DYNAMIC PROPERTIES OF ORIENTATION TO A VISUALLY FIXATED TARGET BY WALKING COLORADO BEETLES

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Summary

The dynamic components of the fixation behaviour of walking Colorado beetles were examined. The beetles walked on top of a locomotion compensator under closed-loop conditions. The fixation target was a yellow disk with small black stripes ('Colorado dummy'). The paths of beetles walking towards the stationary dummy were characterized by oscillations, and were investigated by applying a fast Fourier transform to the turning-velocity time course. The power density peaks near 0.3 Hz with varying amplitude. Films of the fixation reaction revealed that this frequency was much slower than the stepping-pattern frequency of the beetles. During orientation to other stimuli (wind or gravity), the oscillations were not present, showing that they were not an artefact of the motor output. However, they were present in other forms of visual orientation, such as the optomotor response and during positive phototaxis.

A frequency–response curve (Bode diagram) under closed-loop conditions was obtained for the fixation reaction by changing the dummy position sinusoidally and measuring the phase and amplitude of the tracking response. A simple model of this behaviour, including a low-pass filter and an integrator, describes the reaction. Hence, the reaction can be understood as the simple resonance behaviour of an underdamped closed-position loop. The question of whether this can explain zigzagging paths in other species is discussed.

Introduction

The dynamic properties of visual behavioural reactions have only recently received close attention. Static responses can be measured with relatively simple experimental paradigms and lead to an interesting hypothesis for visual input–output relationships. For example, the steady-state fixation reaction, assessed under open-loop conditions with various torque meters (Poggio and Reichardt, 1976; Reichardt and Poggio, 1976) or locomotion recorders (Bülthoff, 1982), gives

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insight into the computation by which the visual input, the position of a fixated object, is converted into the measured output, the turning tendency of the animal. Similar results were obtained for the static parts of the fixation reaction of walking Colorado beetles (Lönnendonker and Scharstein, 1991; Lönnendonker, 1984).

Moreover, the dynamic components of the flight behaviour of large flies can be summarized as a simple process generating random torque fluctuations (Reichardt, 1973). For *Drosophila*, however, Heisenberg and Wolf (1984) showed that the flying behaviour is more structured than expected and it is possible to conclude that *Drosophila* can discriminate between intrinsic flight manoeuvres and the extrinsic shifts of the visual surround (Heisenberg and Wolf, 1988; cf. Möhl, 1989). However, visually guided behavioural reactions of walking beetles differ from those observed in flight. In the closed-loop situation, Colorado beetles fixating a target walked along an oscillating path (Lönnendonker, 1984), which this report will describe in more detail. The oscillations are analyzed to determine whether they are an integral part of the visually guided behaviour or whether they are also basic components of walking in other orientation paradigms. A careful examination of the underlying system will demonstrate that this structured behaviour can be understood by making simple assumptions. The movement can be interpreted as simply a resonance of the fixation loop, which is underdamped.

Materials and methods
Animals

The experimental animals (Colorado beetles, *Leptinotarsa decemlineata* Say) were obtained from J. H. Visser (Agricultural University Wageningen, Netherlands). The sexually mature insects were kept under natural light conditions and fed with potato leaves and tubers. Both sexes were used approximately equally often and, within the limits of the experiments, did not show differences in behaviour. The head and pronotum were normally free to move (but see Fig. 7).

Apparatus

The experimental animal walked on top of a sphere which was actively rotated so as to 'fix' the beetle without restraining its locomotor activity. This locomotion compensator (Kramer, 1975) compensated only translational movements, allowing free rotations. For a detailed description see Weber *et al.* (1981) and Lönnendonker and Scharstein (1991). Briefly, a position sensor above the sphere measured deviations of the animal from the middle of an area illuminated by infrared light. These measured deviations drove two positioning motors, which turned the sphere until the animal was again in the middle of the area. The compensatory movement of the sphere was registered by two optoelectronic angular measuring devices, giving a representation in orthogonal x and y coordinates in a tangential plane with 0.25 mm resolution. That is, the system detects neither translational movements smaller than 0.25 mm nor pure rotations. The pulse-coded data were fed into a computer (DEC PDP 11/40), which sampled

the animal's positions x_i and y_i at preset intervals (normally 0.5 s). Velocity v_i and direction α_i were calculated from the position changes, and the turning velocity ω_i from direction changes, for consecutive intervals (i and i+1). Below a threshold velocity v_1 of $0.1\,\mathrm{cm\,s^{-1}}$, computation of α_i, ω_i and ω_{i+1} was cancelled.

Circular statistics

The straightness of a walk is characterized by the mean vector l: its direction corresponds to the connecting line between the initial and final point of the run, its length |l| is the ratio of the length of the connecting line to the total distance walked. In the normal circular distribution |l| corresponds to the width of the distribution. Therefore, a dispersion value (angular distribution) s (compare Fig. 6) can be given (Batschelet, 1981):

$$s = \sqrt{2(1 - |l|)}. \tag{1}$$

Experimental situation

The experimental paradigms used are described in Lönnendonker and Scharstein (1991). Stationary or oscillating patterns were presented on two concentric cylinders mounted inside a hemispherical lampshade. The optical environment was illuminated indirectly by 12 lamps on the bottom of the inside of the lampshade. Either of the two cylinders could be moved by a belt driven by a motor regulated by a control system. The movement of each cylinder was recorded separately with a pulse-coded angular measuring system like that in the locomotion compensator. These pulses were also fed into the computer to allow an exact positional representation.

To elicit true fixation reactions, a pattern consisting of a yellow disk with black stripes was used. The disk subtended 5° at the beetle's eye, the stripes much less than 1° (Lönnendonker, 1984). In the following this will be called a Colorado dummy to indicate the resemblance to the Colorado beetle wing-case pattern. It was presented on the inner smaller cylinder (height subtending 20°, painted white) at an altitude that subtended an angle of 10°. The outer cylinder was higher, the part of it visible above the inner cylinder subtending an angle of about 30°. This visible area was covered either with vertical ($\lambda=20°$) stripes or with horizontal stripes. In some experiments both cylinders were stationary, and in others the dummy and the white background were oscillated sinusoidally while the outer cylinder was stationary.

Autocorrelation and Fourier transformation

The fast Fourier transform (FFT) was applied here to normalized autocorrelation data of ω. The use of the autocorrelation function allowed me to examine walks of 5 min duration with the FFT (Bendat and Piersol, 1971). The ordinates for the power densities (the squares of the amplitudes) are in arbitrary units, which are, however, the same in each figure. Autocorrelation measurements provide a tool for detecting deterministic data that might be masked in a random back-

ground. Most of the autocorrelation functions shown persisted periodically over all time displacements τ, indicating a periodic component in the turning velocity of the animals. To describe the general frequency composition of these data, the power density function is used (for further details, see Lönnendonker, 1984).

Film

The walking Colorado beetles were filmed with a 16 mm camera (Beaulieux R 16) at 36 frames s^{-1}, through a 200 mm Macro-Zoom objective (Soligor). The brightness in the walking area was fixed at 1000 lx. Three pairs of points were marked on the beetles, indicating the longitudinal axis of the body, the pronotum and the head. The coordinates of these points were transferred to the computer *via* an $x–y$ tablet (Summagraphics HW2-209) by single-frame projection (LW Photo Optical Data Analyzer model 224 A).

Bode diagram

Behaviour was examined in both stationary and oscillating surrounds. In the latter experiments, the maximal angular velocity of the dummy was kept constant ($15°$ s^{-1}) while the frequency of the oscillation was changed. This restriction on stimulus velocity is imposed by the limited turning velocity of the beetle as it follows the movement of the pattern (Lönnendonker and Scharstein, 1991). To evaluate the phase and amplitude relationships of the oscillating Colorado dummy and the animal's tracking reaction, I have calculated the cross-correlation of the two position measures. The phase is given by the time shift at which the correlation coefficient is 'highest'. The amplitude is then found by a modified deviance function (Lönnendonker, 1984).

Results
Comparison of different visual stimuli

Fig. 1 shows that the occurrence of oscillations in the walking path depends on the nature of the visual surround. The figure shows the walking paths, the autocorrelation function of the turning velocity for each path, and the spectra of these autocorrelations. In Fig. 1A the animal walked in a surround consisting only of horizontal black and white stripes (Lönnendonker and Scharstein, 1991; Lönnendonker, 1984). The animal was unoriented, as can be seen from its circling path, and the spectrum was flat (compare Reichardt, 1973). In a vertically striped surround ($\lambda=20°$, Fig. 1B), the course was more spread out and a periodic component appeared in the walking trace. This component can easily be seen as a distinct peak at about 0.2 Hz in the spectrum. Correspondingly, the autocorrelation function shows a periodicity of around 5 s. This periodicity can be seen even more clearly in the isolated fixation reaction (Fig. 1C), where the animal fixated the Colorado dummy. The insect walked in the direction of the fixation object, though the first half of the path shows superimposed turning behaviour (cycloids, see Wendler and Scharstein, 1986). The oscillations, most clearly visible in the la
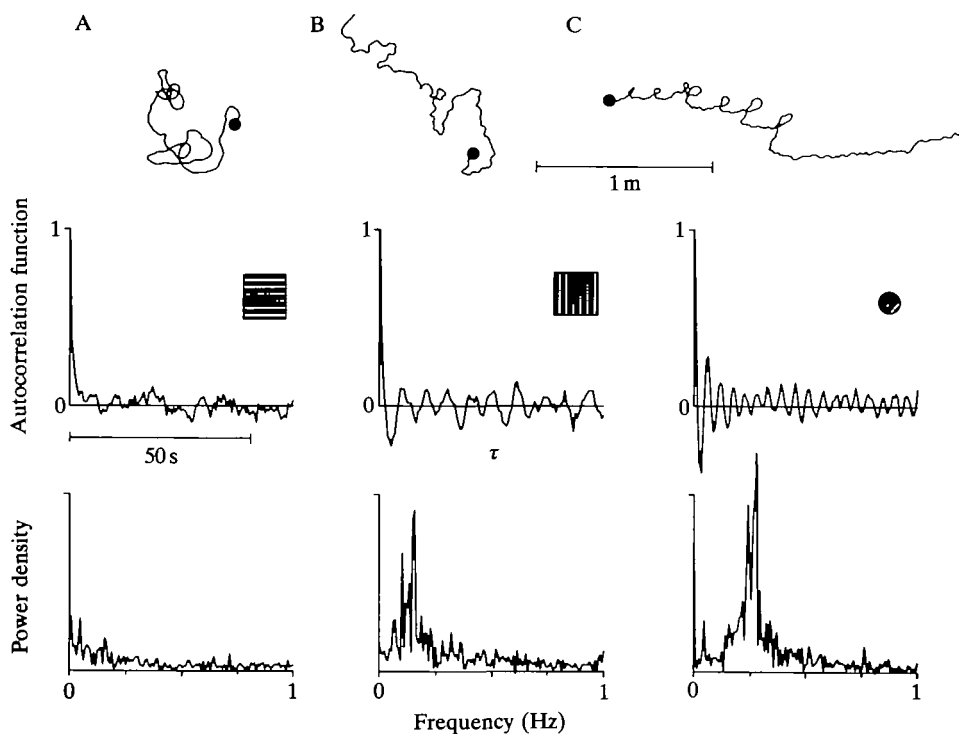
Fig. 1. Comparison of the behavioural reactions of one beetle in three different stimulus situations (symbolized by the insets). (A) An optical environment consisting of horizontal stripes; (B) a standard optomotor environment with stationary vertical stripes; (C) a homogeneous white background with the stationary Colorado dummy. From top to bottom: the walking path of the beetle (origin marked with a black circle), normalized autocorrelation functions of turning velocity and power density spectra of these autocorrelation functions. τ, time delay.

part of the walk, were more pronounced than those in Fig. 1B. The reaction to such dummies will be examined in detail because the response characteristics can be better defined with such small fixation objects than with a pattern of large stripes. Moreover, although the Colorado beetles never displayed menotactic responses (compass orientation) to dummies, they did so to small vertical black stripes (Lönnendonker, 1984).

Comparison of fixation 'modes'

Different 'modes' of fixation could be found when 82 5-min runs of seven animals were examined closely. From this material, five examples were chosen to demonstrate the whole range of this behavioural reaction (Fig. 2). The walking directions are shown over 5 min (the dummy was presented in the direction $\alpha=0°$) and the spectra for the first four examples are presented (A–D). In these four instances the intrinsic oscillation frequencies varied from 0.2 to 0.4 Hz. However, the differences were mainly in the amplitude of the oscillation, not so much in its
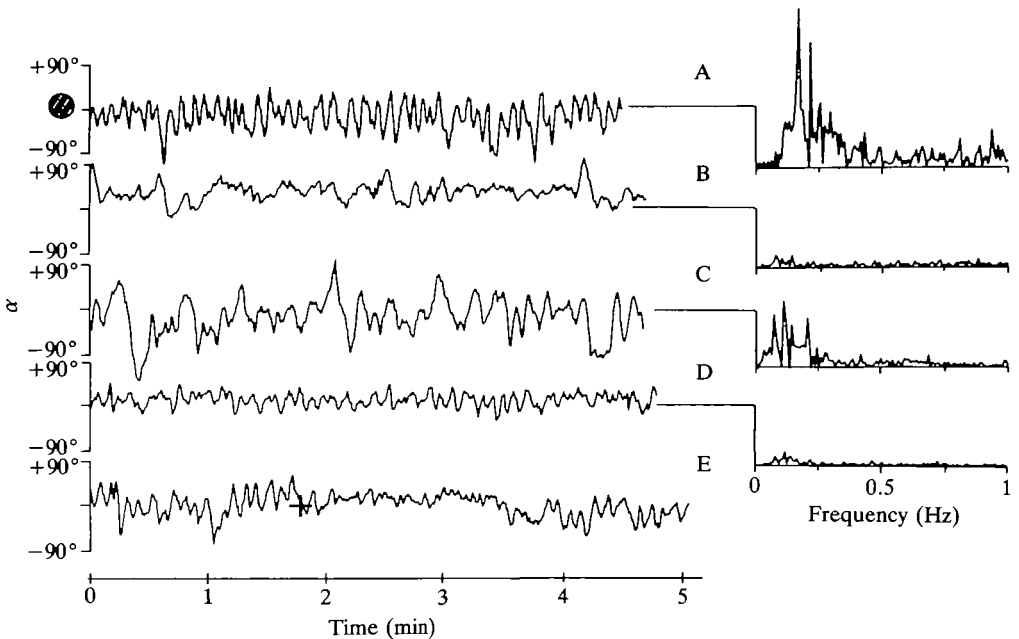
Fig. 2. Fixation 'modes' of different animals (A–E), which walked towards the Colorado dummy at position $\alpha=0°$. On the left are the individual course directions as a function of time and, on the right, the power density spectra from the turning velocity for examples A–D. The example in E shows that the beetle changed its 'mode' of fixation after a visual disturbance (marked with the cross). The background consisted of horizontal stripes.

frequency. The last example in Fig. 2E establishes that the 'mode' could be changed by a disturbance to the visible surroundings (in this case a change of the background from horizontal to vertical stripes).

Orientation to other stimuli

To address the question of whether these oscillations were induced by the visual control loop of Colorado beetles, three other orientation tasks were compared. Fig. 3 shows the results from one beetle walking in four different situations: in the light with the dummy, in a darkened surround with only one small light source, in the dark on a tilted surface (the animal walked upwards Fig. 3C) or in an air current (the animal walked upwind Fig. 3C). Comparison of the autocorrelation functions (Fig. 3A) or the respective spectra (Fig. 3B) from these distinct orientation tasks clearly shows that the frequency of turning in the visually elicited orientation reactions differs from that in the two other responses. Because only visually elicited behaviour exhibited such oscillations, the oscillations are not a fundamental property of the motor system. The velocity (Fig. 3D) was highest for walking in the light, smaller for the darkened surround and very small for orientation to gravity.
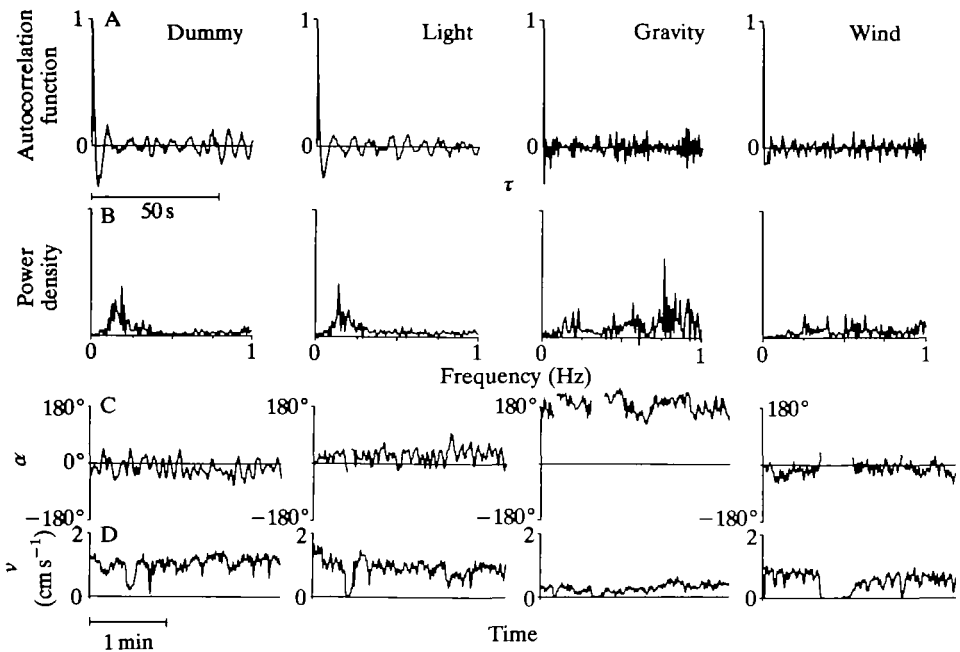
Fig. 3. Walking parameters of one beetle in four different orientation situations. From left to right: dummy, Colorado dummy at position $\alpha=0°$ in front of a white background; light, point light source at position $\alpha=0°$ and room darkened; gravity, plane of inclination 20° (the animal walked upwards); and wind, air current of $1\,\mathrm{m\,s^{-1}}$ from the direction $\alpha=0°$. In the last two examples the beetle walked in darkness. (A) The autocorrelation function of turning velocity, (B) the power density specta of these autocorrelations, (C) the walking direction α *versus* time and (D) the walking velocity v. τ, time delay.

Relative angles of head, pronotum and body

In all the preceding experiments, the beetles were free to move their heads. To examine the possibility that a component of the walking behaviour is induced by movements of the head or the pronotum relative to the body, various walks were filmed and analyzed. In Fig. 4, measurements of the angle of the body axis with respect to the dummy (=walking direction) and of the relative angles of the pronotum (to the body) and the head (to the pronotum) are shown for one oriented walk together with the spectra of the first derivative of the three angles. The walking direction clearly oscillates at a frequency of 0.3 Hz (note the frequency scale), whereas no sign of these oscillations can be found in the data from the pronotum or head. The data from the head were too noisy to make any clear deductions. However, the head and pronotum clearly followed low-frequency motion of the fixation object in other situations, with relative bending angles of ±7° (Lönnendonker, 1984, not shown). The stepping pattern (triplet pattern) could be discerned by the higher frequencies in the spectra for body and pronotum motion (Fig. 4B,C). Moreover, it has been shown that these oscillations
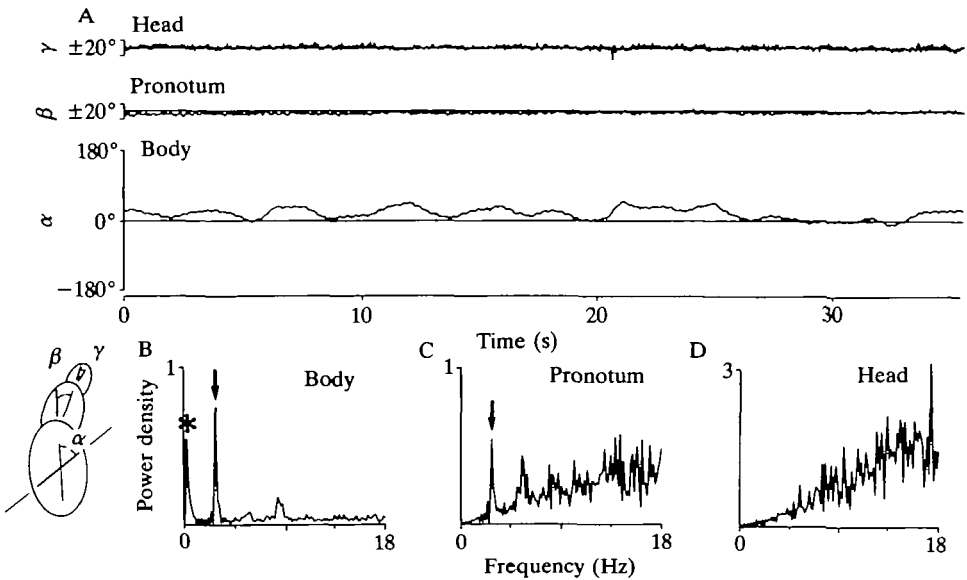
Fig. 4. Single-frame analysis (36 frames s^{-1}) of a fixation sequence of a Colorado beetle walking towards the Colorado dummy. The beetle walked on top of the sphere of the locomotion compensator. (A) The position of the body longitudinal axis α and the angles between the pronotum and body (pronotum β) and the head and pronotum (head γ) during a 30-s period. The diagram on the left shows how the angles are defined. (B–D). The power density spectra of the first derivative of the angles for the entire 4-min run, (B) the body, (C) the pronotum and (D) the head (the ordinate scale is three times larger than in B and C). The positions of the 4 Hz (arrow) and 0.3 Hz (*) peaks are labelled.

in the range 1–4 Hz were dependent on the walking velocity of the beetles (Lönnendonker, 1984).

Frequency response

To examine this intrinsic oscillation behaviour more fully, the frequency response over nearly two decades of stimulus frequencies was tested under closed-loop conditions. The dummy was oscillated sinusoidally at a maximal angular velocity such that a good tracking reaction could be obtained. Fig. 5 demonstrates that the intrinsic oscillation behaviour persisted without interruption, the oscillatory tracking of the fixation object being superimposed on the intrinsic turning. At a frequency of 0.3 Hz a resonance phenomenon was observed; that is, the amplitude of the intrinsic oscillations was clearly increased. The example at 0.75 Hz shows a similar increase. However, this possible interference between stimulus and intrinsic oscillation was not explicitly tested because the beetles do not always react to such high test frequencies. In Fig. 6, the coupling of the animal to the stimulus is depicted in direction units (α and s, see equation 1) for two cycles of dummy oscillations at the different frequencies tested. The amplitude and phase
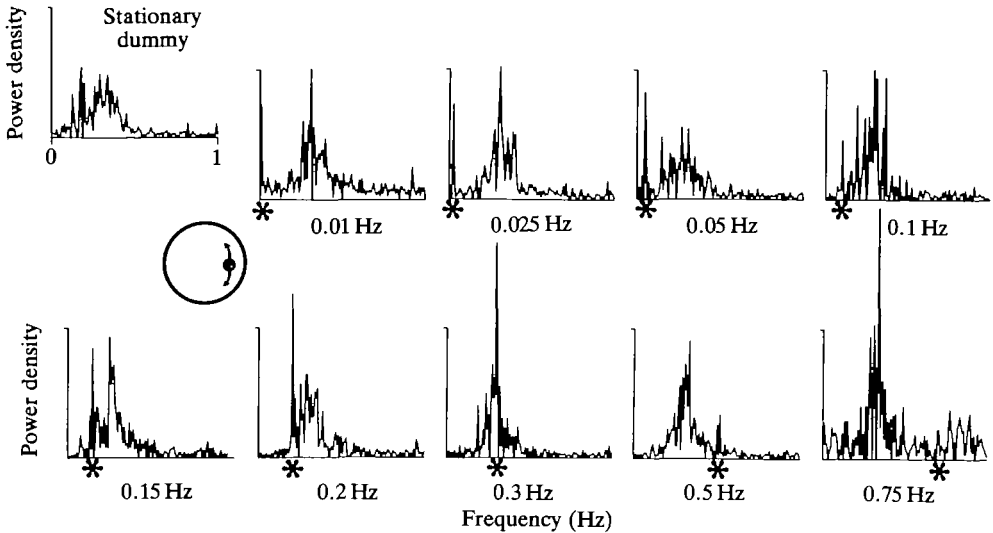
Fig. 5. Power density spectra of turning velocity of one beetle during a frequency response analysis. The Colorado dummy was oscillated on a white background, above which a stationary background of vertical stripes ($\lambda=20°$) was visible; see inset. The upper left spectrum shows the animal's reaction to the stationary dummy. The other spectra depict the frequency response at different oscillation frequencies (marked by asterisks).

of the reaction are discussed below. Complicated couplings of the intrinsic oscillations to the stimulus period can be seen at the lower frequencies. At a stimulus frequency of 0.75 Hz (see above), hardly any coupling could be seen.

Bode diagram

The tracking behaviour of the animal can now be described in a Bode diagram, separate plots of the amplitude and phase of the response *versus* the stimulus frequencies. Fig. 7 summarizes the reactions of various animals with two different stationary backgrounds (white and vertically striped). They are shown together with the best cross-correlation coefficient between the stimulus and the beetle's reaction. These correlation values are always smaller than 1 at a stimulus frequency above 0.3 Hz, which may indicate differences between the 'shapes' of the stimulus and the reaction. However, it is evident that the response followed the stimulus from 0.01 to 0.1 Hz with a nearly negligible phase shift and a 1:1 amplitude ratio. At higher frequencies, the phase lag increased. Moreover, the amplitude increased, because of the resonance mentioned above, to values twice as great as the stimulus amplitude (Fig. 7B). The different animals had slightly different resonant frequencies (compare Fig. 2) and some showed no clear increase in the amplitude (Fig. 7A). The type of stationary background had no detectable influence. That is, there was no detectable dynamic suppression of the beetle's oscillations by stationary vertical stripes (Fig. 7B).
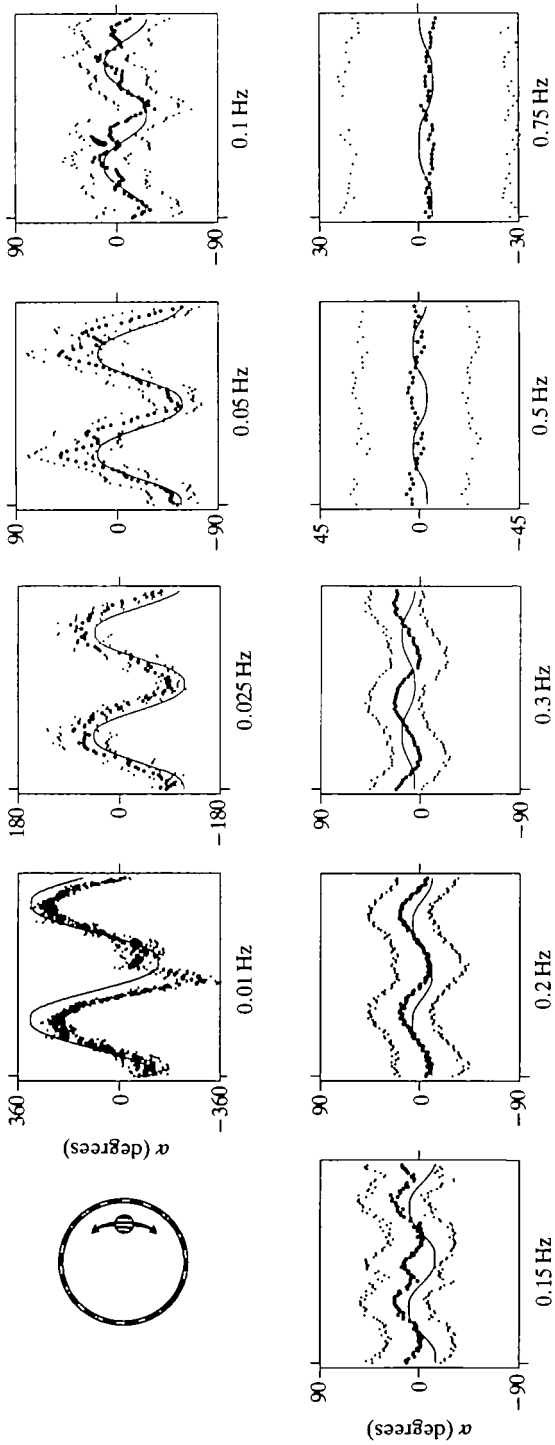
Fig. 6. Demonstration of the dynamic response of the beetle (in turning angle α) for the different stimulus frequencies (marked under each diagram). The same experiment as in Fig. 5. The mean reaction (large dots) and the angular deviation (s, small dots) are shown for two stimulus cycles. The stimulus is shown as a continuous line. Note the different scales.
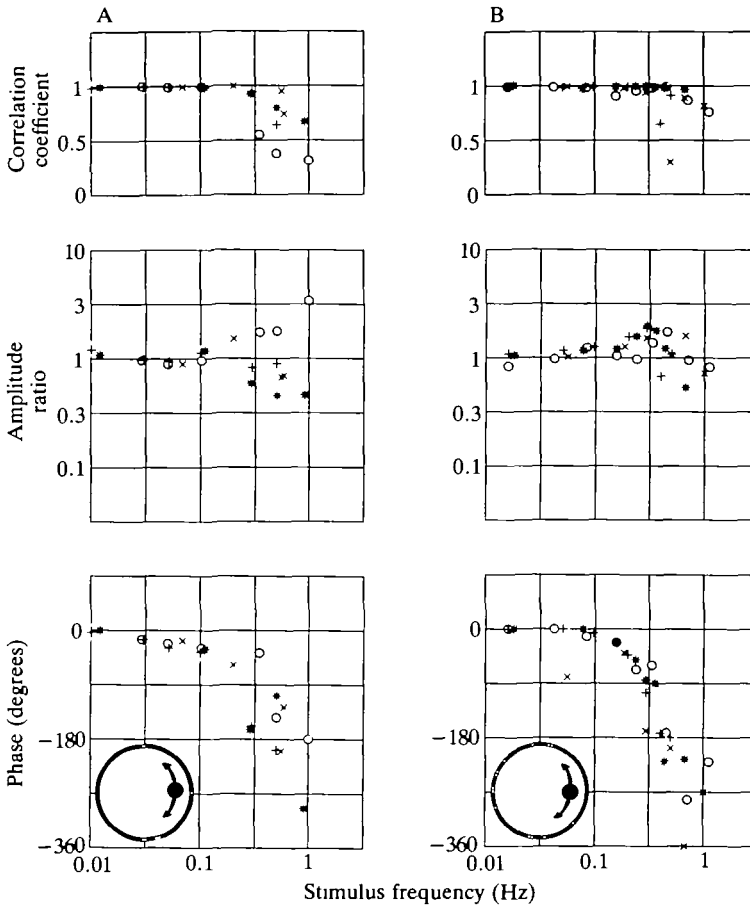
Fig. 7. Bode diagrams (A) without and (B) with the stationary vertically striped background. From the top: the best cross-correlation coefficient between the stimulus and the reaction of the animal, the ratio between the stimulus and response amplitudes and the phase of the reaction. Note that the abscissa and the ordinate for the amplitude ratio are scaled logarithmically. The four symbols in A represent different beetles. The symbols × and * in B represent one animal without (*) and with (×) head and pronotum fixed to the body.

Discussion

Head movements

Dynamic aspects of head movements of fixed walking insects (*Tenebrio molitor*) were examined by Varjú and Bolz (1980). Oscillations were induced by walking and by a visual input. Our study demonstrates that the Colorado beetle, walking freely, showed a clear reaction of the pronotum to body motion at a stepping frequency of 4 Hz (Fig. 4B,C). This is a counter-reaction to the body movement after a delay of 60–140 ms, as was shown by cross-correlation between the two measures (Lönnendonker, 1984). The fixation oscillations at 0.3 Hz were not

present in the pronotum power density function in Fig. 4C. Thus, the oscillating fixation reaction to a stationary dummy was not accompanied by pronotum movements. Moreover, head and pronotum movements were not necessary for the dynamic elements of the walking behaviour of Colorado beetles. The oscillations persisted even after these segments had been fixed to the body (not shown) and the dynamic characteristics were not changed significantly (Fig. 7B, symbol ×).

Comparison of intrinsic behaviour and stimulation

The resonance features of the fixation loop found in Fig. 7 give hints about how the system functions. If a linear system is assumed, the structure must be at least of second order (Varjú, 1977). A simple possible postulate is as follows. The beetle perceives the divergence angle between the position of the dummy and its own long axis. The angle controls the turning velocity of the animal through a first-order low-pass filter. The low-pass features are obvious from the suppression of high frequencies (Fig. 7). In the closed-loop situation, the integral of this turning velocity yields the new direction. Hence, the block diagram of this system (Fig. 8A) has two signal-transmitting elements: a low-pass filter and an integrator connected in series. The closed-loop transfer function in the frequency domain (Fig. 8) is a Laplace transformation of the associated weighting functions (Varjú, 1977). In Fig. 9, three examples of the consequences of such assumptions for the time constant $\tau_a = 1.4\,\mathrm{s}$ and different gains are shown. The values of the amplitude and the phase (Fig. 9) up to $0.3\,\mathrm{Hz}$ can be compared directly with those in Fig. 7. The discrepancy between the phase saturation at $-180°$ in Fig. 9 and the larger
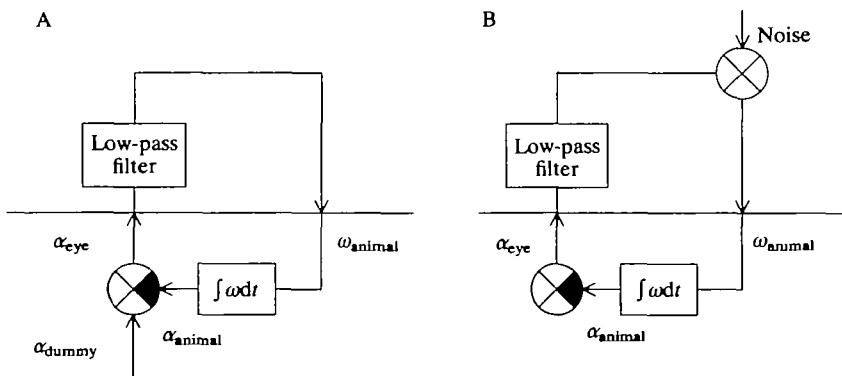

Fig. 8. Block diagrams of the model used to describe the behaviour of walking Colorado beetles. (A) The situation with an oscillating dummy and (B) the situation with a stationary goal (the only input is the internal noise source). Boxes denote the transfer elements (low-pass filter and integrator), lines with arrows symbolize the direction of the signal flow and the crossed circles designate addition or subtraction (filled quadrant).
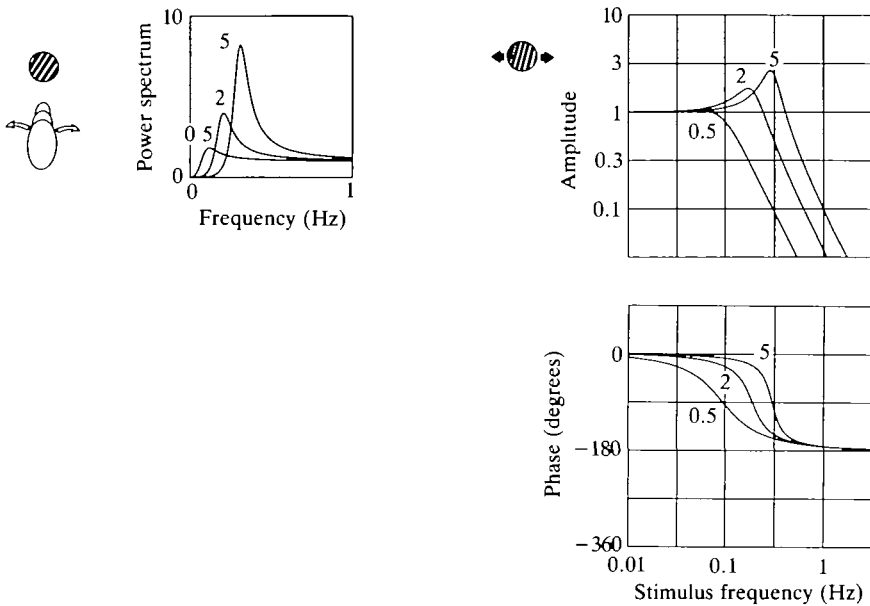
Fig. 9. Normalized power density spectrum (left) and Bode diagram (right) of the postulated fixation loop. The insets illustrate the stimulus conditions and behavioural reactions. The results depicted are calculated using three different values of the gain of the low-pass filter (5, 2 and 0.5 s degree^{-1}) and one time constant τ_a (1.4 s). See text for more details.

phase lags obtained experimentally (Fig. 7) is, of course, expected, because the system as modelled does not include delay times and the simple assumption of only one low-pass filter may possibly not be adequate.

The same fixation loop can now be used to model the intrinsic turning behaviour in a stationary surround. The assumption is that a noise source inside the animal generates deviations from the goal (Fig. 8B). It is assumed that this noise is, under open-loop conditions, a flat function of the frequency (compare Fig. 1A). This would lead, under closed-loop conditions, to an intrinsic oscillation in a similar frequency range to that in the forced situation with the oscillating dummy. This is visualized in Fig. 9 by calculating three different spectra for the three different gains used. Thus, the postulation of a closed fixation loop with resonance seems justified. The loop is underdamped.

The different spectra for the various gains used show that the modes in Fig. 2 can be simply explained by changes in the gains of the fixation loop. This does not exclude, however, the possibility that the time constant τ_a may also vary to some extent. Moreover, this type of description does not reduce insects to small machines. It is simply a technique that allows the behaviour to be treated in a mathematical way and makes useful predictions about the underlying mechanisms.

Comparison with other animals and other orientation tasks

Egelhaaf (1987) has measured the open-loop amplitude of the fixation loop dynamically with fixed flying *Musca domestica*. These flies exhibit a significantly larger response amplitude in fixation (small field) between 1 and 4 Hz than at lower frequencies. Horn and Mittag (1980) found body movements in walking *Calliphora erythrocephala* 'fixating' a stationary object in the frequency range 0.4–1.3 Hz. Böhm (1987) obtained no indication of resonance in the closed anemotaxis loop of walking *Necrophorus humator*; the loop is overdamped. One must assume that similar considerations apply to the wind and gravity orientation of walking Colorado beetles (Fig. 3). The gains and time constants of these two reactions are unknown. Evidently, however, the visual control loops share a common component, since all visually elicited orientation reactions exhibited oscillations (Figs 1, 3).

Bombyx mori walking upwind in a pheromone plume change their walking direction periodically ($\pm 30°$). Kramer (1975) interprets this as a triggered command value (set point) change. Flying moths follow a zigzagging flight path when advancing up a wind-borne sex pheromone plume. However, different control mechanisms have been proposed. Preiss and Kramer (1986) suggest that these manoeuvres are caused by errors or noise in one of the feedback reactions in the horizontal plane. Although David and Kennedy (1987) discuss active counterturning of moths in free flight, it remains to be clarified whether some of these counterturnings can be explained by resonance, as for Colorado beetles.

Strategy or reflex behaviour

One possible explanation for such a structured behavioural reaction would be the transfer of the image of the dummy from one eye to the other. Specialized retinae are observed in different insect species. However, it was found (Lönnendonker, 1984) that beetles can maintain well-defined angular positions relative to a small black stripe (menotaxis), and a beetle walking at 90° to the stripe exhibited the same oscillations. Thus, one 'seeing' eye is likely to be sufficient for this reaction. Moreover, the reaction to a broad stripe ($\lambda=360°$) demonstrates alternating fixation preferences for the edges of the pattern (Lönnendonker, 1984), which are superimposed on the oscillations. This makes it possible to differentiate between (oscillating) set point changes of the fixation loop and oscillations of the loop by resonance.

In the case of insect olfaction, it seems clear that the zigzagging paths play a dominant role in pheromone orientation. However, their function in the visual orientation of Colorado beetles remains unclear. The gain of the controlling fixation loop seems to be too high for visually initiated movements. Moreover, the beetle's turning loop is closed but its translational movements generate no feedback. In a situation where the beetle approaches the dummy, it is possible that other mechanisms may also come into play (Collett, 1988). It is interesting that the large flies show 'tuning' to very similar frequency ranges (Egelhaaf, 1987; Horn

and Mittag, 1980). More experiments with different insect species are necessary to find out if such a resonance behaviour is common in nature.

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