The binding of the phenoloxidase to the mitochondria thus has a significant influence on the catalytic properties of the enzyme. We assume that the binding results in some coupling with the hydrogen transport system of mitochondria, thereby potentiating the monophenoloxidase activity. Some conflicting data in the literature concerning the monophenolase and diphenolase activity of various preparations can be reevaluated in light of these findings.

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Dynamics of Motion Perception in the Desert Locust

Abstract. *The torque produced by the neck muscles of a locust mounted coaxially in an illuminated cylindrical striped drum follows small sinusoidal oscillations of the drum. Peak-to-peak oscillations of 0.03 degree (± 0.02 degree) at 0.1 cy/sec elicit measurable responses. Several features of this visual response to drum oscillation can be expected theoretically on the basis of a formal neural mechanism similar to that inferred by Hassenstein and Reichardt for constant-velocity motion perception in the bettle eye.*

If a locust is mounted horizontally by the sternum in the center of a coaxial cylindrical striped drum, the head will rotate about the roll axis so as to follow angular motion of the drum. If the head is attached to a torque meter of high mechanical input impedance, torques about the roll axis may be measured which vary consistently with the drum motion, illumination, and pattern.

This reflex has been studied in adult males of the desert locust *Schistocerca gregaria* (Forskål) and in nymphs of the grasshopper *Eutropidacris cristata* (L.). The experimental arrangement consisted of a Plexiglas cylinder, 10 cm in diameter, the inner surface of which was covered with translucent white tracing or construction paper bearing equally spaced black stripes (the pattern spatial period, λ, being either 7 degrees or 45 degrees). The cylinder was rotated either at constant velocity or with small, nearly sinusoidal angular oscillations, and illuminated from the outside by either d-c incandescent or a-c fluorescent lamps. No effect of the 120-cy/sec component of the fluorescent lamps was discernible in comparison with d-c illumination.

Torque was measured as follows. The frons of the head was connected by means of wax and a steel rod to a block clamped onto a taut steel band aligned with the longitudinal body axis of the locust. The torsion of the band produced by the locust's head torque was registered as motion of a light beam reflected from a mirror on the block. The image of a 6-volt, long-coiled lamp filament was cast by the mirror on the mutual boundary of two juxtaposed 1- by 2-cm silicon solar cells. The differential voltage output of the two cells under these conditions was nearly a linear measure of head torque over a range of at least ± 2 kdyne-cm with a sensitivity of 25 mv/kdyne-cm. The torsional compliance of the taut band and connecting rod was about 0.04 degree/kdyne-cm. Since most torques measured were less than 500 dyne-cm, motion of the head about the roll axis was generally less than 0.02 degree. The visual feedback normally available to the locust eye was therefore reduced to this extent. The torque meter, d-c amplifier, and stylus drive provided constant gain and negligible phase shift from d-c to 6 cy/sec.

The pronotum of the mounted locust was waxed firmly to the thorax. The head was attached to the torque rod and drawn forward slightly, away from sensory hairs on the pronotum (*1*). Responses were measured with luminance at the outer drum surface of from 10 to 500 lux. Transmission of the diffusing white stripes was from 7 percent to 20 percent for the various papers used. Controls on the response to sinusoidal oscillation included plain white paper in place of the striped pattern, removal of drum illumination, and anesthetization of the insect; all of these conditions eliminated the response. Further, the response may readily be observed by eye in the head motion of a hand-held locust (visual feedback is in this case available to the locust visual system).

Clear following of sinusoidal drum motion was measured at drum frequencies of from 0.0014 cy/sec to 4 cy/sec; it cannot yet be excluded that slight unevenness in the mechanical drive contributed to the response at very low frequencies. Records of torque measured under constant-velocity (CV) rotation and sinusoidal-angle (SA) drum oscillation are illustrated in Fig. 1. After an initial transient, the steady-state response to either input assumed approximately the time behavior of that input. No appreciable adaptation from the level of response attained after 10 to 20 seconds has been noted for CV or SA stimuli lasting several minutes.

The SA response was less sensitive than the CV response to imperfections in the pattern such as the "joint" of the paper cylinder; a sheet of plain white paper used as a control "pattern" induced considerable CV torque but no detectable SA torque. The SA head response was also more reproducible than other optokinetic responses of the locust—for example, isometric yaw torque during tethered flight in a laminar windstream (*2*).

In order to use standard linear harmonic description (*3*) toward analysis of such a system, one must determine the extent to which nonlinearities affect input-output measurements. Several important nonlinearities exist in the neck-torque visual response to SA input. First, if the head is twisted at all when attached to the torque rod, asymmetry can appear in the records. Second, saturable, logarithmic, or other nonlinear processes certainly exist in the sensory, neural, and muscular systems which take part in the response. Although harmonic distortion in the output has not been measured, the curves of torque amplitude versus small SA-input amplitude in Fig. 2 indicate an approach to linearity at peak-to-peak inputs smaller than 0.15 degree for a frequency of 0.1 cy/sec.

If a threshold for the response exists, Fig. 2 shows that it occurs below 0.03

degree peak-to-peak input amplitude. Further nonlinearities are indicated by the asymmetrical responses to the "on" and "off" velocity "steps" (angle "ramps") in Fig. 1*A*. These do not necessarily contradict the small-angle near-linearity inferred from Fig. 2, however, since the angle ramps of Fig. 1*A* involve large angular displacement of the pattern. Finally, in anticipation of the results of the theory developed below, the light intensities at receptors are complicated functions of time if the amplitude of drum-oscillation is not sufficiently small.

Independent of these considerations, it is important to ask, theoretically, what kinds of optokinetic response to drum oscillation would be expected, given certain mechanisms as candidates for the neural processing of intensity changes at photoreceptors. Hassenstein and Reichardt (*4*) have proposed one such mechanism for the formal organization of the steady-state optokinetic response to patterns rotating with constant angular velocity, for the beetle *Chlorophanus*. The model predicts approximately the beetle's reaction to a variety of spatial patterns under constant-velocity drum rotation. The following example shows that a formally similar model permits prediction of the dynamic response reported here, and that there is qualitative agreement with the experimental gain and phase relations of Fig. 1.

Consider the two-sensor system (Fig. 2, inset) in which τ_F and τ_H are the time constants of the through- and cross-channel transfer functions $G_F(\omega)$ and $G_H(\omega)$, respectively, [of form $a/(1 + j\omega\tau)$] having the characteristics of monomolecular reactions, or low-pass filters; ω is the angular frequency, $j = \sqrt{-1}$, and a is a constant. The boxes marked M are multipliers, the difference of the outputs of which drives another first-order low-pass filter of time constant τ_S. This system is identical topologically to Reichardt's two-ommatidium system except for (i) elimination of his "D-filters" (special one-dimensional diffusion processes in series with each sensor) which are required to fit the *Chlorophanus* data, and (ii) the removal of the requirement that the S-filter act as a long-time-constant averager.

In terms of the sinusoidal-angle experiment with the locust the two photoreceptors A and B (whether groups of ommatidia, rhabdomes, or rhabdomeres), separated by an angle Δs, face an approximately sinusoidal spatial brightness pattern, of form $c + b \cos (2\pi s/\lambda)$, on a cylindrical drum oscillating sinusoidally in time. The quantities c and b are average intensity and contrast, respectively. The assumption in this calculation of a sinusoidal spatial pattern is consistent with the use of 7-degree square-wave (striped) patterns in the experiments, due both to the inherent amplitude ratios of the harmonics of a square wave and to the known imperfect resolution by photoreceptors; for receptors with Gaussian off-axis sensitivity of 1-degree width at half-response, several times as sharp as current estimates (*5–7*) indicate, the response of the model to the third harmonic (first "overtone") of a 7-degree square wave is less than 10 percent of the response to the fundamental.

If the drum oscillation amplitude U is small with respect to the pattern spatial period λ, the light intensities $f_A(t)$ and $f_B(t)$ at the two sensors, with appropriate initial conditions and adequate imaging, are represented by the first-order approximations

$$f_A(t) = c + b \cos \frac{2\pi s_A}{\lambda} - \frac{2\pi bU}{\lambda}\left[\sin \frac{2\pi s_A}{\lambda}\right]\left[\sin \omega_u t\right] \qquad (1)$$

$$f_B(t) = c + b \cos \frac{2\pi (s_A + \Delta s)}{\lambda} - \frac{2\pi bU}{\lambda}\left[\sin \frac{2\pi (s_A + \Delta s)}{\lambda}\right]\left[\sin \omega_u t\right] \qquad (2)$$

where s_A is the angular direction of one of the sensors with respect to any stationary reference direction, and ω_u is the angular drum-oscillation frequency. For the case in which U is not small, these functions can be described by the usual treatments of frequency-modulated waveforms.

If these functions are considered as inputs to the two-sensor model described, the reason for removing the D-filters used by Reichardt is clear; since for small input oscillations the two inputs are in phase (both vary as $\sin \omega_u t$), the difference of the outputs of the multipliers will be zero unless some information concerning the constant intensities $c + b \cos(2\pi s_A/\lambda)$ and $c + b \cos[2\pi(s_A + \Delta s)/\lambda]$ is transmitted to them. The D-filters do not pass constant inputs. A further consequence of the small drum oscillations

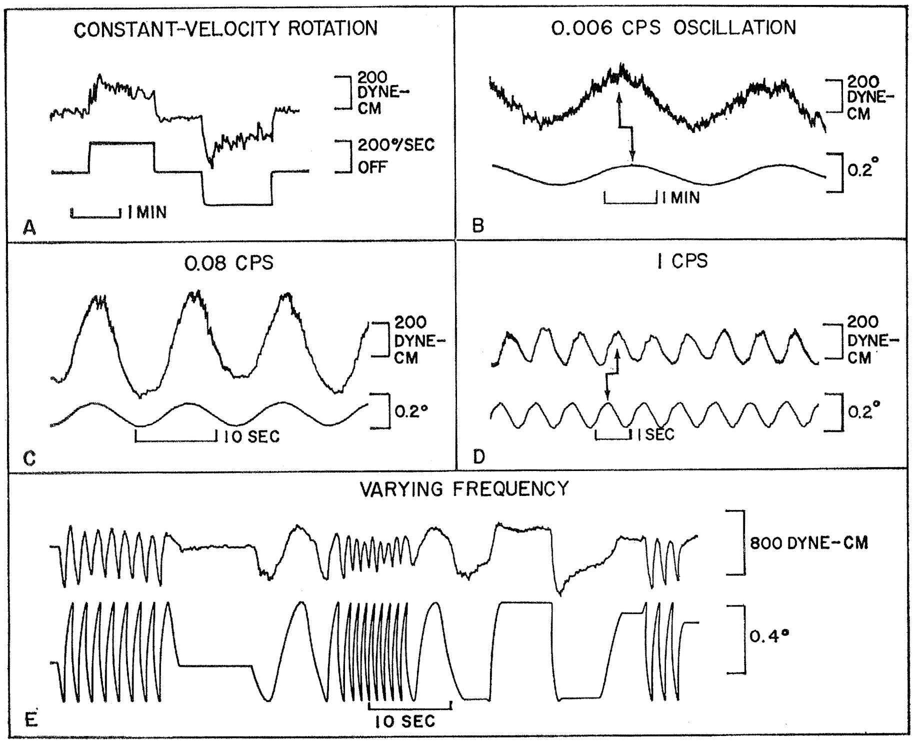

Fig. 1. Records of isometric neck-torque responses (upper traces) to striped-drum motion (lower traces). $\lambda = 7$ degrees. (*A*) *S. gregaria,* "maintained" torque with constant-velocity drum rotation; clockwise rotation followed by counterclockwise rotation. (*B–D*) *E. cristata,* close following of very small drum oscillations; arrows mark phase lead in *B* and lag in *D*. (*E*) *E. cristata,* response to manual variation of drum frequency in the range 0 to 1 cy/sec. Asymmetry due to mounting is particularly apparent in (*C*) and (*E*). Pen arc convex to the left.

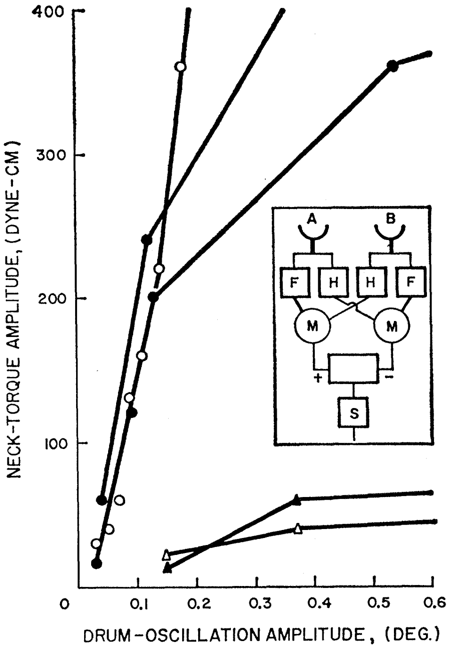

Fig. 2. Peak-to-peak neck-torque amplitude versus peak-to-peak drum-oscillation amplitude. Filled circles: *S. gregaria*, $\lambda = 7$ degrees, 0.1 cy/sec; Open circles: *E. cristata*, $\lambda = 7$ degrees, 0.1 cy/sec; Filled triangles: *S. gregaria*, $\lambda = 45$ degrees, 0.1 cy/sec; Open triangles: *S. gregaria*, $\lambda = 45$ degrees, 0.6 cy/sec. Measurement uncertainty in values of angle ± 0.02 degree. Torque variation about ± 20 percent. Extensions of curves are to measurements outside range of axes (near-linearity of *E. cristata* response extends beyond 500 dyne-cm). *Inset:* two-sensor motion-perception system related to Reichardt's for which harmonic response is calculated (see text).

is that $f_A(t)$ and $f_B(t)$ contain, to first-order approximation, only the frequency ω_u, independent of the drum spatial pattern. This situation offers an important experimental convenience. That is, "single-frequency" visual inputs are in principle available from quite imperfect striped drums.

The output of the S-filter in the frequency domain (*3*) is given by

$$R(\omega) = G_S(\omega) \int_{-\infty}^{+\infty} f_A^*(\theta) f_B^*(\omega - \theta) D_{FH} d\theta \qquad (3)$$

where D_{FH} is the determinant

$$\begin{vmatrix} G_F(\theta) & G_H(\theta) \\ G_F(\omega - \theta) & G_H(\omega - \theta) \end{vmatrix}$$

$f_i^*(\omega)$ is the Fourier transform of $f_i(t)$, $i =$ A, B; $G_k(\omega)$ is the transfer function of filter k, $k =$ F, H, S; θ is an integration variable. Expression of the output in terms of correlation functions (*4*) offers no economy in the general dynamic case since the two inputs at A and B do not differ simply by a constant time delay.

The transfer function $G(j\omega)$ of the two-sensor system, with the drum angle $U \sin \omega_u t$ considered as input, and the pattern and sensor geometries left as parameters, is equal to $R(\omega)$ divided by the Fourier transform of the input. Substitution of the expressions already chosen for $f_i(t)$ and $G_k(\omega)$, with $c = 0$, gives the result

$$G(j\omega) = \frac{j\omega(2\pi N/\lambda) \sin (2\pi \Delta s/\lambda)}{(1 + j\omega\tau_F)\,(1 + j\omega\tau_H)\,(1 + j\omega\tau_S)} \qquad (4)$$

where $N = a_F a_H a_S b^2(\tau_F - \tau_H)$. In this calculation c was set equal to zero, as if the two sensors measure only departure from average intensity over the whole eye. If c is not zero, gain and phase dependence upon frequency are unchanged, but the gain becomes a function of s_A.

Gain and phase behavior with frequency may be read directly (*8*) from $G(j\omega)$: Thus the predicted output of the two-sensor model, for small sinusoidal drum oscillations, (i) is sinusoidal and of the same frequency as the drum frequency, (ii) exhibits low-frequency phase lead (with respect to the drum) and smooth transition to high-frequency phase lag of 180 degrees and (iii) has gain increase of 6 db/octave at low frequency, maximal gain at some frequency, and gain reduction of 12 db/octave at high frequency. Qualitative agreement with these predictions is evident in Fig. 1, *B* to *D*, from a single experiment on *E. cristata*. The approximately sinusoidal neck torque shows some phase lead at low frequency and a lag at 1 cy/sec, while gain is greatest at 0.08 cy/sec in *C*. More detailed gain and phase measurements (seven animals) provide more quantitative agreement with the calculation. However, the fitting of transfer functions to such data and estimation of rate constants properly await further study of the effects of the illumination and geometrical parameters mentioned. The correspondence noted here in no way invokes the two-sensor model as a unique basis for the locust optokinetic response, nor does it argue against processes existing in the insect visual system which correlate with the D-filters. It is striking, however, that a formal organization deduced for constant-velocity motion perception in the beetle is consistent with the gross dynamics of motion perception in the locust.

The 0.03-degree motion acuity of the SA response is on the order of the "motion perception threshold" reported for the human (*9*). It is important that this sensitivity to small displacement of 7-degree stripes should not be confused with other criteria for visual "resolution." In particular, Burtt and Catton (*5, 10*) and Rodgers (*11*), for several insect species, interpret electrophysiological responses to *large* displacement of 0.3-degree stripes as anomalous with respect to diffractive limitations upon single-ommatidium resolution; they suggest as an adequate dioptric apparatus that several neighboring ommatidial lenslets may cooperate in producing "intermediate Fourier diffraction images."

The motion acuity measured here with 7-degree stripes does not require the diffractive theory of Burtt and Catton. Fermi and Reichardt (*12*) have recently measured optokinetic flight torque of the housefly *Musca*, in a rotating striped drum, for pattern contrast of 0.5 percent. If a similar sensitivity to small $\Delta I/I$ were to hold for receptors in the locust visual system, then motion acuity of 0.03 degree would be compatible with current estimates of ommatidial off-axis response distribution (*5–7*). To the extent that individual rhabdomeres—even within "fused" rhabdomes—might act as separate receptors, with spatial resolution better than that of the ommatidium (*6*), still less sensitivity to contrast will account for the measured motion acuity.

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