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A Special Class of Nonlinear Interactions in the Visual System of the Fly

Leo Heimburger, Tomaso Poggio, and Werner Reichardt
Max-Planck-Institut für biologische Kybernetik, Tübingen, FRG

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Abstract

Flies can detect a small object in front of a randomly contrasted background if the object undergoes small motions. The effect was investigated in fixed flying flies under open-loop conditions. The results suggest that nonlinear inhibitory interactions underly this elementary case of figure-ground discrimination.

Flies (*Musca domestica*) orientate towards a black object in front of a white background [1]. This orientation behaviour and its relation to object tracking and pattern discrimination was investigated in a sequence of papers [2–10].

Recently [4–6] it has been shown in behavioural experiments under natural (closed loop) conditions that flies orient towards a small black object in front of a noiselike contrasted background if the object undergoes at least small motions relative to the background. This effect can also be demonstrated when the foreground and the background are moved relative to the fly's eyes and when the (fixed flying) fly is not coupled to its environment (open loop conditions). Measurements of the time average of the flight torque show that the fly is not attracted by a small object if the object and the background are oscillating together coherently with the same amplitudes. However when the degree of coherence is reduced the object is detected by the fly, which tries to turn towards it [4].

Open loop experiments [11] show that the "attractiveness" of a narrow object (like a stripe less than 5° wide) which underlies the fixation behaviour probably does not require nonlinear lateral interaction of signals between two or more light receptors. However the non-coherence effect described before requires nonlinear interactions between the signals from two or more receptors. The underlying interactions must be nonlinear since the time averaged responses depend upon the input modulation to the receptors. In order to characterize this effect, we have carried out the following experiment under open-loop conditions: a black vertical stripe (3° width) was oscillated around the positions ±30° (the flight direction of the fly, suspended from a torque compensator, is defined as 0°) with an amplitude of ±5° and a frequency of 2.5 Hz. The cylindrical background panorama consisting of randomly distributed contrast elements was oscillated with the same frequency and at the same amplitude in different phases relative to the object. The average "attractiveness" of the object (expressed by the average torque generated by the fly) was measured as a function of the relative phase between foreground (stripe) and background (random pattern). The average response is given in units of a "standard" response to an oscillating stripe in front of the resting background. The figure shows that the fly does not "detect" the object when the phase relation amounts either to 0° (in phase) or to 180° (antiphase). The detection effect reaches its maximum for a 90° phase shift. If the object and the background are oscillated with different frequencies (foreground 1.8 Hz, background 2.5 Hz) the effect is again found to be strong. About half of the 55 experiments included in the figure were performed with a stationary white screen of 13° angular width interposed between the stripe and the background. No difference in the response has been found under the two experimental conditions. The finding that the screen does not effect the detection phenomenon, suggests the existence of laterally interacting units which receive their inputs from receptors that are stimulated by the oscillating stripe and from receptors which receive stimuli from the pattern either side and beyond the borders of the screen. The hypothesis of lateral nonlinear interactions is also supported by the following control experiments: the visual field of the two compound eyes was divided into two halves – above and below the eye's equator. A black vertically oriented stripe was positioned in the lower part of the visual field, whereas the background pattern covered either the lower or the upper part of the field. Again, stripe and background pattern were optically separated by a 13°

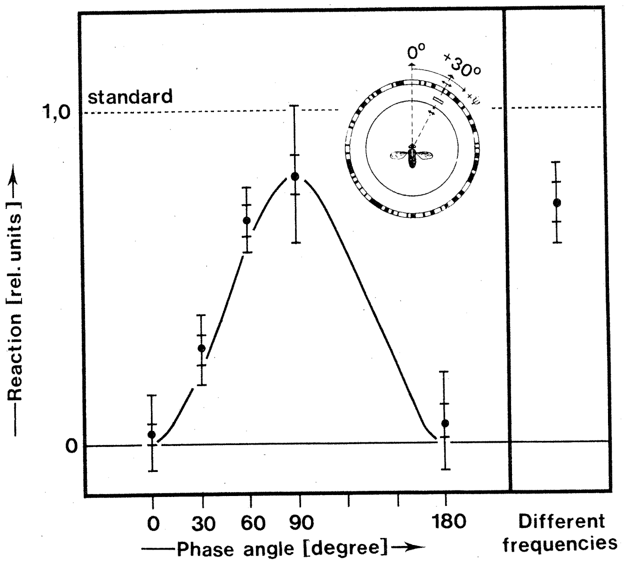

Fig. 1. Average torque responses from 55 experiments plotted as a function of the phase angle between sinusoidally moving foreground and background. The frequency was 2.5 Hz; amplitude to ±5°. In the case of different frequencies, the foreground was moved with 1.8 Hz, the background with 2.5 Hz. Average positions of the stripe were ±30°. The average torque indicated in the figure by filled circles was derived from the difference of the average reactions at the stripe positions −30° and +30°. The inset shows a cross-section of the experimental set-up. The dot on the inner circle indicates the stripe, the oblong between the inner circle and outer circle (random pattern) is the white, non-transparent screen. See text for further details

white screen. When both the stripe and the random pattern were located in the lower half, the same effect described before was found, but the effect was not observed when the random pattern was located in the upper part of the visual field. This finding suggests that a) lateral nonlinear interactions are present in the lower parts of the compound eyes, b) since under both conditions the amount of stimuli received by the compound eyes is the same, saturation at the motor output cannot play an essential role in the effect, showed in Fig. 1.

In previous papers [12–18] the functional interactions in the visual system of the fly underlying either movement detection or orientation behaviour have been described and in most cases conceptually classified in terms of a Volterra series formalism. Movement detection requires second order, multiplication-like interactions between pairs of inputs whereas the orientation response to small objects is most likely due to nonlinear selfinteractions of signals from individual receptors. Lateral inhibitions affecting the orientation response were observed in open- and closed-loop behavioural experiments [5, 9, 19]. The class of interactions underlying the orientation response were theoretically characterized and general criteria, to specify experimentally their order, were thereby available [12, 20]. Experiments employing two flickering light sources with defined phase relations have recently suggested the existence of lateral interactions of order four and/or higher than four [17]. The phase dependence of the effect shown in the figure can be fully accounted for by *fourth order nonlinear inhibitory interactions* between the signals received from two to four receptors. The fourth order interactions are likely to underly both effects; however further experiments will clarify this point. It is possible to give a more detailed description of these interaction properties in terms of the Volterra formalism: this will be given in a forthcoming paper.

The foreground—background discrimination by the fly and our interpretation of it may also be relevant to some psychophysical [21–24] and electrophysiological data [25–30].

It seems to us especially important that the detection effect is found under closed-loop as well as under open-loop conditions; moreover, the closed-loop behaviour can be fully derived from open-loop observations [3, 9]. This implies that the “Reafferenz-Prinzip” [31] is not needed for the explanation of our results.

The lateral nonlinear interactive network involved in the effect which we have described in this paper may play a crucial role in pattern discrimination and perception since nonlinear interactions of input channels could provide a powerful mechanism for pattern selectivity [13]. For instance the discrimination of the environment into figure and ground, which is one of the basic processes in perception, could be performed by interactions of the special class considered here.

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Mr. Leo Heimburger
Dr. Tomaso Poggio
Prof. Werner Reichardt
Max-Planck-Institut
für biologische Kybernetik
D-7400 Tübingen, Spemannstr. 38
Federal Republic of Germany