Visual Flicker Induces Orientation Behaviour in the Fly *Musca*

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Visual Flicker, Orientation Behaviour, Dipteran Fly

Flies navigate under visual control[1]. When a fly perceives an object within its visual surroundings, it may turn towards the object. This orientation behaviour plays an important role in the fixation of objects and image stabilization, tracking and possibly even more complex phenomena such as pattern perception (see for example[2–6]). Although this kind of behaviour normally occurs in a “closed-loop” situation, it can be explained by “open-loop” experiments under steady state conditions. This has been shown in a quantitative behavioural analysis of object fixation by tethered flying flies[3]. As reported by Reichardt[3], stabilized retinal images of stationary objects fail to elicit a turning reaction whereas moving objects do. These observations are incorporated in a phenomenological theory describing the basic logical structure of the flight orientation by means of a stochastic equation of motion[7]: The angular velocity of the surrounding panorama (around the fly’s vertical axis) provides the visual feedback. However, from this one cannot conclude that the fly’s visual system computes instantaneous angular velocities. When looking for the visual stimuli which may induce orientation, one has to bear in mind the variety of events that may be evoked by movement. It is known from earlier experiments[8–12] that the *direction-sensitive* perception of motion in the steady state is described by the *correlation* of signals coming from different receptor channels. In the case of stationary (open-loop) *orientation* behaviour, however, the results to be reported here suggest a *superposition* of signals from different receptor channels.

Flies (*Musca domestica* females) with fixed heads were suspended on a torque compensator[11, 12] and placed in the centre of an evenly illuminated white drum. Two vertically oriented filament lamps, placed closely together, were positioned at 15° to the right (or to the left) of the direction of flight. Each lamp subtended an angle at the fly of 2.7° width by 40° height (the divergence of neighbouring vertical rows of ommatidia is about 2.5°). Predominantly the ventral parts of the compound eyes were exposed to the visual stimulation. By means of current control, the intensity of the two lamps could be modulated sinusoidally and independently of one another at a standard frequency of 3 Hz. The maximum luminance of the lamps equaled the background luminance of about 60 cd/m², the minimum reached 40% of this value. In-phase modulation led to synchronous flicker stimulation, whereas a phase shift $\Delta\Omega$ of π radians resulted in “antiflicker”. When the light modulation of the right filament lamp followed that of the left lamp, $\Delta\Omega$ was defined to be positive and between 0 and π. With positive phase shifts $\Delta\Omega$, a motion to the right was simulated, whereas negative phase shifts $\Delta\Omega$ (between 0 and $-\pi$) simulated a motion to the left. The response obtained was the fly’s torque around it’s vertical axis, averaged over 1 minute of steady flight. The zero level of the response was measured when the luminance of the two lamps remained unmodulated at a level of 70% of the maximum. Changes of the colour spectra of the tungsten lamps result from current modulation but do not seem to affect the experimental results reported here[13].

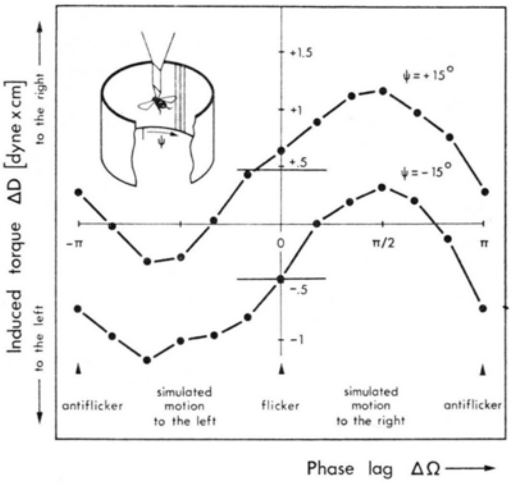

Fig. 1. A single fly’s mean torque response ΔD, which is induced by two vertically oriented filament lamps (2.7° wide by 40° high each). The intensities are modulated sinusoidally and phase-shifted by $\Delta\Omega$ with respect to one another in order to simulate motion or flicker. The phase lag $\Delta\Omega$ is defined to be positive if the luminance modulation of the right lamp follows that of the left lamp. The background luminance is about 60 cd/m². The two horizontal bars in the graph at about ±0.5 dyne cm indicate the phase-independent reaction level. The amplitude of the sine-wave is about 0.7 dyne cm.

Fig. 1 shows the mean induced torque response ΔD measured on a single test fly as a function of the phase lag $\Delta\Omega$ of the two flickering filament lamps. The upper curve results when the two lamps

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are positioned at $\psi = +15^\circ$ to the right side of the midline of the animal (see figure inset), the lower one when the lamps are positioned at $\psi = -15^\circ$ (left side). It turns out that the expression $A + B \sin \Delta\Omega$ closely approximates the torque response ΔD, if all experiments of the series are taken into account:

1. The sinusoidal dependence of the torque response ΔD is represented by the term $B \sin \Delta\Omega$. The amplitude B is positive and of the same size for both positions of the two lamps (*e. g.* B is about $+0.7$ dyne cm in the example shown in Fig. 1): Positive phase shifts (simulation of a motion to the right) contribute a positive torque component to the right, whereas negative phase shifts contribute a negative torque component (to the left). This component of the total response ΔD reflects exactly the *direction-dependent* response to the perceived motion mentioned above, as predicted by the correlation model[9]. In a rather general treatment of movement detection models applying Volterra series[14], this experimental result is related to the symmetric part of the *second order cross-kernels*. Higher order nonlinearities seem to be negligible, since the data are described sufficiently well by the expression $\sin \Delta\Omega$. Recently, Marmarelis and McCann[15] came to a similar conclusion concerning electrophysiological recordings of class II units under white noise stimulation.

2. The term A describes the mean reaction level which is positive, if the two lamps are positioned at $\psi = -15^\circ$, and negative, if the lamps are at $\psi = -15^\circ$. Therefore, A depends on the position: $A = A(\psi)$ (Fig. 1: $A(+15^\circ) = -A(-15^\circ) \cong 0.5$ dyne cm). The mean torque response A of the fly is directed towards the two lamps. In earlier experiments[3, 16], a glow modulator lamp was used to apply in-phase flicker without background illumination. Only a small effect was observed, presumably because the light source was too dim and the modulation too small to induce significant torque responses. In terms of the Volterra-description[14, 17], the *self-kernels* may provide the phase-independence which is necessary to account for the position-dependent reaction recorded in the present experiments. This conclusion is however only tentative. The complete specification of all kernels of a multi-input system with one output requires input signals independent of each other. To obtain strong reactions in the present experiments, however, groups of about 15 ommatidia were stimulated simultaneously[18]. This could be improved upon in an experiment where one or more receptors are stimulated discretely, as has been done for the direction-sensitive perception of motion in walking flies[19]. Discrete stimulations of this kind are not yet possible for the flying fly. If we assume, however, that only second order nonlinearities exist for the position-dependent component of the response, then the receptors which are stimulated by the left stripe interact with the ones stimulated by the right stripe in a linear (therefore phase-indifferent) manner to provide orientation responses. The "sequential stimulation", which is characteristic for movement, is not required.

Since the phase shift $\Delta\Omega$ is not accounted for in the fly's orientation, this component $A(\psi)$ of the torque response can be studied selectively if one stimulates using a single flickering filament lamp (subtending in this experiment an angle of about 4.5°). In what manner does the orientation depend on the position ψ of the vertical filament lamp? Fig. 2 shows the term $A(\psi)$ measured on a single fly. The absolute values of the torque responses of corresponding positions ψ and $-\psi$ are averaged to account for the bilateral symmetry of the animal. The results of a single experiment often do not precisely reflect the bilateral symmetry due to *e. g.* inaccurate alignment of the fly. At $\psi = 0^\circ$, corresponding to the direction of flight, no turning reaction is observed. If the lamp is positioned at the right side, the torque response is positive (to the right); it increases with increasing ψ, reaches a maximum at about $\psi = 20^\circ$, and from there on decreases towards the back. Correspondingly the torque response is negative if the lamp is positioned at the left side of the animal: The profile of "attractiveness" $A(\psi)$ is antisymmetric with respect to $\psi = 0^\circ$. One would expect therefore that under "closed-loop" conditions, the fly would hold a single

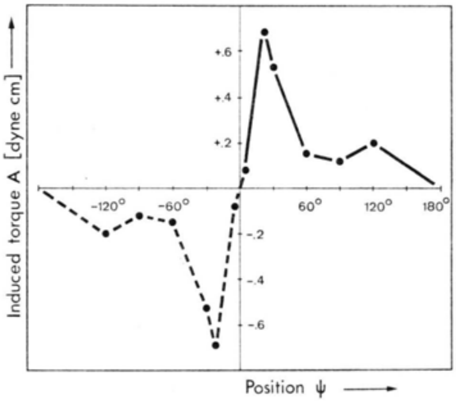

Fig. 2. The phase-independent term $A(\psi)$ measured on a single test fly. The torque response is induced by a single flickering lamp subtending 4.5° at the fly. The absolute values of the original responses measured at corresponding positions ψ and $-\psi$ are averaged (solid line) to suppress the influence of oblique tethering.

vertical stripe at the stable position $\psi = 0^\circ$: The fly would fixate, as has been observed by Reichardt[3]. In those experiments the torque distribution $D_{\text{ind}}(\psi)$ was measured using small oscillations of a thin black stripe. $D_{\text{ind}}(\psi)$ roughly fits into the profile $A(\psi)$ of a flickering lamp. Therefore, from flicker-induced, "open-loop" torque responses one can derive $D_{\text{ind}}(\psi)$, which is essential to formulate the phenomenological theory describing the dynamics of the orientation behaviour. A similar position-dependent perception of objects is known for the lateral eyes of the jumping spider and may elicit a turning motion of the animal, which results in facing the target[20, 21]. Object movements from front to back or from back to front induce the turning reaction; flicker is reported to be an inadequate stimulus. One can easily imagine a type of sensory network (or a processing in terms of Volterra kernels) which is motion-sensitive in either direction but does not respond to flicker. Or, on the other hand, the situation might resemble the one found in the fly where the adequate stimulus is not the movement *per se* but the flicker signal extracted from the movement: Using a relatively small flickering stripe (angular width of up to about 6°) the results are as described above. However, preliminary experiments have shown that broader fields ($\sim 13^\circ$) are often ineffective indicating lateral inhibition. The fine structure of this spatially integrating process is closely related to the optimum stimulus and may be relevant to pattern perception.

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[1] K. G. Götz, Kyb. **4**, 199 [1968].

[2] W. Kirmse and P. Lässig, Biol. Zbl. **90**, 175 [1971].

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

[4] M. F. Land, Nature **243**, 299 [1973].

[5] R. Virsik and W. Reichardt, Naturwissenschaften, in print [1974].

[6] M. F. Land and T. S. Collett, J. Comparat. Physiol., in print [1974].

[7] T. Poggio and W. Reichardt, Kyb. **12**, 185 [1973].

[8] B. Hassenstein and W. Reichardt, Z. Naturforsch. **11 b**, 513 [1956].

[9] W. Reichardt, Z. Naturforsch. **12 b**, 448 [1957].

[10] W. Reichardt, Sensory Communication (W. A. Rosenblith, ed.), pp. 303–317, M. I. T. Press, Cambridge, Mass. 1961.

[11] G. Fermi and W. Reichardt, Kyb. **2**, 15 [1963].

[12] K. G. Götz, Kyb. **2**, 77 [1964].

[13] B. Pick, in preparation.

[14] T. Poggio and W. Reichardt, Kyb. **13**, 223 [1973].

[15] P. Z. Marmarelis and G. D. McCann, Kyb. **12**, 74 [1973].

[16] W. Reichardt, personal communication.

[17] T. Poggio, Biocybernetics **VI**, (H. Drischel, ed.), Fischer-Verlag, Leipzig, in print 1973.

[18] In a similar way the phase-sensitive term $B \sin \Delta\Omega$ represents an average response.

[19] K. Kirschfeld, Information Processing in the Visual System of Arthropods (R. Wehner, ed.), p. 61, Springer-Verlag-Heidelberg, Berlin, New York 1972.

[20] H. Homann, Z. vergleich. Physiol. **7**, 201 [1928].

[21] M. F. Land, J. exp. Biol. **54**, 119 [1971].