

Analogous motion illusion in man and fly

SINCE Wertheimer's classic paper¹, research in motion perception has been concerned with the study of visual illusions such as ϕ -motion. Various phenomena of this type are easy to elicit by successive changes of the light flux in spatially distinct photoreceptors, and easy to explain by the specific properties of the motion detectors, although there are reports to the contrary². The present account deals with a less easily comprehensible illusion which is elicited by simultaneous changes of the light flux in differently illuminated receptors³⁻⁵. The phenomenon has previously been ascribed to the prolonged latency of the 'light-on' responses at lower levels of illumination which converts simultaneous stimuli into successive signals⁶, but this does not explain the illusion satisfactorily³. MacKay and co-workers were the first to attribute the apparent motion to the adaptive properties of the input channels of the motion detectors⁴. We show that the illusion can be induced in the fruitfly, *Drosophila melanogaster*, as well as in man. The course control response to motion provides a quantitative assay of the illusion in the fly. The results suggest that the illusion originates in the distortion of the visual signals before motion detection.

To elicit the illusion in humans we illuminated transparent optical wedge filters of linearly graded density with a variable light source. The observer of the circular array in Fig. 1a usually perceives a spurious 'propeller' behind the pattern which rotates a few degrees towards the less transparent side of the wedge filters during light increase, and in the reverse direction during light decrease. The predominant sensation is oscillatory rotation at modulation frequencies of 0.3-2 Hz, continuous rotation towards the less transparent side of the filters at 5-12 Hz and ambiguity at 2-5 Hz.

Motion around a fly evokes vigorous turning in the direction of the horizontal displacement. The response counteracts involuntary deviations from a straight course in a stationary environment. Turning is induced by a regular network of elementary motion detectors. The network accepts stimuli from all

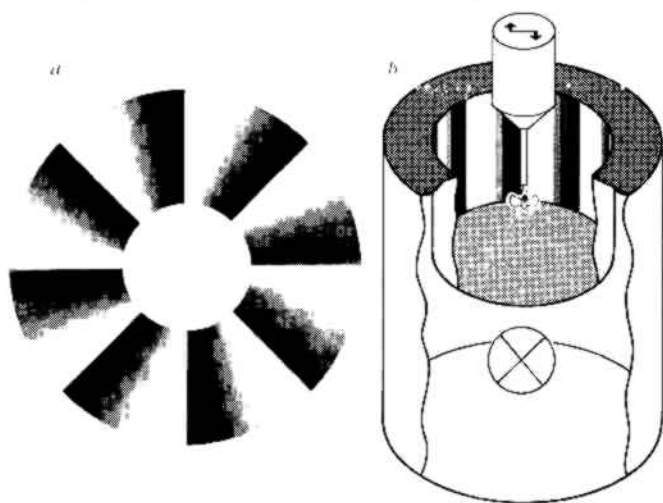


Fig. 1 *a*, Circular array of wedge filters used to elicit, stroboscopically, the illusion of oscillatory (0.3-2 Hz) or continuous (5-12 Hz) rotation in the human observer. The best results were obtained with a transparency of the pattern (absorbance 0-2), illuminated from behind by a sinusoidally modulated light source of almost arbitrary colour and intensity. It may be difficult to see the illusion when the figure is directly exposed to flickering light. *b*, Cylindrical array of wedge filters surrounding the fruitfly *Drosophila* during fixed flight on a torque meter which is used to record the course control response. The stationary pattern was illuminated from outside by a programme-controlled central light source in the lower compartment. The panorama was inverted between experiments and was presented in arbitrary angular positions to minimise lateral disparities of stimulus and response.

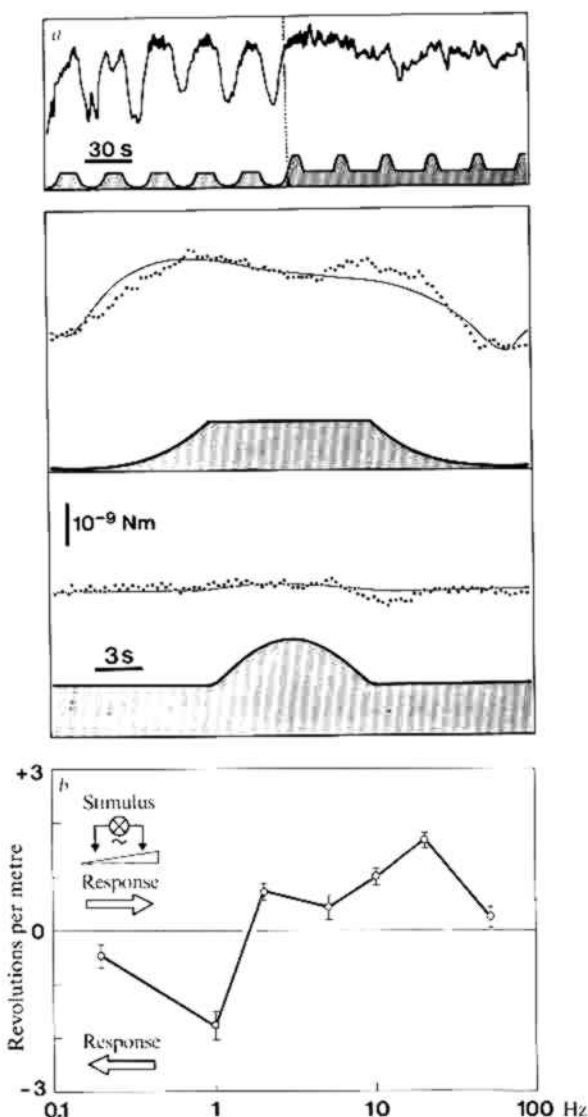


Fig. 2 *a*, Oscillatory motion illusion response of the fruitfly during fixed flight in the experimental set-up of Fig. 1*b*. The shaded area shows the actual light programme ($I_{\max} = 0.003 \text{ cd m}^{-2}$). The upper diagram shows the torque about the vertical axis produced in a single experiment. Increasing torque indicates the increasing tendency to turn towards the less transparent side of the filters, and vice versa. The dots in the lower diagrams refer to the responses of 12 flies, or the averages of 257 subsequent cycles of stimulation. The solid curves represent the motion illusion response of the model in Fig. 3. The oscillatory motion illusion of the fly is predictable and resembles the illusion induced in the human observer. *b*, Continuous motion illusion response of the stationary walking fruitfly as a function of the frequency of sinusoidal light modulation in the panorama of Fig. 1*b*. The tendency to turn was measured in revolutions per metre pathlength. The means and s.e.m. refer to the time averages of the responses of 11 flies which covered a total pathlength of 2,200 m in 250 h.

parts of the visual field, and acts on the difference between the propulsive forces on either side. With the fly held in a stationary position the course control responses of wings⁷ or legs⁸ can be measured quantitatively. Figure 1*b* illustrates the paradigm used to assay apparent motion during fixed flight. The results in Fig. 2 reveal the existence of a motion illusion in *Drosophila* which is strikingly analogous to the corresponding illusion in man. The illusions coincide with respect to the phase and direction of the oscillatory component at low modulation frequencies, and with respect to the direction of the continuous component at high modulation frequencies of the illumination. Maximum intensity and spectral composition of the light source

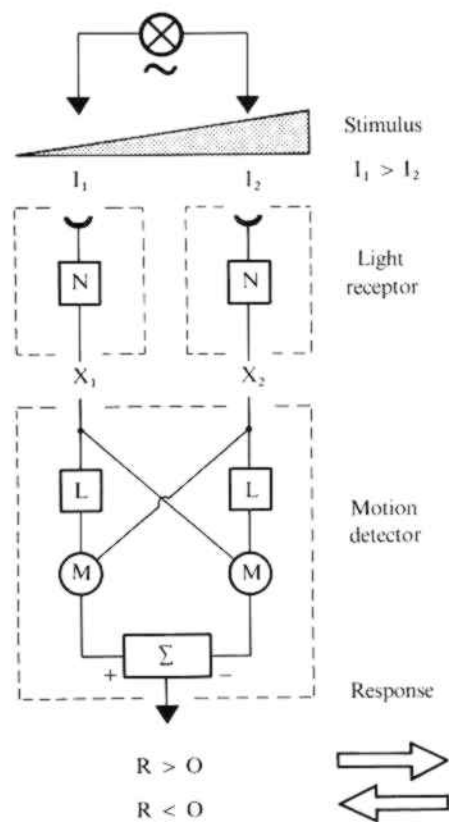


Fig. 3 Motion detector model used to describe the perception of both true and apparent motion in man and fly. The figure shows the attenuation of a sinusoidally modulated light source by a wedge filter. The simultaneous signals, I_1 and I_2 , are nonlinearly transformed (N) into the input signals, X_1 and X_2 , of a motion detector of the Reichardt-Hassenstein type⁹. The model consists of linear elements (L) for the retardation, and nonlinear elements (M) for the multiplication, of the input signals. It produces responses R of opposite sign if the direction of motion is reversed. Partition of the bi-directional motion detector into uni-directional antagonists imposes no constraints on the present results. The motion illusion obtained with the model is due to the nonlinear properties of N . The responses disappear if N becomes linear.

do not seem to be critical in the range $0.003\text{--}300\text{ cd m}^{-2}$.

In the fly the illusion originates within the network of bidirectional motion detectors, each comprising motion-specific interactions between neighbouring input units of the visual system⁸. The steady-state responses of the detectors are adequately described by the correlation model in Fig. 3, where the interaction is achieved by multiplication of two input signals. The model is representative of all 'simple' motion detectors which do not require more than the theoretical minimum of two input units in second-order nonlinear interaction⁹. Models of this type are equivalent in their steady-state responses, and seem to be sufficient to describe the properties of entirely different motion detection systems, such as the direction-selective retinal ganglion cells in vertebrates^{10,11}. The models respond to successive stimulation of their input units and cannot discriminate true motion from the corresponding φ -motion. Figure 3 shows the simultaneous sinusoidal stimulation of the receptors in the present paradigms. The visual input is characterised by the transmission-dependent mean intensities $\bar{I}_1 > \bar{I}_2$, and by the transmission-independent relative amplitude, or modulation, $\Delta I/\bar{I} = \Delta I_1/\bar{I}_1 = \Delta I_2/\bar{I}_2$. In the linear range of signal processing at the receptor level (N) the gain factor of the response, R , of the model is $\bar{I}_1\bar{I}_2(\Delta I_2/\bar{I}_2 - \Delta I_1/\bar{I}_1) = 0$. This is easy to show by application of the operations specified in Fig. 3. The absence of responses at the level of motion detection excludes the genera-

tion of the expected responses at subsequent levels. Nonlinear processing of the simultaneous signals before motion detection becomes necessary to elicit non-zero responses from the detector model.

Surprisingly, the characteristics describing the apparent saturation of photoreceptors in quasi-static conditions, $X(t) \sim I(t)/(I(t) + I_0)$; $I_0 = \text{constant}$ (refs 12, 13), are apparently sufficient to elicit the expected oscillatory responses. To calculate R , the receptor output, $X(t)$, may be developed into a power series about \bar{I} . The first-order term accounts for a positive gain factor $I_0(\bar{I}_1 - \bar{I}_2)\Delta I/\bar{I} > 0$ and describes the illusion qualitatively. The results of a quantitative simulation are shown in the lower sections of Fig. 2a. The solid curves approximate the oscillatory responses of the fly with respect to (1) the light-on effect, (2) the light-off effect, (3) the phase lead on the periodic stimulus¹⁴, and (4) the decrease of the response with increasing background illumination. The matched parameters $I_0 = 0.04I_{\text{max}}$ of the receptor characteristics (N), and the matched time constant $T = 10\text{ s}$ of the low pass filters (L), are also appropriate for the simulation of the response to true motion.

The simulated illusion decreases with progressing linearisation of the receptor characteristics at higher frequencies of stimulation. Concurrently, dynamic receptor nonlinearities become important, in particular, the prolonged latency of the light-on signal of the receptor output at lower levels of illumination^{15,16}. Latency differences between the light-on signals in the present experiments lead to successive stimulation of the input units of the motion detectors in the expected direction, towards the less transparent side of the wedge filters. The oscillatory motion illusion cannot be explained by prolonged latency. Qualitatively, there is no resemblance between the rebound of the transient light-on response $R > 0$ of the model and the marked light-off effect shown in Fig. 2a. Quantitatively, latency differences of 0–25 ms in man⁶, or 0–5 ms in the fly¹⁷, seem to be too small to contribute significantly to the oscillatory motion illusion³. However, accumulation and fusion of latency-induced transients $R > 0$ seem to account for the continuous motion illusion at higher frequencies of stimulation in Fig. 2b. The negative responses at medium frequencies are possibly due to the inversion of the brightness gradient at the edges between neighbouring wedge filters.

The results obtained permit the classification of various types of motion illusion according to their origin within the visual system. Unlike φ -motion² the present illusion requires nonlinear signal processing before motion detection, and is adequately, though not necessarily⁴, explained by the intensity dependence of gain and latency at the receptor level.

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