

DYNAMIC PROPERTIES OF ORIENTATION TO TURBULENT AIR CURRENT BY WALKING CARRION BEETLES

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Accepted 5 May 1995

Summary

A beetle orients its walk with respect to the direction of even a brief air current lasting only a few seconds. In a discontinuous current, the degree of orientation increases with the proportion of time during which the air flows. In the absence of wind, a walking beetle generates its own opposing airstream, the velocity of which is rhythmically modulated.

Sinusoidal modulation of the wind direction elicits approximately sinusoidal changes in walking direction. The amplitude of the following response at frequencies below 0.1 s^{-1} is almost as large as the amplitude of the change in wind direction. As the stimulus frequency increases, the response amplitude decreases. The Bode plot

shows that at frequencies above 1 s^{-1} the phase of the following response lags by almost 360° .

The dynamic temporal behaviour of the wind-orientation system is comparable with that of a control mechanism having low-pass characteristics of at least second order. It follows that rapid changes in wind direction do not immediately affect orientation behaviour. The wind-orientation system is thus well adapted to the air currents recorded in nature which, at the level of a walking beetle, can change very quickly and erratically in both direction and velocity.

Key words: wind-orientation, anemotaxis, Bode plot, *Necrophorus humator*, hot-wire anemometer.

Introduction

Many organisms depend to a great extent on information about currents in the ambient medium (Vogel, 1981; Bleckmann, 1991). Terrestrial arthropods very accurately detect changes in the air-current field surrounding them and often respond with life-preserving behaviour. For example, a cockroach can save its life by scuttling away as soon as it has been warned (Camhi, 1984) by the air current produced when a toad flicks out its tongue. In defending themselves from attack by a flying predator, caterpillars (Tautz, 1977) and crickets (Gnatzy and Heußlein, 1986) detect the enemy by means of the fluctuating air flow generated by the beating wings. But orientation to air currents is not limited to defensive or escape reactions; it can also help an animal find food and contribute to sexual behaviour. Orientation to scented air currents is used to find food sources (Kramer, 1976; Böhm and Wendler, 1987) or, if the odour substance is a pheromone, to locate a sexual partner (Kramer, 1975, 1986; Kaissling and Kramer, 1991). Many insects select a walking direction with reference to the direction of air flow (anemotaxis) even when the air current is carrying no attractive or repellent odour substances (Birukow, 1958; Heran, 1962; Linsenmair, 1969; Preiss, 1980; Heinzel and Böhm, 1983; Schöne, 1984), using the current as a cue to locate the nest entrance (Wehner and Duelli, 1971) or some other target.

Beetles are capable of anemotaxis when exposed to an air current with a velocity as low as 0.05 m s^{-1} (Linsenmair, 1973; Preiss, 1980; Heinzel and Böhm, 1989). The sense organs used for this purpose are restricted entirely to the antennae (Linsenmair, 1970; Heinzel and Böhm, 1989). Called Johnston's organs and Hicks' organs, they can detect the velocity and direction of an air current (Gewecke, 1972; Heinzel and Gewecke, 1979).

As a rule, a beetle uses the air-current information it receives from the antennae to compensate for changes in direction of air flow, so that it can maintain a chosen course with respect to the wind. Models developed for the wind-orientation systems of carrion beetles *Necrophorus humator* (Böhm *et al.* 1991) and gypsy moths *Lymantria dispar* (Preiss, 1980) not only describe a means of processing directional information in the central nervous system for the purpose of course control, but they also allow spontaneous alteration of the preferred walking direction with respect to the wind (Linsenmair, 1973; Heinzel and Böhm, 1989). Certain elements in the central nervous system that could play a role here have been described for the silkworm moth *Bombyx mori* (Olberg, 1983; Kanzaki and Shibuya, 1986).

However, very little is known about the structure of an air current in the boundary layer within which an insect walks. As

a rule, air currents are measured (Oliver and Mayhead, 1974; Baldocchi *et al.* 1983) in order to determine the large-scale distribution of abiotic factors in the biotope. For this reason, the few available velocity profiles have been recorded (Olzweski, 1974; Scott, 1978) or modelled (Elkinton *et al.* 1984; Cionco, 1985) in a region far above the boundary layer, at large temporal intervals.

Thus, when the question of interest is how an insect can orient its walk with respect to natural air currents, it is essential to record these currents. The experiments on which the present analysis of the dynamic properties of the wind-orientation system are based were therefore concerned not only with the behaviour of a walking beetle in a predetermined, dynamically changing air-current field, but also with the actual air flow to which the beetle was exposed. Finally, it is only by measuring the air currents naturally present that new information about the wind-orientation system can be viewed in a biologically relevant context.

Materials and methods

Animals

Carrion beetles *Necrophorus humator* F. were captured in woods near Cologne, Germany, using carrion traps. They were kept in boxes filled with moist soil at 18 °C and 70% relative humidity, and fed on the carcasses of a small vertebrate and on meat. These dark-active beetles (Müller and Cordes, 1987) were exposed to an inverted 12 h:12 h light:dark cycle, so that the experiments could be performed during the day.

Measurement of air flow

Air-current velocity was measured with a thermistor anemometer, either with temperature compensation (Testovent 4100, TestoTherm) or without (type G41 N, Lamprecht). To measure rapid changes in air-flow velocity (up to 10^4 s^{-1}) in the field, a constant-temperature hot-wire anemometer (ASM, Teltron) was used; the anemometer signal was recorded with an analogue tape recorder (Store 4, Racal) and later analyzed with a digital computer (PDP 11, DEC). For some measurements, the hot-wire probe (tungsten, 5 μm diameter, 1.5 mm long) was modified by adding a protective cap so that it could be used to measure the change in direction of a constant-velocity current (Neuerburg, 1969); for example, to measure the quality of the flow in the experimental apparatus.

In a second method of wind-direction measurement, dandelion seeds (*Taraxacum officinale*) were used as direction indicators. The seeds were glued individually to the closed ends of small glass tubes (diameter 0.1 mm), the open ends of which were slipped onto insect pins, and the direction in which the seeds were deflected was monitored (see below). Using this method, Sagakami (1977) measured fluctuations in wind direction of up to 400 s^{-1} .

The air currents were recorded in the woodland in which the animals had been caught. Nine current-direction indicators were arranged in a square area measuring 100 cm^2 , so that each indicator was 4 cm away from its neighbours at a height of

20 mm. Simultaneously with the direction measurement, signals representing wind velocity were obtained using the hot-wire anemometer 10 mm, 20 mm and 70 cm above the ground. A video camera was used to record both the positions of the direction indicators and the read-outs from the velocity sensors. The values for direction and velocity of air flow at the various positions were then obtained by single-frame analysis.

Recording of walking direction

A locomotion compensator was used to record continuously the walking direction and walking speed of the animals (Fig. 1; for details, see Kramer, 1976) with or without an air-current stimulus. The beetle was free to walk on the apex of a ball which compensated for the animal's movement, thus keeping it in the same position in space. The walk could thus be monitored by the movement of the ball, which was represented by four trains of electric pulses corresponding to the x , y , $-x$ and $-y$ -coordinates of the walking track.

A free-ranging beetle walking without external air-current stimulus was recorded with a high-speed camera (Locam, model 51, Red Lake; filmed at $100 \text{ frames s}^{-1}$). The coordinates of parts of the beetle's body (antennae, left tarsus and pronotum) were digitized (Summagraphics HW2-209) and drawn frame by frame.

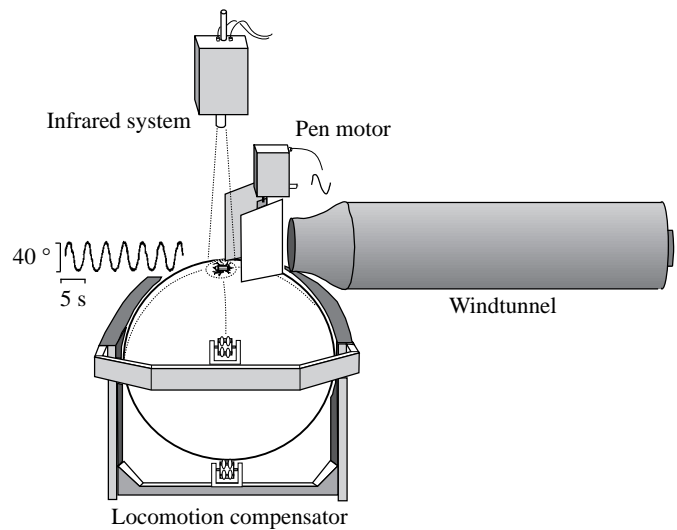


Fig. 1. The experimental apparatus. The beetle was free to walk on the apex of a ball. An infrared system monitored each change in the position of the animal. Correspondingly, two servomotors of the locomotion compensator compensated for the animal's movement, thus keeping it in the same position in space. The movement of the ball was coded into a train of electric pulses, which represented the x - and y -coordinates of the walking track. A windtunnel, which generated an air current with a low level of turbulence, was placed 15 cm from the beetle. Two plates in front of the mouth of the windtunnel, which were moved sinusoidally by a pen motor, produced the modulation in air-current direction, which was recorded with a constant-temperature hot-wire anemometer at the position of the animal (see trace on the left-hand side).

Stimulation by air currents

Animals walking on the locomotion compensator were stimulated by currents from two different windtunnels.

A small windtunnel (length 60 cm; mouth diameter 10 cm) produced a low-turbulence air current at 1 m s^{-1} , which could be switched on and off by a step-motor-driven valve inside the windtunnel tube. The valve opened and closed in 450 ms. The duration of the air-current stimulus and the stimulus period were controlled by a microcomputer (Mikroprofessor, Multitech). As stimulus duration was varied, the inter-stimulus interval was changed correspondingly so that the stimulus period, and hence the duration of the whole stimulus series, would be constant.

A large windtunnel (Fig. 1, length 140 cm) produced an air current whose direction was modulated sinusoidally within $\pm 20^\circ$. The modulation was produced by two plates (10 cm \times 20 cm) in front of the mouth (diameter 18 cm) of the windtunnel, which were sinusoidally moved by a pen motor. The constant-temperature hot-wire anemometer was used to measure rapid changes in direction of a constant-velocity current in the field at the apex of the ball. Except for the change in air-current direction caused by the plates, there were no vortices or turbulence in the apparatus at low and high frequencies. Moving the plates without an air current had no effect on the walk of the animal.

Data processing

All experiments on the locomotion compensator were conducted in the dark at a room temperature of 21–24 °C. The walking velocity v , walking direction α and the animal's path were computed and reconstructed by analysing the rate of the four electric pulse trains at sampling interval Δt . Each individual run was characterised by a vector with its origin at the starting point and its tip at the end point of the run. The vector length L is calculated from the shortest distance between the starting and end points, divided by the length of the actual distance walked. Hence, an increase of vector length corresponded to an increase in straightness of the path. When the animal walks in a straight line, the maximum value of L will be 1.

To calculate the mean change in an animal's walking direction during stimulation with sinusoidally changing wind direction, the walking direction was averaged for several stimulus cycles (Lönendonker, 1991). In this way, only those components of the animal's response that are coupled to the stimulus frequency are evaluated. Power-density spectra of walking direction with no stimulus showed that in these circumstances the direction of a beetle's walk fluctuates with components between 3 and 10 s^{-1} (Böhm, 1987). When the carrion beetle is walking in a constant air current, peak angular velocities as great as 90° s^{-1} to the left and right can be recorded (Heinzel and Böhm, 1989), so that a beetle walking on the locomotion compensator should be able to give an unrestricted response to the largest directional change tested, $\pm 20^\circ$ at 1.5 s^{-1} .

The frequency response of an individual animal was tested with up to eight frequencies in a single day. The duration of

an experiment was determined by the number of stimuli and the period of the oscillation. When the stimulus period was short, the sampling interval was correspondingly reduced so that there would be sufficient data points per cycle. If the preferred walking direction with respect to the air-current direction changed during an experiment, the cycle during which the change occurred was eliminated from the analysis.

The data points for mean walking direction in every measured phase of the stimulus cycle were fitted using sinusoidal functions (least-squares method, Batschelet, 1981). The cross-correlation coefficient (Varjù, 1977) was calculated as a test of every fit (Lönendonker, 1984), and as a rule was found to be 0.75 or higher. Only for the highest frequency tested, 1.5 Hz, was it lower, because here the scatter of the walking-direction values was large in comparison with the amplitude.

Thus, the animal's reaction was represented by the amplitude and phase of this fitted sinusoid, shown as a function of the frequency of the sinusoidal stimulus in a Bode plot.

Results*Air currents generated by the animal itself*

The antennae of carrion beetles are the only air-flow sensors involved in orientation to the wind. They are sited on the head capsule, articulated by a type of ball joint and can be actively bent at the scapus–pedicellus joint (Heinzel and Böhm, 1989). Because of this arrangement, not only every antennal movement but also any movement of other parts of the body can, in some circumstances, produce an air current relative to the antennae. As a first step, to test for an influence of self-generated air currents on the wind-orientation system, walking in the absence of wind was examined.

Because insect walking involves a rhythmically coordinated pattern of leg movements, the velocities of the body and its appendages also change rhythmically. For instance, a point on the midline of the pronotum of the carrion beetle advances at a speed that fluctuates rhythmically between 3 and 18 cm s^{-1} at a frequency of about 12 s^{-1} (Fig. 2, upper trace; see asterisks); in the process, it oscillates to the right and left of the mean walking direction at the stepping rhythm of approximately 6 s^{-1} (Fig. 2, top).

The right and left antennae also oscillate at the stepping rhythm, approximately in synchrony with the foreleg (Fig. 2, top). The range over which velocity changes is the same for the antennae as for any other point on the body. However, the periodicity in ground speed is not so clear for the antennae, because their forward progress is affected by the passive coupling of the antennae to the head and the head to the pronotum. Although the antennae also swing to the left and right of the mean walking direction, the angles between their actively movable segments are kept very constant, as has previously been shown for the range setting of the locust antenna during flight (Gewecke, 1972).

An air-current velocity of 5 cm s^{-1} stimulated carrion beetles to orient their walking direction with respect to the wind

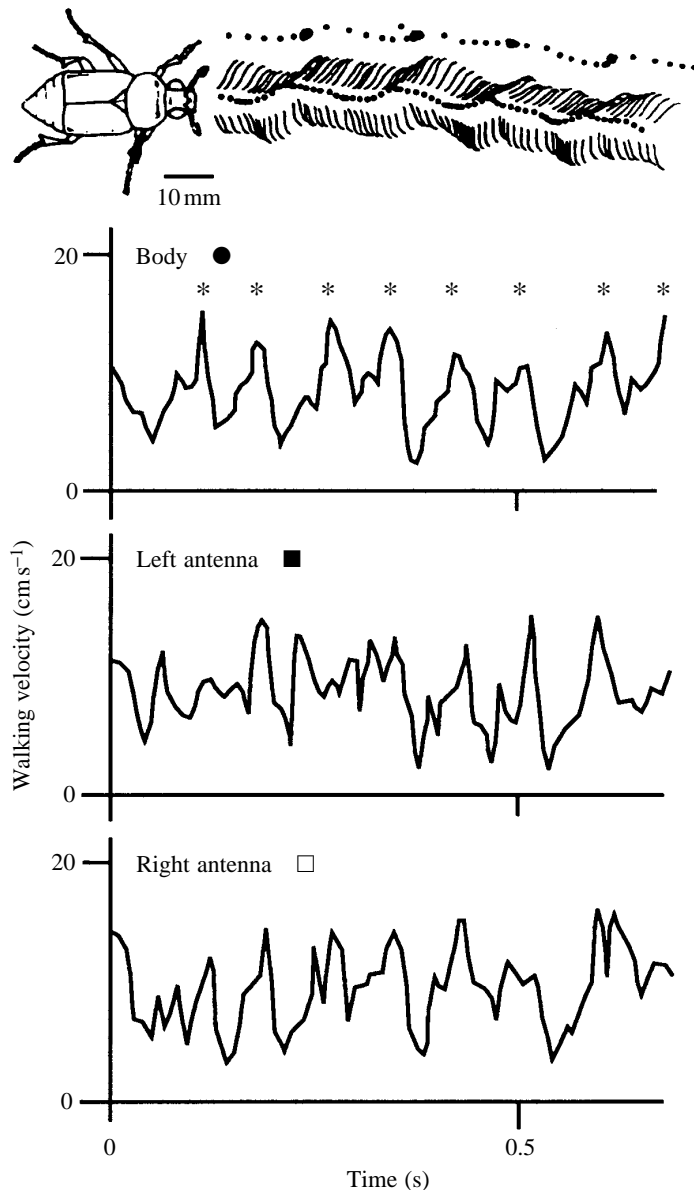


Fig. 2. Relative air flow generated by walking. The drawing at the top shows the positions of the antennae, the left front tarsus and the pronotum with respect to the ground at intervals of 10 ms. In the graphs below, movement velocity is plotted as a function of time for a point in the midline of the pronotum (●) and the tips of the two antennae (right □; left ■). The asterisks mark maxima in the forward velocity of the point on the body.

(Heinzel and Böhm, 1989), and the self-generated relative air currents measured here exceed this threshold. The following experiments demonstrate the influence of marked changes in air-current velocity on the beetles' walking and show how modulation of air-current direction affects the animals.

Wind-orientation in air currents of various durations

When a beetle walking in the dark with no other directional stimuli is presented with a single pulse of flowing air, i.e. a temporary increase in air velocity from 0 to 1 m s^{-1} in a

constant direction (0°), its first visible response is to reduce its walking speed and then to pause (Fig. 3). Every such stimulus, however brief, caused the beetle to stop walking, although the duration of the pause varied and was independent of the air-pulse duration.

When the beetle begins to walk again after stopping, it is most likely to proceed at a particular, steady angle with respect to the direction of the air pulse. That is, whereas in the dark with no directional cues it had changed direction continuously so as to walk on a circular path, during air-pulse stimulation it walked in a relatively straight line. From moment to moment, its walking direction is corrected towards the preferred direction relative to the air-current direction, with the result that the recorded instantaneous walking direction fluctuated over only a small range ($\pm 45^\circ$) around the preferred, mean walking direction (Fig. 3, upper trace within the hatched columns).

The preferred walking direction can be at any angle with respect to the air-pulse direction (anemomenotaxis). From one stimulation to the next, a given animal can choose a different menotactic course (Fig. 3, upper trace: $+125^\circ$ during the first stimulus, -130° during the second stimulus). The preferred courses are not individual-specific; they vary from animal to animal.

When the air pulse lasts as long as the animal's pause or is shorter (Fig. 3: fourth and fifth stimuli, less than 4 s), the direction of the subsequent walk is not controlled with respect to the stimulus direction.

Although a beetle can orient its walk in the presence of a single brief air current, in ordinary life it is usually confronted with many such events. To imitate such natural stimulation under specific conditions, four animals were each presented with 18 series of uniform air-flow pulses (velocity 1 m s^{-1}) from a constant direction, with a different temporal structure in each series.

When a beetle walking in the dark is presented with a series of pulses in which the pulse duration is greater than 5 s, with a 10 s interval between pulses, the animal responds to each pulse as it would to a single pulse, orienting its walk with respect to the direction of the air current. As the inter-pulse intervals are progressively reduced, only the first pulses in the series cause the beetle to stop walking, for varying periods. This response habituates so strongly that, when pulses occur in rapid succession, the walking velocity is hardly reduced at all, with little dependence on pulse duration. As a result, after the initial, momentary reduction in walking velocity, beetles in a discontinuous air current proceed almost as fast during the air pulse as before or after stimulation.

In response to the air-flow patterns presented here, all the animals tested exhibited a preference in the distribution of their walking directions, although here again the menotactic course could vary from animal to animal and from walk to walk. The strength of the preference for a certain direction relative to the wind, reflected in the straightness of the chosen course and thus in the vector length, depends on the ratio of pulse duration to pulse period (Fig. 4).

Apart from one value ($N=64$), the mean vector lengths for

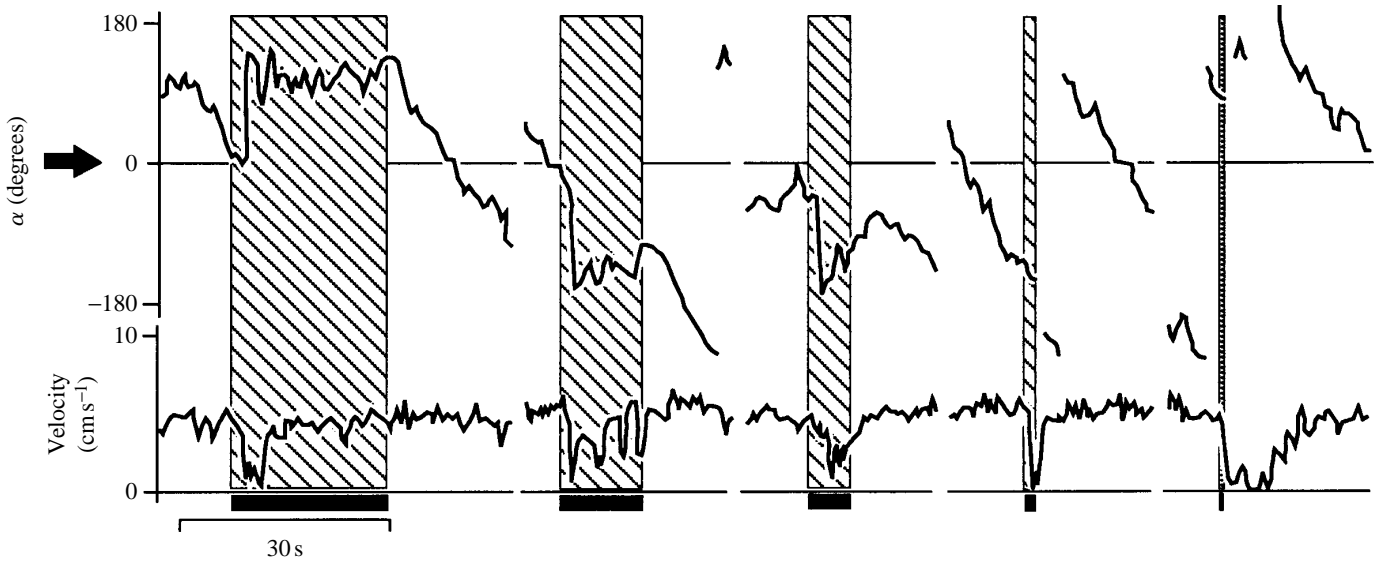


Fig. 3. Walking during wind pulses. Time course of walking velocity v and walking direction α of a beetle exposed at intervals of 2.4 min to an air current (1 m s^{-1}) of various durations from the direction 0° . The presence of the wind stimulus is indicated by the hatched columns. The arrow shows the direction of air flow.

walks with air-current pulses are greater than for those without stimulation (Fig. 4: dashed line at $L=0.17$). Although the values of L for a few walks exceed 0.9, the fluctuations about the mean walking direction are usually greater in discontinuous air currents, because of more pronounced corrective turning, than in a continuous current. Therefore, the average of these values is below the mean vector length of 0.88 (Fig. 4: dot-dashed line) obtained from 109 experiments in a continuous air current at 1 m s^{-1} .

The vector length of a walk in which an air current is present for about 30% of the total duration of the trial is approximately 0.7. An increase in flow velocity of a discontinuous air current would presumably give a greater degree of orientation, but this effect was not investigated.

Wind-orientation when the air-current direction changes

The fluctuations in walking direction produced spontaneously in the absence of wind amount to only a few degrees, and their frequency spectrum is characterized by the stepping rhythm of the individual beetle. Even in a continuous air current, the power-density spectrum includes no conspicuous frequency components in addition to those associated with these changes of direction (Böhm, 1987). However, if the direction of an air current is suddenly altered, a large change in angle almost always induces a corresponding change in the beetle's mean walking direction within a few seconds (Böhm *et al.* 1991).

To quantify precisely the dynamic properties of the wind-orientation system, a frequency-response analysis was carried out for five individuals, with the aim of discovering the transfer characteristics for changes in air-current direction. The stimulus was an air current flowing in a direction that was modulated sinusoidally with an amplitude of $\pm 20^\circ$ about the 0° direction. The modulation frequency was varied to see how

the fluctuations in walking direction would be affected, for an air-current field with constant flow velocity of 1 m s^{-1} .

In the example shown (Fig. 5, upper right) the animal is following the low-frequency stimulus ($f=0.02 \text{ s}^{-1}$) in phase. The amplitude of its response corresponds to the amplitude of the change in air-current direction. When the stimulus frequency is

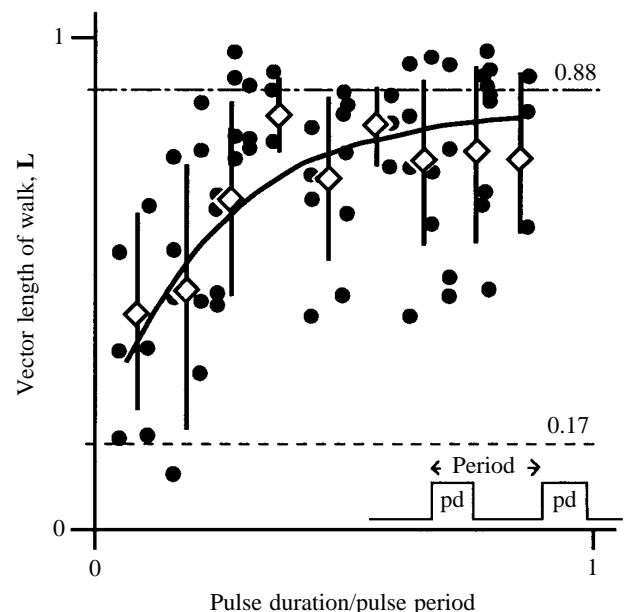


Fig. 4. The quality of orientation during wind pulses. The vector length L of a walk is plotted as a function of the relative duration of the air-current stimulus (pd =pulse duration). The graph shows both the individual (\bullet) and the mean (\diamond) \pm s.d. values subdivided into 10 classes. The dot-dashed line marks the mean vector length found in a continuous air current at 1 m s^{-1} . The dashed line shows the mean vector length in the absence of an air current. The curve was fitted by eye to the mean values for orientation in wind pulses.

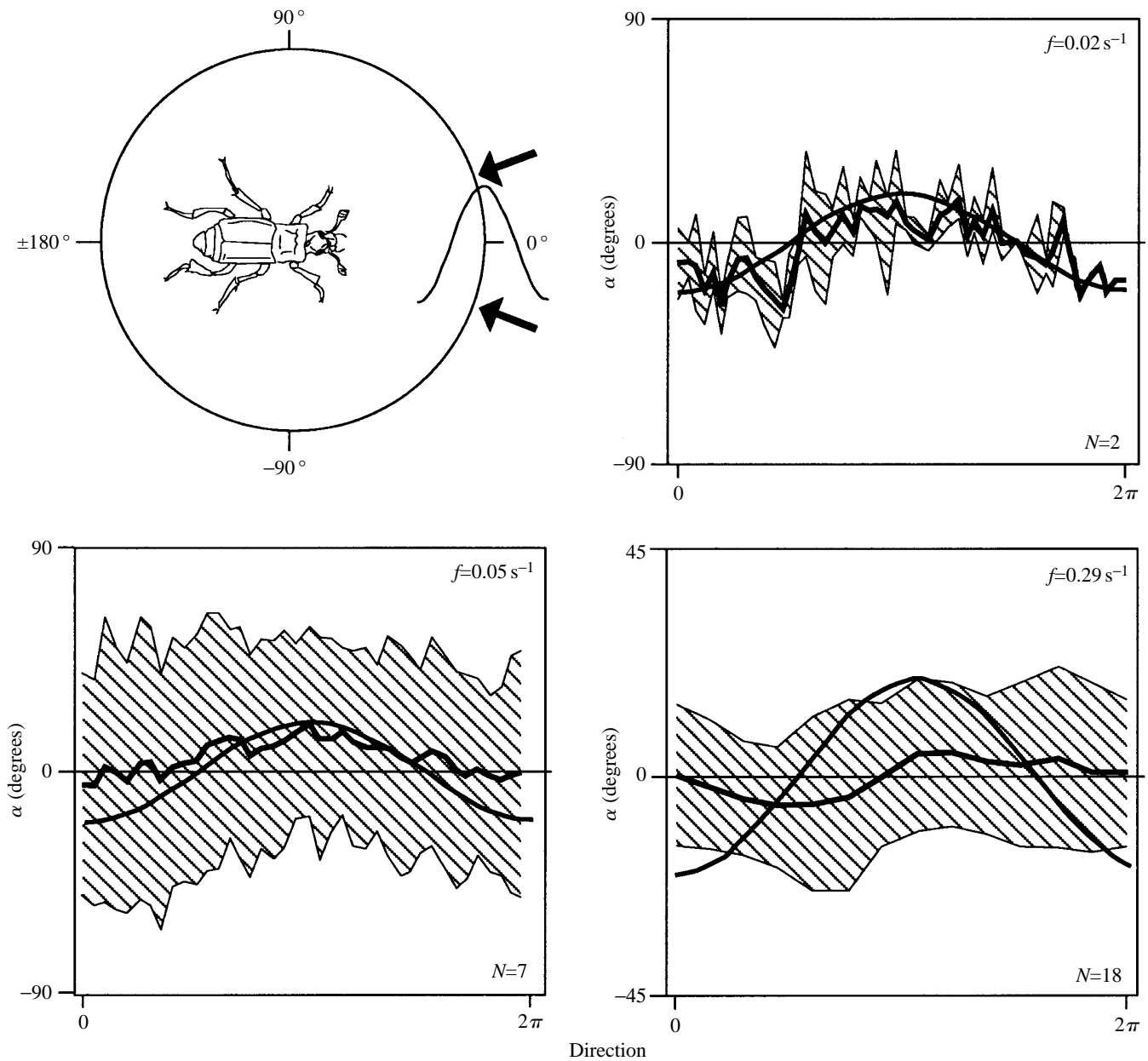


Fig. 5. The frequency-response analysis. Each graph shows mean walking direction and angular standard deviation (hatched region, N indicates how many cycles were averaged) over the stimulus cycle, superimposed on a sine wave representing wind direction. The animal's response is shifted symmetrically with respect to the 0° direction, so that the ordinates are to be interpreted as directional change. The drawing at the upper left shows the stimulus situation. The beetle walks on the locomotion compensator in the 0° direction, while the direction of the air current oscillates as shown by the sine wave. Minimum and maximum changes in current direction are indicated by the arrows.

raised to 0.05 s^{-1} (Fig. 5, lower left), the response amplitude is distinctly reduced. This trend continues as the stimulus frequency is further increased, and the animal's response begins to lag distinctly behind the stimulus. With stimulus frequencies exceeding 1.5 s^{-1} , none of the individuals tested showed any response to the change in direction of the air current.

Although walking beetles are entirely capable of changing their walking direction by 90° within 1 s, the beetles in air currents that changed direction by $\pm 20^\circ$ with a frequency greater than 1.5 s^{-1} failed to follow the direction of the wind

at all. Only low frequencies are detected by the wind-orientation system without being attenuated (Fig. 6A). As the response amplitude decreases with increasing stimulus frequency, the change in walking direction lags progressively further behind the stimulus. In the region between 0.1 and 0.3 s^{-1} , the phase of the following response is shifted by -90° . Above 0.3 s^{-1} , all the phase values fall sharply, so that at frequencies greater than 1 s^{-1} the phase lag is almost 360° . The 180° line is crossed with negative slope at values around 0.8 s^{-1} (Fig. 6B). At this frequency, the gain is less than 1 for

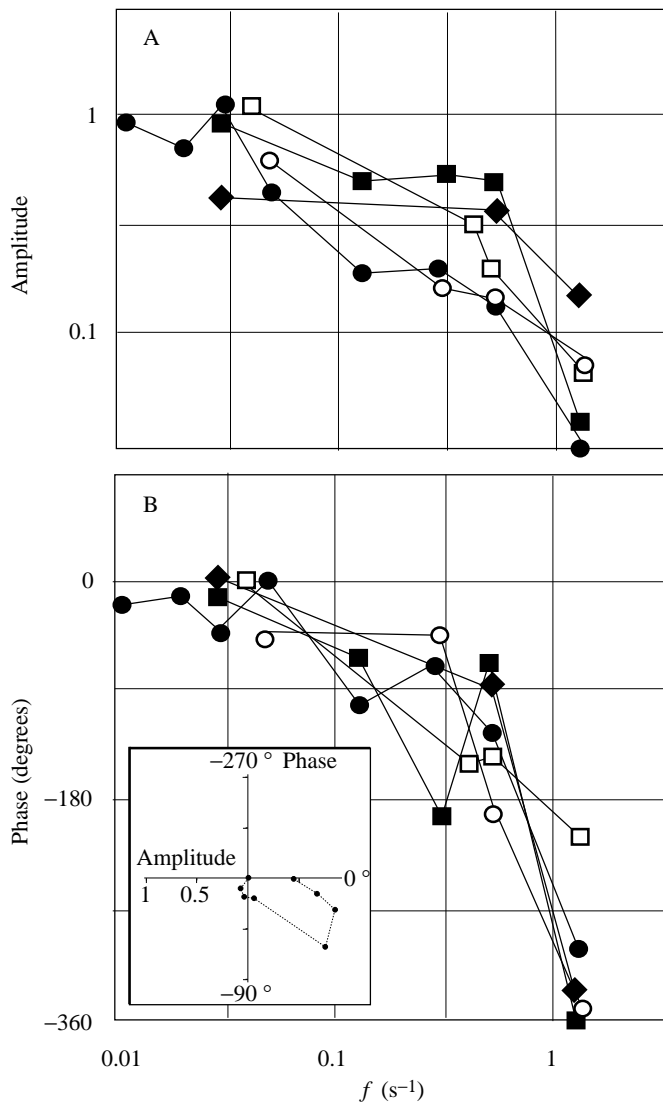


Fig. 6. The Bode plot: amplitude (A) and phase (B) of the sine wave fitted to the mean walking direction of the beetle, as a function of stimulus frequency. The values obtained from an individual animal ($N=5$) are represented by the same symbol in the amplitude and phase diagrams. The inset in B is a Nyquist diagram showing the phase and corresponding amplitude for the animal represented by the filled circle (●) in a polar plot.

all the curves. Because of the broad intra-individual scatter of the amplitude and phase values in this biological system, no attempt has been made here to give specific values for corner frequency and order of the system, or for the characteristic time constants that are ordinarily used in technical descriptions.

Natural air-current structure

Given that the dynamic properties of the wind-orientation system have been established using the transfer function (Bode plot; Nyquist diagram), it is evident that the relative air currents generated by the beetle itself would not be expected to affect course control directly because they are in a frequency range too high to be passed by the system to the components involved

in walking. In nature, an insect walking on the ground, with its antennae at a height of about 20 mm, is exposed not only to these self-generated air currents but also to the ambient air movements characteristic of that region (Fig. 7).

In woodland, the wind velocity 20 mm above ground is on average only 20–30% of that 70 cm above ground (e.g. top trace in Fig. 7 from 0 to 0.5 min: mean velocity at 20 mm is 0.2 m s^{-1} ; mean velocity at 70 cm is 1.1 m s^{-1}). The detailed changes in wind velocity over time at 70 cm differ considerably from those in the boundary layer near the ground.

High-resolution measurements in the boundary layer (approximately 10 mm above ground) with the hot-wire anemometer (Fig. 7C) reveal peaks that can be interpreted as microturbulence. These are produced as the air moves among leaves and grass in the boundary layer. Within a few milliseconds, the air velocity near the ground can change by as much as 0.5 m s^{-1} , so that the air flow becomes pulsatile. However, the duration of such bursts of pulsatile air flow and the intervals between them are in the range of seconds rather than milliseconds.

In the video frames, two direction indicators 4 cm apart were rarely observed to point in opposite directions. When the air-current velocity was above 0.10 m s^{-1} , the direction of air flow at neighbouring measurement points was usually the same, and the pattern of directional change over time was also the same at each point. However, the direction recorded for the array of indicators could be very different from one frame to the next. At a sampling interval of 0.5 s, an air current with a velocity v_w of approximately 0.5 m s^{-1} could change direction by as much as 105° between samples (see Fig. 7; angle β). Higher-velocity air currents, as a rule, change direction more slowly ($20\text{--}30^\circ$ in 0.5 s) and can maintain a relatively constant direction for several seconds.

The time course of air flow in the boundary layer near the ground, within which a beetle walks, varies unpredictably. Although the changes in direction and velocity measured for these air currents were greater than those found for the self-generated air flow during walking, the frequency components of velocity and direction changes are within the same spectral region (not illustrated) in both cases, mainly between 0 and 10 s^{-1} . They are thus in the same range as those of the stimuli used for the frequency-response analysis and for the experiments with air pulses.

Discussion

As would be expected given the magnitudes and rates of change measured for natural air currents, a carrion beetle orienting its walk to the wind is relatively undisturbed by irregular changes in the movement of the ambient air. When exposed to an air current with pulsatile velocity fluctuations, the beetles can still make use of it to maintain a preferred walking direction with respect to the air-current direction. This sort of anemotaxis in a discontinuous air current has been

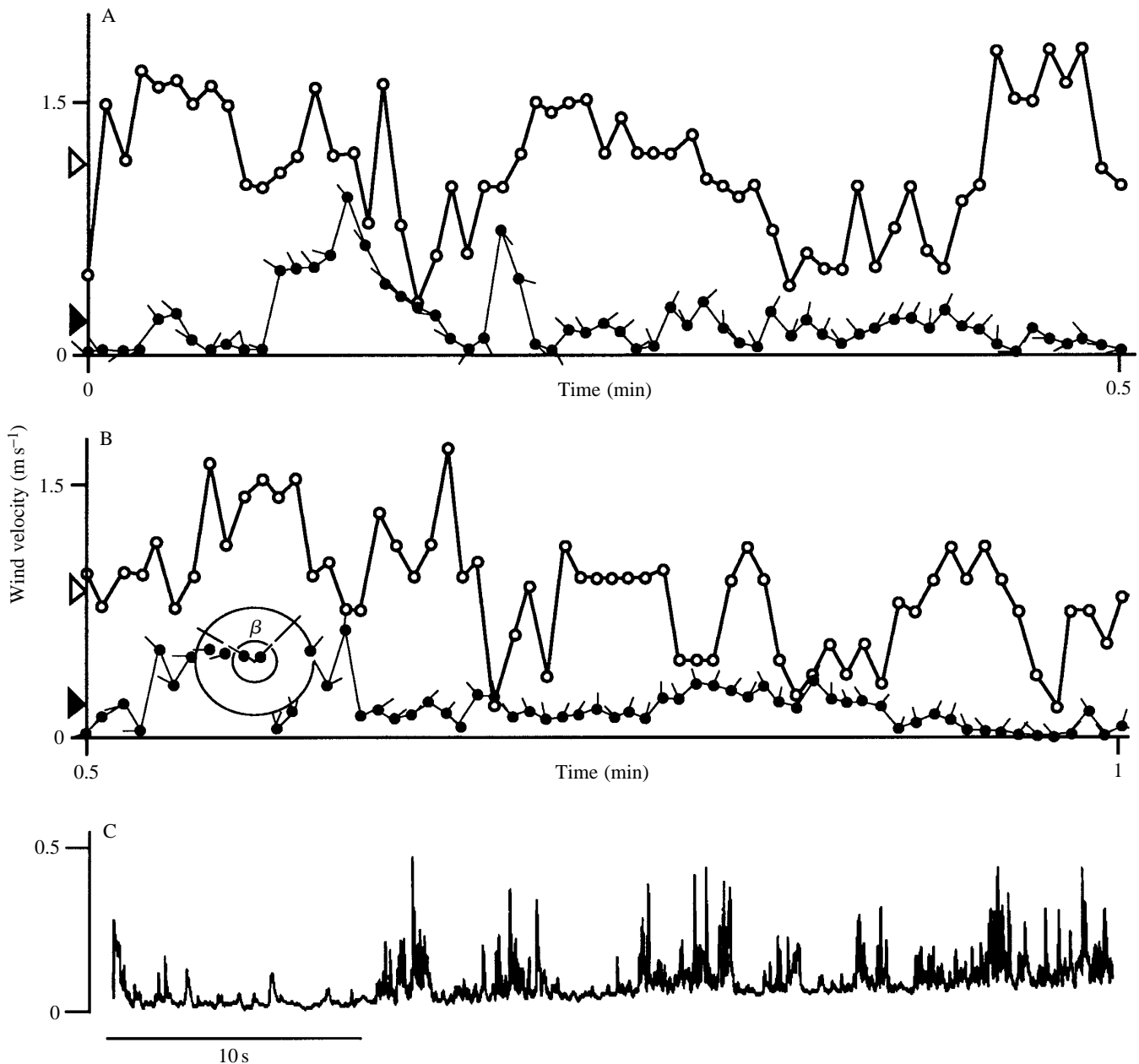


Fig. 7. Wind velocity as a function of time. A and B show consecutive values of air-current velocity v_w measured over 1 min at a height of 700 mm (○) and 20 mm (●) above the ground. The lines leading away from the filled circles indicate the direction of air flow. The arrowheads on the ordinate indicate the mean values over each 0.5 min period (▷, 70 cm above the ground, ►, 20 mm above the ground). The angle β in B is the maximum difference in the direction of air flow between two consecutive frames (105°). In C, the air-current velocity is shown at higher temporal resolution, as measured in the boundary layer in the environment at the height of a beetle (approximately 10 mm) with the hot-wire anemometer.

described previously by Linsenmair (1969) for Tenebrionidae and dung beetles.

Insects such as cockroaches *Periplaneta americana* (Camhi and Tom, 1978) and crickets *Acheta domesticus* (Stabel *et al.* 1985) usually respond to air pulses with an escape reaction; that is, they walk faster and choose an unpredictable walking direction that takes them away from the direction of the stimulus. During courtship, African crickets *Phaeophilacris spectrum* presumably use low-frequency air-current signals

(near-field medium motion) for intraspecific communication (Heinzel and Dambach, 1987), as has been reported for the infrasonic signals produced by bees *Apis mellifera* (Michelsen *et al.* 1986).

The organization of the mechanosensory systems that process such air-current signals and the underlying central nervous filtering mechanisms have so far been worked out in only a few cases in arthropods (Barth, 1986). It remains an open question whether the different observed behavioural

responses, (1) an initial reduction of walking velocity and orientation to the air current (Bell and Kramer, 1979), (2) an undirected escape reaction with increased walking velocity (both can be found in cockroaches), or (3) an increased passivity (as in the African cave cricket), are brought about by the spatial structure of an air current or by the temporal interaction, in the central nervous system, of the signals from various organs that sense air flow.

Unlike the insects with escape reactions cited above, carrion beetles do not try to escape when they are in danger, or when a puff of air is blown at them. Instead, they use passive defensive behaviour to protect themselves from enemies (Pukowski, 1933). They also lack the cercal sensory system that contributes to escape behaviour in other insects; the antennae of carrion beetles are their only sensors for air currents. When the antennae were cut, the beetles lost their capability for wind-orientated walking (Heinzel and Böhm, 1989) and their walking velocities were reduced immediately after ablation of both antennae.

In order for a carrion beetle to orient its walking direction with respect to an air current, each individual gust of wind must last for at least 4–5 s. This inertia in the wind-orientation of walking beetles is certainly not due to the organization of the mechanosensory system in their antennae. Experiments on the locust antenna (Heinzel, 1978) have shown that changes in air-flow velocity are well transmitted up to frequencies of 70–130 s⁻¹. The mechanoreceptors in locusts very accurately signal changes in direction (0.01°) or velocity of an air current in the region of the wingbeat frequency (20 s⁻¹). If the flow velocity changes, they can correct their wing movements within only one wingbeat cycle. It has been demonstrated that locusts are dependent on rapid, phasic information about the modulation of air-current velocity, which is self-generated by the wing beat (Horsmann *et al.* 1983), in order to maintain stable flight (Wendler, 1974).

Walking beetles can also make course corrections relatively rapidly, e.g. within one stepping cycle (approximately 160 ms). The rhythmically fluctuating air currents caused by the act of walking are also within the range of velocities that can be detected by the beetles (Heinzel and Böhm, 1989). Like flying locusts, walking carrion beetles could possibly use the self-generated change in air current to monitor their rhythmic walking pattern in order to maintain a stable course.

But not all changes in an air current elicit an equally strong response. Indeed, it is to the beetle's advantage for some to be ignored. The relatively high-frequency microturbulence measured in the boundary layer near the ground, for instance, should not have much influence on the beetle's orientation, or too much energy would be expended in making the many small, rapid corrections necessary to maintain a straight course. Besides, the success of an anemotactic search for a carcass would be reduced, because less space could be covered in the same time if the beetles were to react to every small change in the air current. Only gusts of wind that carry an appropriate odour should modify the anemotactic behaviour. Therefore, it

would make sense to collect sufficient information about the quality of an air current and then to modify the preferred course.

The Bode plot for direction-tracking in the wind-orientation system gives important insights into the function of information-processing mechanisms in the central nervous system of the carrion beetle. From the measured transfer function for oscillatory changes in wind direction it follows (1) that low-pass characteristics must be included in the wind-orientation system (a previous study of the anemoreceptive system of walking moths of the species *Lymantria dispar* has also implicated a low-pass characteristic; Preiss, 1980); and (2) that the instantaneous walking direction of a beetle results from the integration of turning tendencies that have the effect of compensating for deviations from the preferred walking direction (Böhm *et al.* 1991).

These two properties indicate a system of at least second order, which is capable of oscillation (Cruse, 1981; Lönnendonker, 1984). Because the Bode plot does not reflect any resonance phenomena in the form of overcompensation for a change in direction, it follows that the present system must have low gain (high damping). In theory, under such conditions, the phase lag cannot be greater than -180° (Cruse, 1981). Here, however, phase lags of up to 360° were measured. This behaviour must reside in a third property. This third property is a dead time, which is always present in biological systems if only to allow time for neural conduction.

The combination of low-pass characteristics, an integrator and a dead time explains the dynamic properties of the orientation of the carrion beetle to changing air currents. In fact, the transfer function was calculated for the feedback control loop of walking direction based on low-pass, integrator and dead-time elements (Böhm and Scharstein, 1988). In that transfer function were three constants, which depended on the properties of the different elements, namely the gain, the integration time constant and the dead time of the feedback loop. Mathematical simulations which took into consideration variations of these constants in the range 0.2–0.7 for the gain, less than 0.5 s for the integration constant and less than 0.5 s for the dead time led to a set of transfer functions which covered the range of data points measured for the beetle's walk (Böhm, 1987; Böhm and Scharstein, 1988).

The time constants obtained here are similar to those found for other orientation systems, such as the visual fixation system of the fly *Musca* (Guo and Reichardt, 1987) or the potato beetle *Leptinotarsa decemlineata* (Lönnendonker, 1984) and the auditory system of the cricket *Gryllus bimaculatus* (Wiese, 1986). To determine just where these filter characteristics reside in the carrion beetle, however, it will be necessary to examine the individual components of the wind-orientation system in greater detail.

I thank Professor Wendler for many valuable discussions on the subject of wind orientation. Professor H.-G. Heinzel was always ready to help with the solution of aerodynamic problems and was a critical reader of the manuscript. I am

grateful to Dr H. Scharstein and Dr U. Lönnendonker for their friendly, computer-assisted advice regarding data processing with the PDP. The manuscript was kindly translated by Dr M. A. Biederman-Thorson. This work was supported by funds from the DFG We719, He1118.

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