

The Effect of Pattern Movement on the Impulse Activity of the Cervical Connective of *Drosophila melanogaster*

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Action potentials of some of the 3578 nerve fibres in the cervical connective of *Drosophila melanogaster* can be recorded with extracellular electrodes. The spike rate increases if moving striped patterns are presented to the compound eyes, especially with horizontal front-to-back movement. The response is small or absent with the reverse (or with vertical) directions of movement. The main properties of this response are described, and briefly discussed.

Introduction

In insects the two prominent parts of the central nervous system, the cephalic and the thoracic ganglia, are connected by a pair of cervical connectives, which in most Diptera are fused into one. A cross section through the connective of a wild type female of *Drosophila melanogaster* (Fig. 1*) shows 3578 nerve fibre profiles. Their mean diameter is about $5\ \mu\text{m}$ in the two dorsally situated "giant fibres"¹, $1-3\ \mu\text{m}$ in another set of 70 fibres, and less than $1\ \mu\text{m}$ in the remaining 3506 fibres (Fig. 2).

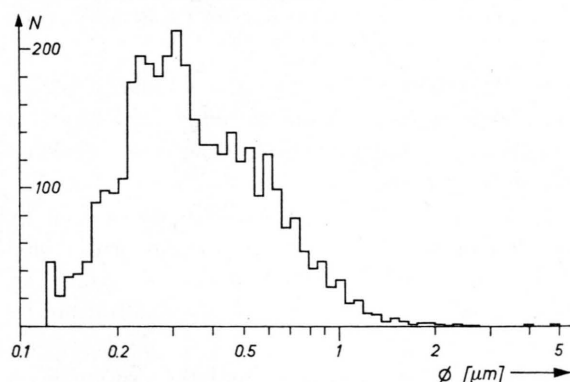


Fig. 2. Frequency distribution of mean fibre diameters in the cervical connective shown in Fig. 1. The mean fibre diameters were determined by matching circles of approximately equal area. The total number of fibres is 3578.

To record the action potentials of at least some of these comparatively thin fibres, the forelegs and parts of the prothoracic sternite are removed. A low impedance hook electrode is *in situ* attached to the

intact connective, and the reference electrode is placed at the posterior edge of the incision. The preparation is then sealed with an insulating dental cement (Scutan®), which reduces the extracellular shunt conductance, and preserves the preparation from rapidly drying out. High-gain/low-noise amplification ($\cdot 10^5$), and narrow band frequency filtering ($0.5-2\ \text{kHz}-16\ \text{dB/oct.}$) reveal nerve spikes of $5-50\ \mu\text{V}$ peak-to-peak amplitude. The experiments were continuously recorded on magnetic tape ($\text{dc}-2.5\ \text{kHz}$). Repeated evaluation of these records with a variable threshold discriminator plus event counter ($\leq 15\ \text{kHz}$) showed a. that the count rate decreases exponentially with increasing threshold voltage; this is to say that the impulses of individual fibres cannot be discriminated by their particular amplitudes, and b. that the results reported below become – within certain limits – independent of the threshold, if allowance is made for a common count rate factor which is due to the selected threshold of the discriminator.

Results

1. In the *absence of stimuli* there is a continuous activity in the cervical connective which fluctuates in time. There are regularly recurring spike bursts, which correlate with respiratory movements and there are irregular periods of high activity, which might be due to spontaneously intended movements. This impulse activity can be modified by a variety of stimuli, including visual ones.

To investigate the responses of the cervical connective to continuously moving patterns on the left and/or the right side of the fly, the visual stimulus was presented to the anterior monocular visual field

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* Fig. 1 see Table on page 596 a.



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of the corresponding eye or eyes. The pattern on either side consisted of a continuous sequence of bright and dark stripes, moving at constant angular speeds w in the range of 0.4–400 degr./sec across a translucent screen. The angular period of the patterns was $\lambda = 40^\circ$ and the contrast between bright and dark stripes was $m \approx 0.9$. The average luminance was $\bar{I} = 500$ cd/m² unless otherwise stated. The direction of pattern movement M with respect to the anterior body axis A of the fly is given by the angle $\angle MA$. Pattern movement along M is either *progressing* towards or *regressing* from the vertex of $\angle MA$. If not otherwise stated $\angle MA$ is $\pm 0^\circ$. "Progressive" stimulation thus denotes horizontal front-to-back movement either on the left (\swarrow), or on the right (\searrow), or on both sides ($\swarrow \searrow$), whereas "regressive" stimulation denotes horizontal back-to-front movement, either on the left (\nwarrow), or on the right (\nearrow) or on both sides ($\nwarrow \nearrow$).

2. The following responses to the *pattern movement* are obtained from the cervical connective:

- Binocular progressive movement increases the impulse activity. This effect lasts until the movement comes to rest (Fig. 3, left side).
- Binocular regressive movement elicits comparatively weak, if any, responses (Fig. 3, right side). A small transient

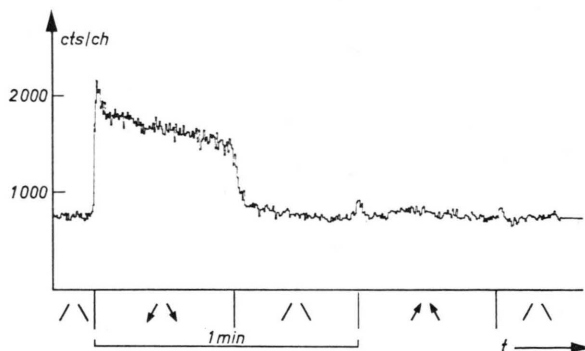


Fig. 3. Time course of the response to binocular progressive ($\swarrow \searrow$), and regressive ($\nwarrow \nearrow$) pattern movement at a contrast frequency $w/\lambda = 1.8$ Hz; 15 stimulus presentations to one fly were summed with a 400-channel signal analyzer.

increase of activity at the onset and at the end of movement is significant in most of the experiments. This result is in contrast to the properties of the bi-directionally responding, wide-field movement-sensitive units in the optic lobe of other flies, which show a marked inhibition of their spontaneous activity if the pattern moves opposite to the preferred direction².

Rapid permutation of stimulus conditions (movement/rest, progressive/regressive, left eye/right eye/both eyes), and averaging of samples of 5 sec duration for each of the combinations is used to suppress the influence of fluctuations of the background activity in the following experiments.

3. Monocular progressive stimulation on the left or on the right eye is only somewhat less efficient than binocular progressive stimulation (Fig. 4). It

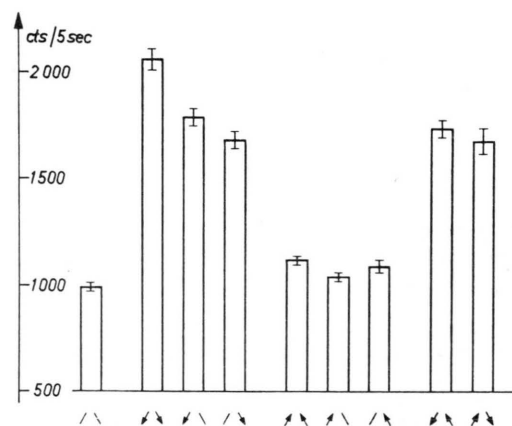


Fig. 4. Responses to different combinations of movement stimuli as specified by the arrow symbols. The patterns were continuously illuminated, and the movement stimuli ($w/\lambda = 4.5$ Hz) were sequentially presented for 5 sec at 15 sec intervals. Mean values \pm standard error of the mean³; $n = 30$; one fly.

is not yet clear whether this non-additivity of the monocular responses is due to binocular interaction or to the increased probability of spike coincidence at high count rates.

4. A similar effect of non-additivity is seen by comparison of the responses to monocular and binocular regressive stimulation (Fig. 4). However, the differences of the comparatively small responses are not significant.

5. Rotatory movement around the test fly gives rise to almost the same responses as monocular progressive stimulation alone (Fig. 4). The monocular regressive component of the rotatory stimulus is apparently ineffective.

6. The flies respond equally well to binocular progressive movement, no matter whether this stimulus is presented to the dorsal or the ventral halves of the compound eyes (Fig. 5). This property of the cervical connective response agrees well with the optomotor flight torque response, where partial responses, elicited by stimulation of different

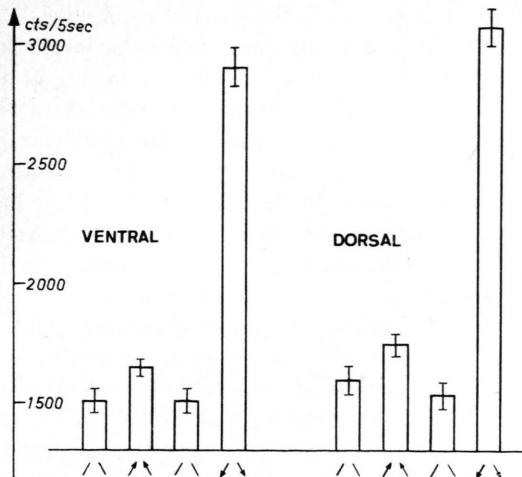


Fig. 5. Responses to binocular progressive (regressive) movement, presented in alternating sequence to the dorsal and ventral halves of the eyes for 5 sec at 15 sec intervals; $w/\lambda = 3$ Hz; means \pm S.E.; $n=30$; one fly.

(dorsal and ventral) eye regions, are added to yield the total response⁴. The cervical connective response is not consistent with the process of object fixation^{5, 6}, which in the housefly was shown to originate from pattern movements in the ventral half of the visual field⁵.

7. If the elevation $\angle MA$ of the pattern movement is varied, a maximum of the response is found for progressive movement in approximately horizontal direction ($\angle MA = \pm 0^\circ$). The response to pattern movement in vertical direction ($\angle MA = \pm 90^\circ$) is not significantly different from the resting

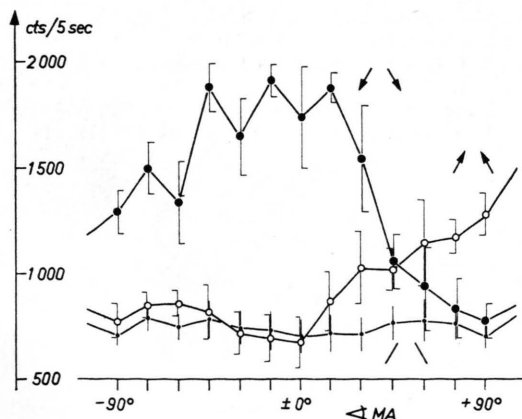


Fig. 6. Cervical connective response as a function of the direction ($\angle MA$) of pattern movement. The maximum response is obtained with movement progressing in horizontal direction ($\angle MA = \pm 0^\circ$) from anterior to posterior. No significant inhibition occurs with movement in the opposite direction. $w/\lambda = 3$ Hz; mean \pm S.E.; $n=5$; one fly.

activity for downward movement ($\angle MA = +90^\circ$) and somewhat larger for upward movement ($\angle MA = -90^\circ$). A significant effect of regressive pattern movement is missing even at $\angle MA = \pm 0^\circ$ (Fig. 6).

8. If the temporal contrast frequency w/λ of the pattern (i.e. the number of periods/sec) is varied from 0.009 Hz to 9 Hz at comparatively high luminance ($\bar{I} = 500$ cd/m²), the response to binocular progressive stimuli increases monotonically. The maximum and decline of the response, due to flicker fusion, occur obviously beyond the maximum speed of 9 Hz, which has been achieved with the present apparatus. Under similar conditions, binocular regressive movement elicits much smaller responses with a broad maximum near $w/\lambda = 3$ Hz (Fig. 7). Quite different results are obtained at

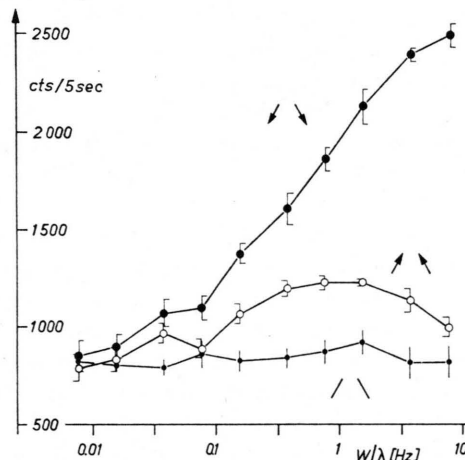


Fig. 7. Cervical connective response to binocular progressive (regressive) movement as a function of the contrast frequency w/λ . The average luminance of the pattern is $\bar{I} = 500$ cd/m². The maximum and decline of the response to progressive movement is expected beyond $w/\lambda = 9$ Hz. Means \pm S.E.; $n=7$; one fly.

comparatively low pattern luminance ($\bar{I} = 2$ cd/m²). The progressive stimulus elicits the maximum response at about $w/\lambda = 3$ Hz. Almost no response is obtained at $w/\lambda = 9$ Hz. The regressive stimulus evokes no measurable response at low pattern luminance. The effect of the luminance on the maximum of the response to different contrast frequencies, which was primarily derived from responses of different preparations under different conditions, has been verified by permutating selected combinations of \bar{I} and w/λ in experiments with individual flies.

9. Some of the experiments reported here for *Drosophila melanogaster* (35 flies) have also been

performed with *D. immigrans* (5), *Musca domestica* (12), and *Calliphora erythrocephala* (7), and yielded very similar results.

Discussion

The results show that specific changes in the nervous activity of the cervical connective of *Drosophila* can be observed in response to moving visual patterns, even though the recording technique does not allow to isolate single units. The involved fibres respond with a pronounced directional preference to horizontal pattern movement from front to back. In principle such a system of movement sensitive elements would be sufficient to establish the orientation control reflex or the optomotor torque response of the insect. We know however from behavioral studies that the animals do respond to the reverse movement. In flying fruit flies, the response to regressive stimuli is about one third of the response to progressive stimulation^{6,7}, and in walking fruit flies the responses are of almost equal size⁸. Furthermore, the investigation of the lift control response⁸ of the flying fruit fly has established the ability to evaluate also the vertical component of the moving stimulus. In order to explain the apparent discrepancy between the properties of the cervical connective response and the behaviour of intact fruit flies, one may assume that information, concerning progressive and regressive movements within the visual environment, is conveyed to the thoracic motor system by fibres of different size

and/or location within the cervical connective.

Some of the visually controlled behavioral traits depend differently upon certain parameters of the stimulus. The location of the neural networks, which provide the control patterns for the particular behavioral traits, is not yet known. If these networks were located within the thoracic compound ganglion, rather general output fibres of the visual system should pass through the cervical connective. In this case one would expect to find no direct correspondence between the response characteristics of the movement sensitive elements in the cervical connective, and any one of the specific behavioral traits. One would gain though, from the cervical connective responses direct access to the output of a general movement perception system, located within the cephalic ganglia. If on the other hand the networks which control the different behavioral traits were located within the fly's head, one would get access to only a limited part of the movement perception system, but one would gain detailed information about the neural basis of a specific, yet unknown, type of behaviour.

Studies are under way to analyze, in more detail, the response properties of the movement sensitive elements in the cervical connective, and to establish their relation to visually controlled behavioral traits. The objective of the forthcoming studies is to understand the particular nature of behavioral mutations, which have recently been induced in *Drosophila melanogaster*^{9,10}.

¹ M. E. Power, J. comparat. Neurol. **88**, 347 [1948].

² L. G. Bishop, D. G. Keehn, and G. D. McCann, J. Neurophysiol. **31**, 509 [1968].

³ Standard error of the mean: $S.E. = \pm \sqrt{\sum(x_i - \bar{x})^2 / n(n-1)}$.

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⁵ W. Reichardt, Naturwissenschaften **60**, 122 [1973].

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⁷ K. G. Götz, Kybernetik **4**, 199 [1968].

⁸ K. G. Götz and H. Wenking, J. comparat. Physiol. **85**, 235 [1973].

⁹ Y. Hotta and S. Benzer, Nature [London] **222**, 354 [1969].

¹⁰ M. Heisenberg, J. comparat. Physiol. **80**, 119 [1972].

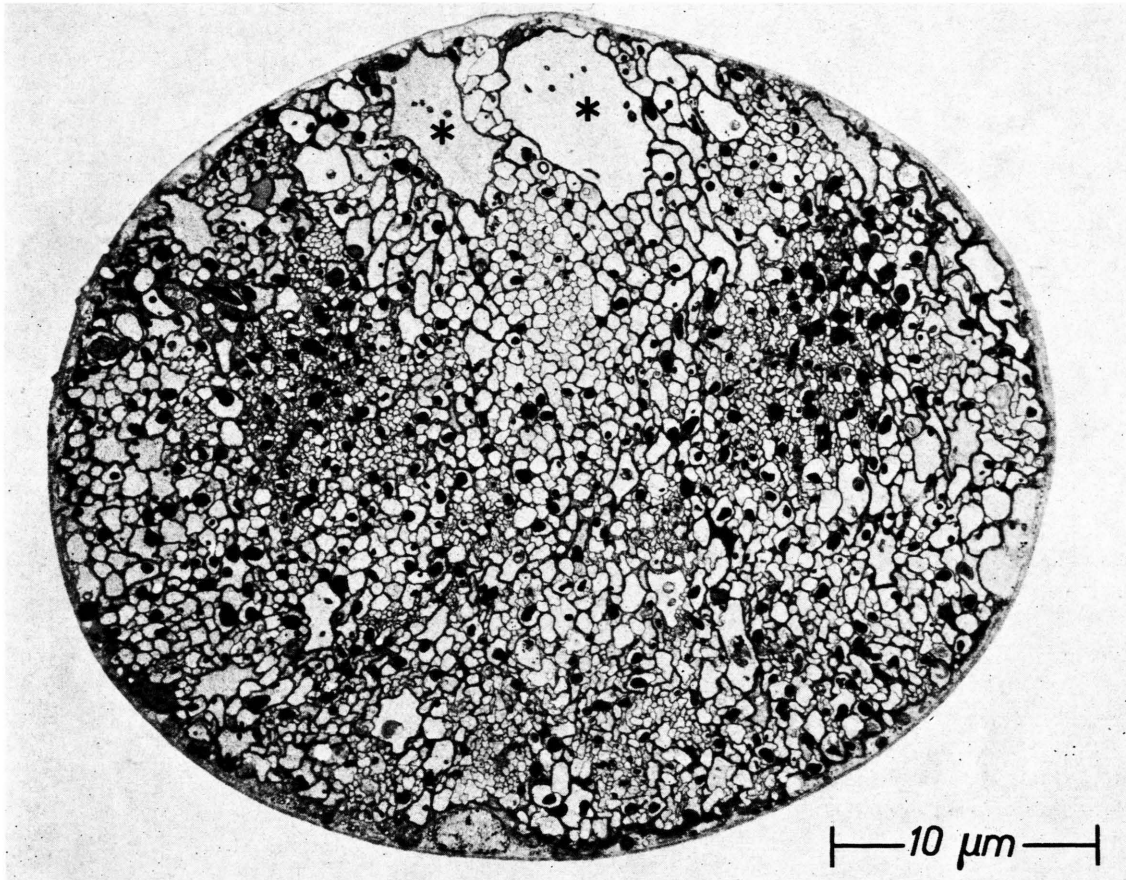


Fig. 1. Cross section through the cervical connective of a wild-type *Drosophila melanogaster* female. The dorsally located "giant fibres" are marked with * (Courtesy Dr. C. B. Boschek).

