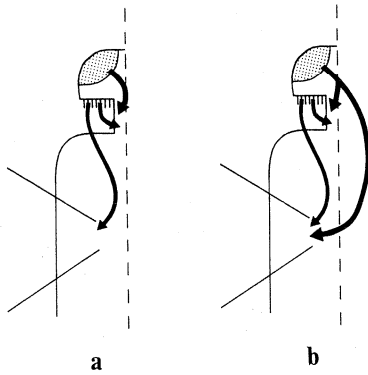


**Fig. 3a and b.** Record of head and body movements of *Calliphora erythrocephala* (female) during fixation of the same vertical black stripe with **b** and without **a** an additional inertial load about 10 times the fly's own inertia. Observe the different type of head and body movements in the two cases. The arrows in **b** point to saccadic-like movements of the head: the body trajectory is much smoother and lags consistently behind the head, due to the higher inertia. In **a** various types of head and body movements can be observed: for instance, simultaneous for head and body (**s** arrows) or initiated by the body **b** (arrows) with an opposite movement of the neck. In **a** one can recognize two "saccadic-like" movements of the head (however, head and body initiate the jump simultaneously): they are, in the 40 s record of which this is a sample, extremely rare

<sup>4</sup> The time scales measured by Land (1973) are 100/200 ms for the body against 20/40 ms for the head

<sup>5</sup> The aerodynamic friction coefficient [ $k$  in Reichardt and Poggio (1976); see also Land and Collett (1974)] could in principle also take, in ours and Land's (1973) "pivot" experiments, unphysiological values, because of the absence of forward motion. For the experiments described in this paper, preliminary data (on *Musca*) seem to exclude this possible artefact; both the moment of inertia ( $\Theta \approx 1.6 \cdot 10^{-3}$  dyn cm s/rad) and the friction coefficient ( $k \approx 0.24$  dyn cm s/rad) are in the physiological range (Reichardt and Poggio, 1976; Land and Collett, 1974)

receptors between the head and the thorax serve such a purpose (Mittelstaedt, 1950; Liske, 1976). Figure 4 shows diagrammatically two different basic hypothesis about the organization of the control system which underlies head and body movements. Our data exclude the first hypothesis (Fig. 4a) and are consistent with the second one (Fig. 4b), while Land's data are consistent with both hypothesis and, superficially, seem to suggest the first one (but see Land, 1975). Interestingly, Figure 4b is very similar to the known organization of eye-head coordination in monkeys (Bizzi et al., 1972).



**Fig. 4a and b.** Two possible hypothesis about the organization of the system controlling head and body movements. In **a** visual input controls neck movements; mechanoreceptors (for instance, sensory hairs between head and thorax) determine corrective body- (and perhaps neck-) movements. In **b** visual input controls simultaneously neck and body movements; peripheral feedback loops (probably the prosternal organ), activated by the head-body movements, induce corrective body- (and possibly also neck-) compensatory movements. Our data (see Table 1) exclude the first possibility **a**, which is also inconsistent with head-fixed fixation and tracking experiments (Reichardt, 1970; Reichardt and Poggio, 1976). The general scheme of **b**, beside possible evolutionary advantages, serves also better the purpose of maintaining a visual target in the relatively small "foveal" region (see Reichardt and Poggio, 1976) of the complex eye. When there is no visual pattern, neck movements, although present (Fig. 2), apparently fail to be "coherent" with body movements (Table 1). This seems to imply that random search commands [noise commands, in the terminology of Reichardt and Poggio (1976)] are not equivalent to visual input for the head-body control system

Moreover, Table 1 and Figure 2 suggest that in absence of a visual pattern the "search" movements of head and body are significantly more independent than during fixation. From Figure 4b more detailed organization structures can be conjectured on the basis of this and a few other data. Additional experiments, however, are necessary to clarify such questions.

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Dr. T. Poggio  
MPI für biolog. Kybernetik  
Spemannstr. 38  
D-7400 Tübingen  
Federal Republic of Germany