

VISUAL AND ACOUSTIC COURSE CONTROL IN THE CRICKET *GRYLLUS BIMACULATUS*

BY HARTMUT BÖHM, KLAUS SCHILDBERGER AND FRANZ HUBER
Max-Planck-Institut für Verhaltensphysiologie, 8130 Seewiesen, Germany

Accepted 23 April 1991

Summary

The influence of visual and acoustic stimuli on course control was studied in crickets walking on an air-supported sphere under open-loop conditions. The speed of walking elicited by a calling song was greater in the presence of visual targets than it was in the dark. The precision of phonotactic orientation was improved in the presence of visual cues. Visual and acoustic stimuli induced turning and when both stimuli were present at the same time their effects were additive. A further enhancement was observed when visual and acoustic stimuli were presented from the same direction. Optomotor stimuli also shifted the response to the calling song in an additive way.

Introduction

A female cricket can find a singing male in the dark by meandering over the ground in the direction from which the sound comes, thus tracking the sound source (Wendler *et al.* 1980; Weber and Thorson, 1989). In their habitat, however, crickets orient in a complex environment (Hissmann, 1990) in which visual cues may play a role.

Studies on vision and visually guided behaviour in crickets have been performed to investigate the ontogeny of visual orientation (Campan *et al.* 1987) and the use of terrestrial cues (Campan and Gautier, 1975; Atkins *et al.* 1987; Honegger and Campan, 1989). Visual landmarks and even the plane of polarization of sunlight can be used for orientation (Labhart, 1988).

Female *Acheta domesticus* track acoustic and visual targets using different walking modes (Stout *et al.* 1987; Weber *et al.* 1987). The phonotactic walking course is less meandering when there is a visual stimulus coming from the same direction as the acoustic signal (Weber, 1990).

Although the effects of visual stimuli on orientation and on phonotaxis have been described, little is known about the mechanisms of this multimodal control of orientation. Some understanding of course-control mechanisms underlying phonotaxis has been derived from turning-tendency curves measured under open-loop conditions (Stabel *et al.* 1989; Schildberger and Kleindienst, 1989). This paper investigates the effects of visual and acoustic stimuli on locomotion and course

Key words: course control, *Gryllus bimaculatus*, optomotor response, phonotaxis.

control under open-loop conditions, thus contributing to an understanding of the ways in which multimodal information is processed. This study will guide the search for the mechanisms involved in course control at the level of neurones descending from the brain (H. Böhm and K. Schildberger, in preparation).

Materials and methods

Freshly moulted, adult female *Gryllus bimaculatus* De Geer were taken from a laboratory culture and kept individually in small glass jars at 24°C at a relative humidity of about 80% and a light:dark cycle of 12 h:12 h. They were fed with lettuce, apple and carrot. Animals were taken for experiments after 2–4 weeks of adulthood.

Experimental apparatus

The cricket was tethered on a counterweight balance and walked on top of an air-supported, hollow styrofoam sphere (Fig. 1, radius of the ball 6 cm). The rotation of the ball, and thus the intended movement of the animal, was registered

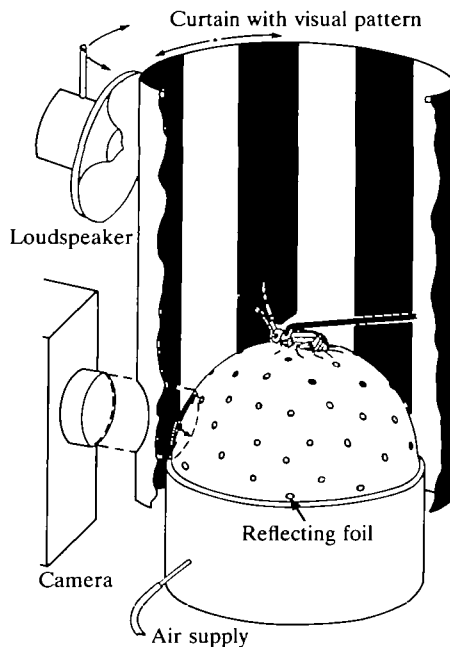


Fig. 1. Design of the experimental apparatus. The female cricket is fixed to a holder and placed on top of an air-supported, hollow styrofoam sphere. The ball can be rotated by the animal, and rotations of the sphere about the transverse and vertical axes (arrows), corresponding to yaw turns and forward walking of the cricket, respectively, were measured by an optical sensor. A loudspeaker can be moved around the animal and an acoustically transparent curtain provides a visual environment. Drawing is not to scale; see text for details.

by means of a camera of the type used in the Kramer walking compensator (Kramer, 1976; Weber *et al.* 1981). In front of the animal and at the height of the equator of the sphere, the camera illuminated a round section of the sphere's surface (diameter 30 mm) with infrared light. The emitted light was reflected from dots on the sphere to a photodiode in the camera and the positions of the dots were registered separately as x - and y -components in the measuring field.

Because the measurement area was situated on the equator and in front of the sphere, the change in x - and y -values specified, respectively, the length (d) of rotational and translational components of the walk (Fig. 1, arrows).

Data processing

The sampling rate ($\Delta t=0.01$ s) of the system corresponded to a spatial resolution of 0.3 mm and a linear range of velocities from 0.3 to 100 cm s⁻¹ (Schildberger and Hörner, 1988). The instantaneous forward speed (translational velocity component measured in cm s⁻¹, $v=d/\Delta t$, where v is velocity, d is distance moved and t is time) and the angular velocity (rotational velocity component $\omega=180d/\pi R\Delta t$ measured in degrees s⁻¹, where R is the radius of the sphere) were each calculated by averaging separately for the two axes of rotation over a time interval of 100 ms. The standard deviations of instantaneous forward speed (σv) and angular velocity ($\sigma\omega$), sampled in this way, were calculated. In the time course of translational velocity negative values occasionally occurred, but were not plotted. Positive values of angular velocity indicated an intended turn to the right, negative values an intended turn to the left. In each sampling interval, the path on the ball was reconstructed by adding the vector of x - and y -components.

To determine the relationship between the motor output of the animal and the stimulus angle, the angular velocity, averaged over a 2-min trial, was measured for the whole range of stimulus directions in each stimulus paradigm. This was termed the characteristic curve. Characteristic curves were obtained from each individual responding to the calling song and to a single black stripe, as well as for the optomotor response. The slope at the zero crossing of the characteristic curve was approximated by the slope of the linear regression line calculated from the values $\pm 30^\circ$ from frontal.

In control experiments carried out in total darkness, the mean rotational velocity varied from individual to individual. There was no systematic bias and, therefore, the characteristic curves were averaged for all animals tested under the same conditions.

In a first approximation, data values of the characteristic curve under the open-loop condition were fitted by a sinusoidal function. In some experiments a stepwise Fourier analysis was made and the values of the characteristic curves were fitted by an algorithm according to the abbreviated Doolittle method (Bennet and Franklin, 1954; Mittelstaedt, 1986). The data values were then approximated to the third harmonics of the sine and cosine components. However, only the significant components were plotted and used in the subsequent analysis.

Acoustic stimulation

An artificial calling song with four syllables of 20 ms duration and a 20 ms pause, with a chirp period of 350 ms and a carrier frequency of 5 kHz was presented *via* a loudspeaker, which could be rotated around the cricket by a motor (Fig. 1). The sound intensity was 80 dB SPL at the position of the cricket and varied by ± 2 dB SPL. The sound direction (α) was changed in steps of 30° in an unsystematic way. All tests with stationary acoustic and visual stimuli or an optomotor stimulus were made in random sequences. Owing to the large number of paradigms, tests with the same crickets were performed on different days.

Visual stimulation

The whole apparatus was placed in a closed, anechoic chamber. The temperature varied between 21 and 26°C . A 38 cm diameter circular fluorescent lamp (40 W) provided diffuse light, when required. A 24 cm diameter white, cylindrical and acoustically transparent curtain provided a visually featureless environment for the cricket. The lower edge of the curtain was positioned at the horizon of the cricket and was 20 cm in height, thus subtending an angle of about 60° for the experimental animal.

Black, acoustically transparent targets of different shapes could be fixed to the inner side of the curtain (Fig. 1). The light intensity at the position of the animal varied from 460 to 1100 lx depending on the visual pattern used. Either a single stripe (width 40°), which seems to be an attractive visual target, or gratings (vertical stripe width 30° , horizontal stripe height 30°) were used.

The cylinder was driven by a motor to move the single stripe in any desired direction relative to the animal or to produce continuous turning of the vertical pattern with different contrast frequencies.

Results

Walking in a visually and acoustically structured environment

Tethered crickets showed the typical intermittent walking pattern that can also be observed in freely walking animals. The pattern of forward movement in darkness differed from that observed in the light. In the dark, the walk was characterized by phases of relatively constant speed (Fig. 2A). In the light, more short stops and short walking bouts occurred, regardless of acoustic stimulation (Fig. 2B,C). The change in walking mode resulted in a shift of the corresponding distribution of momentary translational velocities towards higher values and an increase in the breadth of the distribution.

The translational speed of a typical individual was low in the dark in the absence of acoustic stimulation (mean velocity of the single run 1.54 cm s^{-1}), but it increased when the calling song was added (2.24 cm s^{-1}). A further increase in forward speed was observed in conditions of diffuse light (3.91 cm s^{-1}). The presence of a visual target did not increase walking speed, whether an acoustic

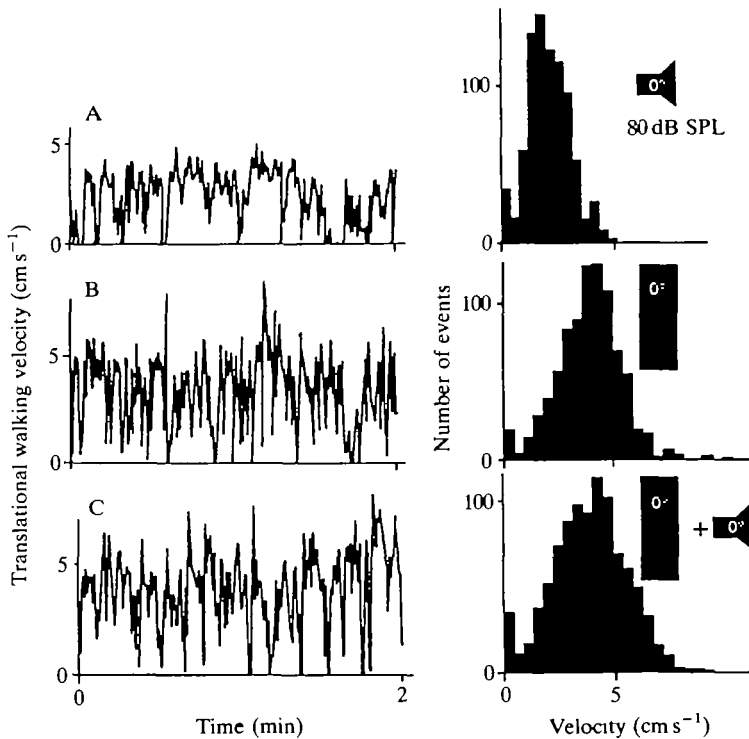


Fig. 2. Translational walking velocity of an individual female under various stimulus conditions. Left, recording traces for a 2-min period (sample time 100 ms). Right, distribution of the momentary translational walking velocities of the traces shown on the left, showing the number of events at a particular speed in a 2-min period. (A) In darkness with a calling song from the front (0°); (B) in the light and with a single vertical stripe (width 40°) at 0° ; (C) in the light, with both the sound and the stripe at 0° .

stimulus was presented or not. This result was typical of all the different animals tested (Fig. 3A).

The increase in mean walking speed was accompanied by an increase in the standard deviation of momentary walking speed; that is, the standard deviation was higher in the light, whatever visual pattern was present, than it was in the dark (Fig. 3B).

The instantaneous rotational component fluctuated about a mean with a maximal deviation of more than 100°s^{-1} to the left and right (Fig. 4B). With lateral sound stimulation, the distribution was shifted towards the stimulated side (Fig. 4A). The distributions were broad and sometimes asymmetrical, owing to short periods of marked intended turning away from the speaker. The mean turning tendency depended on the stimulus direction in a roughly sinusoidal manner (Fig. 4C). However, the zero crossings of the characteristic curve were not necessarily at 180° and 0° for a given individual. This shift reflected a small bias in

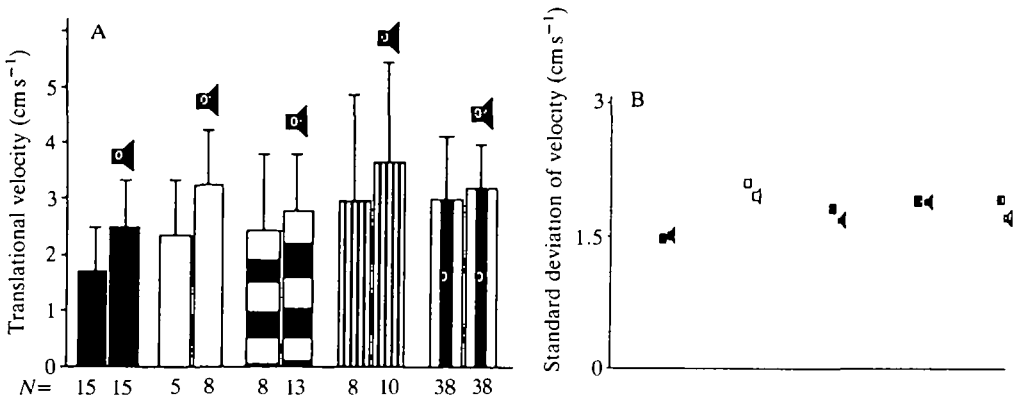


Fig. 3. (A) Means and standard deviations of translational velocities for various visual cues without and with a calling song (loudspeaker symbol) from the front (0°) obtained from different animals. (B) Mean of the single standard deviations of the translational velocity. From left to right the columns represent the responses in darkness (black), in homogeneous light (white), with horizontal stripes (horizontal bars), with vertical stripes (vertical bars) and with a single stripe at 0° (one vertical bar). N is the number of runs.

the turning tendency in the absence of the sound stimulus. The mean bias for the experimental population was close to zero.

The mean forward walking velocity was constant, irrespective of stimulus direction (Fig. 4C), and, therefore, was not studied further.

Interaction of visual and acoustic information

Under open-loop conditions, crickets responded to sound with a direction-dependent turning tendency that could be fitted by a sinusoidal function (Fig. 5). Higher orders of sine and cosine components played no important role.

In the dark, when the calling song was the only orientational cue, the turning tendency curve was shallow (Fig. 5A). In a visually patterned environment, the amplitude of the frontal region of the characteristic curve increased. Thus, the response to the calling song was quantitatively changed by the visual cues (Fig. 5B–D).

Placing one vertical stripe or a striped pattern in front of the animal caused an increase in the slope by a factor of two compared to that in darkness (Fig. 6). When a single black stripe was paired with sound from the direction of the stripe, the slope was nearly three times as high as in the dark.

The interactions of the effects of visual and acoustic stimuli on course control can now be explained quantitatively in terms of combinations of song and stripe, for walking behaviour in the presence of (i) the single stripe alone, (ii) the song alone and (iii) a combination of the two. Therefore, the turning tendency was first measured without sound, with the stripe alone being presented at various angles (Fig. 7B).

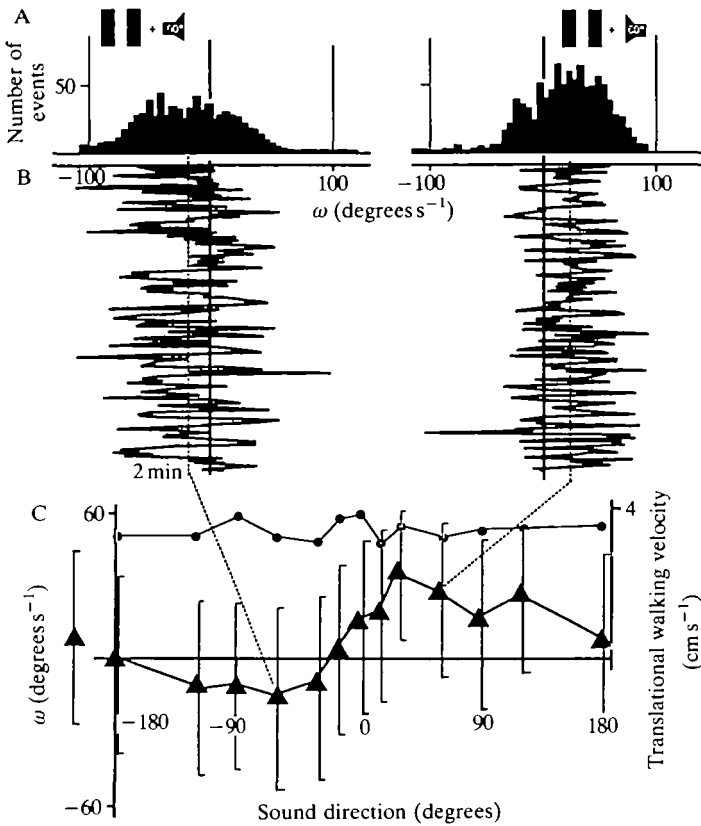


Fig. 4. Rotational walking velocity (ω) of an individual female presented with a stationary vertical grating and a calling song coming from the left (left at 60°) or the right (right at 60°). (A) Distribution of the rotational component (100 ms sample time). (B) Actual recording trace lasting 2 min. Dashed lines indicate the mean values. (C) Mean (\blacktriangle) and standard deviation of the rotational component of walking of the same animal for various sound directions (characteristic curve, left ordinate). Negative values indicate intended turning to the left. The single data point on the left gives the average for the condition with no acoustic stimulus. In addition, the circles show means of the translational component in the same experiment (right ordinate).

A single black stripe was an attractive stimulus: the crickets tended to turn towards it. Maximal responses occurred when the stripe was positioned at about $\pm 45^\circ$ (Fig. 7B). The zero crossing of the curve for the stripe was close to the 0° direction.

The slope of the curve for responses to a single stripe at angles near to the zero crossing was high compared with that of the curve in response to the calling song in homogeneous light. The shape of the curve was not simply sinusoidal, as seen for the calling song curves (Fig. 7A). The fit suggested that the first three sine components were significant parts of the characteristic curve for a single stripe.

When sound direction and single stripe position were the same, the characteristic curve (Fig. 7C) differed in amplitude and shape from those for diffuse light

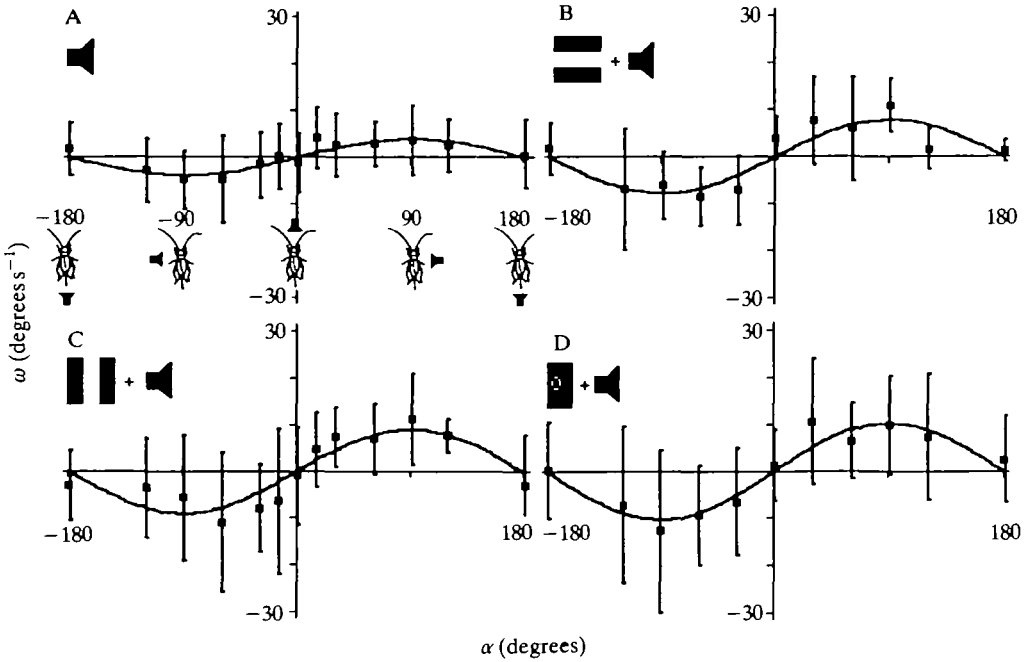


Fig. 5. Characteristic curves in response to a calling song in combination with various visual stimuli for a group of females. (A) Calling song presented in darkness; (B) calling song together with a stationary horizontal grating; (C) calling song together with a stationary vertical grating; (D) calling song together with a single black bar at 0° . The line gives the sinusoidal fit on the basis of single data points. ω , rotational velocity component; α , sound direction. Values are mean \pm s.d.

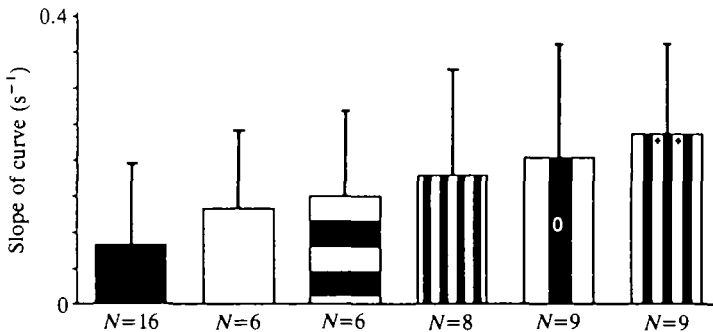


Fig. 6. Mean slope of the rotational component of the characteristic curves for calling songs presented $\pm 30^\circ$ to frontal under various visual stimulus conditions obtained from individual curves (N is the number of individuals). Patterns within the columns represent the visual environment, as in Fig. 3, except on the far right, where a single stripe was always presented from the respective sound direction. Bars represent standard deviation.

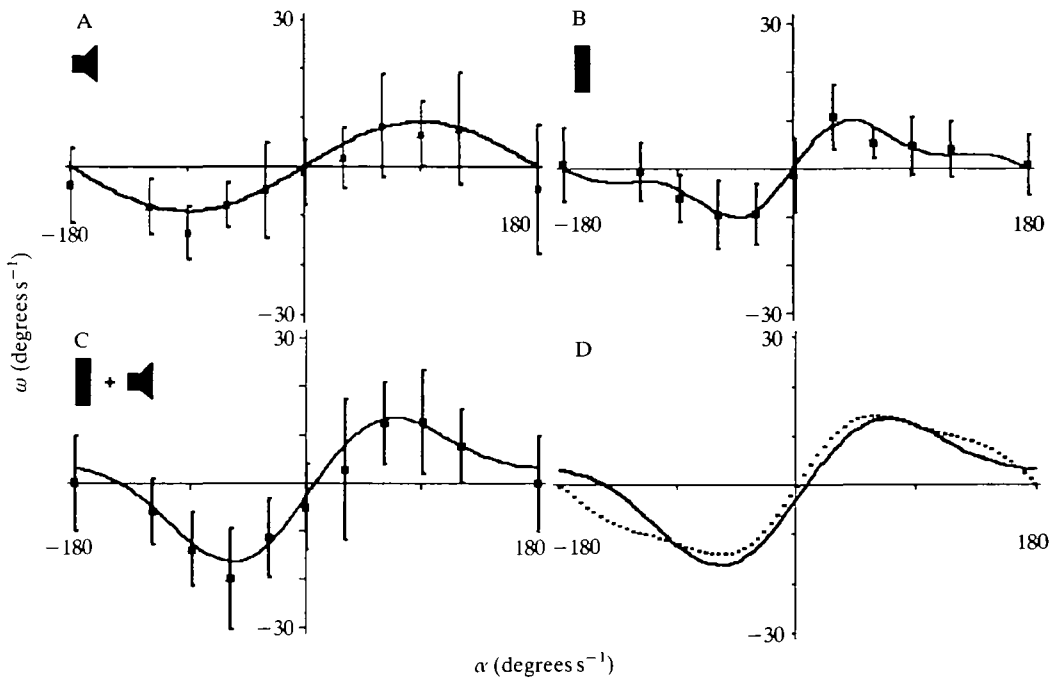


Fig. 7. Characteristic curves under various conditions. (A) Homogeneous light with a calling song; (B) a single stripe without sound; (C) a single stripe and a calling song from the same direction. In each condition the continuous line represents the sum of the first three significant sine and cosine components for the single data points. (D) A comparison of the function in C (continuous thick line) with a function (dashed line) obtained by weighted summation of A and B. α , sound direction; ω , rotational component of velocity; values are mean \pm s.d.

with sound (Fig. 7A), for a stripe without sound (Fig. 7B) and for the stationary frontal stripe with sound presented from various directions (Fig. 5D).

If information concerning visual and acoustic stimuli is processed synergistically it might be expected that the contributions of the two stimuli would be simply superimposed. Therefore, the sum of the visually and acoustically induced turning tendencies was calculated and compared with the experimentally obtained curve for the combined stimulation (Fig. 7D). On the basis of area integration, the differences between the predicted and the measured curves were minimal when the sound curve and the stripe curve were summed with a weighting factor of 1:0.7. In the frontal range, between $\pm 90^\circ$, the estimated and measured curves were nearly identical.

Phonotaxis in a moving visual environment

To test whether the acoustically induced turning tendency also interacts with the response to moving visual stimuli (optomotor stimuli), a drum with vertical stripes was moved around the animal at a constant angular velocity while the characteristic curve for an attractive calling song was measured (Fig. 8A). In the converse

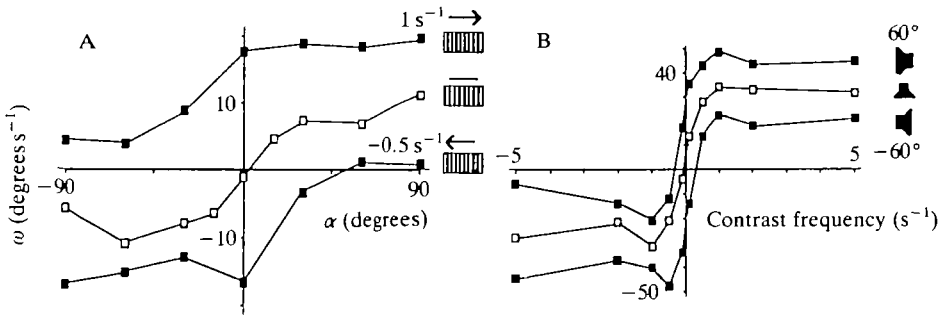


Fig. 8. The mean rotational component of velocity (ω) in response to acoustic and optomotor stimuli. (A) Characteristic curve for phonotaxis with a stationary vertical grating (centre, open symbols), with the grating moving clockwise (top) and with the grating moving counterclockwise (bottom). $N=3$. (B) Characteristic curve for the optomotor response to sound from the front and from 60° to the right or left. $N=5$.

experiment, the turning tendency was recorded for different contrast frequencies (optomotor response curve) during the simultaneous presentation of calling song from one direction (Fig. 8B).

Since information originating from acoustic and moving visual stimuli was present at the same time, a mutual interaction was again found in the characteristic curves. The curve for phonotaxis was shifted by a constant turning tendency induced by the moving striped drum. Sound from a given direction on the left or the right shifted the characteristic curve of the optomotor response. At least for contrast frequencies below $5 s^{-1}$, the optomotor response seems to be additively superimposed on an acoustically induced response. The same effect was also seen in the converse experiment. Therefore, any combination of optomotor and sound stimuli caused a turning tendency that can be explained as the weighted sum of the turning tendencies evoked by the two individual stimuli.

Discussion

Walking under open-loop conditions

Tethered crickets walking on the air-supported sphere exhibit a walking pattern similar to that of freely walking animals (Weber *et al.* 1981). Both exhibit the typical stop-and-go mode and the average durations of continuous walking periods measured under open-loop and closed-loop conditions are similar (Schmitz, 1983).

Nevertheless, the restriction of the animal in the open-loop condition is known to have some effects on walking behaviour. Animals walking on top of a wheel decrease their walking speed (Graham, 1981) and the turning tendencies can become unstable (Stabel, 1987). The forward speed on the sphere is slightly lower than that on a Kramer walking compensator. In our study, instability in the turning tendency was seen only when the animal was not properly mounted. The degree of freedom of rotation is greater on the air-supported sphere than on a wheel. The

maximal fluctuation of the rotational component may be enhanced because of the inertia of the sphere, but, on average, this will not affect the turning tendency.

The quantitative relationship between turning tendency and stimulus direction described here can only be compared qualitatively with the relationships found in studies on other species where the motor output was measured differently, for example, in terms of torque (Götz, 1980; Preiss and Gewecke, 1988), difference in speed of left and right legs (Wendler *et al.* 1984) or angular velocity (Dahmen, 1980). Quantitative predictions and a comparison of the walking paths of freely walking animals from open-loop data make no sense as long as the gain and coupling factors of the motor output remain unknown. Moreover, additional mechanisms for orientation are excluded under open-loop conditions, e.g. scanning the sound field (Schildberger and Kleindienst, 1989). In spite of these limitations, the characteristic curves have quite similar properties.

Orientation to the calling song

Male crickets may call from dawn until late in the night (Rost and Honegger, 1987). Females can find the male in total darkness with song as the only orientational cue (Wendler *et al.* 1980). The phonotactic course on the walking compensator is characterized by meandering, i.e. alternating deviations (30–60°) from the direction of the sound source (Weber *et al.* 1981).

In darkness and under open-loop conditions, the characteristic curves of phonotaxis display average zero crossings at 0° and 180°. For crickets walking on top of a split treadmill (Stabel *et al.* 1989) or on top of a sphere, the characteristic curves can be approximated by a sinusoid for the population, but not necessarily for the individual.

The ear and the auditory interneurons exhibit a cardioid directionality (Boyan, 1979; Boyd and Lewis, 1983; Schildberger and Kleindienst, 1989). Thus, the sinusoidal shape of the characteristic behavioural curve does not reflect simply the directional properties of the first auditory elements. For example, mutual inhibition of central auditory neurons on the left and right sides can enhance the amplitude of the directionality curve (Horseman, 1988).

Orientation to visual stimuli

Field studies on freely walking wood crickets demonstrated the use of terrestrial cues for orientation (Beugnon, 1983). *Oecanthus pellucens*, living on bushes, prefers vertical stripes; *Nemobius silvestris*, living below dead leaves in the forest, chooses horizontally oriented stimuli (Campan *et al.* 1987).

Presentation of a black stripe to a cricket in the absence of sound gives a characteristic curve which, in the open-loop condition, does not have a pure sinusoidal shape. Compared to the curve in darkness and with sound, its slope is steeper in the frontal direction. This should lead to faster compensation for deviation from a visually guided course than from a phonotactically guided course. Indeed, under closed-loop conditions, deviations from a purely visually guided

course are on average, smaller than those guided by song (C. Nilges, personal communication).

Because the motor elements (motorneurons and muscles) are the same for acoustically and visually controlled courses, the differences in the shapes of the characteristic curves may largely reflect the properties of the visual and auditory sensory systems and central nervous components. Whether the increase in amplitude of the visual characteristic curve is due to the greater precision of the directional information from the eyes, compared with that from the ears, is unclear.

As to the mechanisms by which the visual curve is generated in the cricket's nervous system, less is known than for the acoustic curve (Stabel, 1987), though some details of the anatomy and function of the cricket's eye are known (Honegger and Schürmann, 1975; Honegger and Campan, 1989), and some neurones at different levels of the visual system have been described (Honegger, 1980; Richard *et al.* 1985; Labhart, 1988; Zufall *et al.* 1989; Böhm and Schildberger, 1990).

Interaction of acoustic and visual information

Visual surrounds have an effect on cricket phonotaxis (Weber *et al.* 1981; Stout *et al.* 1987): the course towards a sound source is more precise if the cricket can see its surroundings (Weber, 1990). In the presence of a visual target, the walking pattern is changed (Weber *et al.* 1987). The increase in straightness of course seen in freely walking crickets matches the conclusions drawn from our experiments under open-loop conditions. The summation of visually and acoustically induced turning tendencies with different weighting factors results in an increase in the slope of the frontal region of the characteristic curve. Therefore, deviations from the preferred course are corrected more rapidly, and less meandering should occur.

Experiments in which moving gratings were combined with sound also showed that optomotor responses and phonotaxis are added. In contrast to results for flying locusts, there was no decision to follow one or the other stimulus based on a hierarchical order (Robert, 1989); the optomotor response of crickets seems to contribute continuously to the stabilization of the phonotactic course.

These restricted laboratory experiments, which by no means mimic the complex stimulus configurations encountered in nature, indicate that we must expect powerful multimodal and multifunctional operations in the nervous system.

We thank P. Heinecke and F. Antoni for developing electronic and mechanical equipment, W. Mohren for kindly providing the curve-fitting program, G. Horseman, A. Biedermann-Thorson and J. Thorson for helpful discussion and for correcting the English. E. Staudacher and R. B'Shany helped with some of the data acquisitions. Heidrun Bamberg assisted with preparing the figures. The work was supported by a stipendium from the Max-Planck-Gesellschaft to H.B.

References

- ATKINS, G., ATKINS, S., SCHOUN, D. AND STOUT, J. F. (1987). Scototaxis and shape discrimination in the female cricket *Acheta domestica* in an arena and on a compensatory treadmill. *Physiol. Ent.* **12**, 125–133.
- BENNETT, C. A. AND FRANKLIN, N. L. (1954). *Statistical Analysis in Chemistry and the Chemical Industry*. New York: John Wiley and Sons.
- BEUGNON, G. (1983). Terrestrial and celestial cues in visual orientation of the wood cricket *Nemobius sylvestris* (Bosc.). *Biol. Behav.* **8**, 159–169.
- BÖHM, H. AND SCHILDBERGER, K. (1990). Influence of visual and acoustic information on the course control of the cricket *Gryllus bimaculatus*. In *Brain, Perception, Cognition*, Proceedings of the 18th Göttingen Neurobiology Conference (ed. N. Elsner and G. Roth), p. 113. Stuttgart: Thieme Verlag.
- BOYAN, G. S. (1979). Directional responses to sound in the central nervous system of the cricket *Teleogryllus commodus* (Orthoptera, Gryllidae). I. Ascending interneurons. *J. comp. Physiol.* **130**, 137–150.
- BOYD, P. AND LEWIS, B. (1983). Peripheral auditory directionality in the cricket (*Gryllus campestris* L., *Teleogryllus oceanicus* Le Guillou). *J. comp. Physiol.* **153**, 523–532.
- CAMPAN, R., BEUGNON, G. AND LAMBIN, M. (1987). Ontogenetic development of behaviour: The cricket visual world. *Adv. Study Behav.* **17**, 165–212.
- CAMPAN, R. AND GAUTIER, J. Y. (1975). Orientation of the cricket *Nemobius sylvestris* (Bosc.) towards forest trees. Daily variations and ontogenetic development. *Anim. Behav.* **23**, 640–649.
- DAHMEN, H. J. (1980). A simple apparatus to investigate the orientation of walking insects. *Experientia* **36**, 685–687.
- GRAHAM, D. (1981). Walking kinetics of the stick insect using a low inertia counter-balanced, pair of independent treadmill. *Biol. Cybernetics* **40**, 49–57.
- GÖTZ, K. G. (1980). Visual guidance in *Drosophila*. In *Development and Neurobiology of Drosophila* (ed. O. Siddiqi, P. Babu and L. M. Hall), pp. 391–407. New York: Plenum Press.
- HISSMANN, K. (1990). Strategies of mate finding in the European field cricket (*Gryllus campestris*) at different population densities: a field study. *Ecol. Ent.* **15**, 281–291.
- HONEGGER, H.-W. (1980). Receptive fields of sustained medulla neurons in crickets. *J. comp. Physiol.* **136**, 191–201.
- HONEGGER, H.-W. AND CAMPAN, R. (1989). Vision and visually guided behaviour. In *Cricket Behaviour and Neurobiology* (ed. F. Huber, T. E. Moore and W. Loher), pp. 147–177. Ithaca, London: Cornell University Press.
- HONEGGER, H.-W. AND SCHÜRMAN, F. W. (1975). Cobalt sulfide staining of optic fibers in the brain of the cricket *Gryllus campestris*. *Cell Tissue Res.* **159**, 213–225.
- HORSEMAN, G. (1988). Contralateral inhibition of a low-frequency-tuned ascending auditory interneuron in the cricket *Gryllus bimaculatus*. In *Sense Organs, Interfaces Between Environment and Behaviour*, Proceedings of the 16th Göttingen Neurobiology Conference (ed. N. Elsner and F. G. Barth), p. 144. Stuttgart: Thieme Verlag.
- KRAMER, E. (1976). The orientation of walking honeybees in odour fields with small concentration gradients. *Physiol. Ent.* **1**, 27–37.
- LABHART, T. (1988). Polarization-opponent interneurons in the insect visual system. *Nature* **331**, 435–437.
- LABHART, T., HODEL, B. AND VALENZUELA, I. (1984). The physiology of the cricket's compound eye with particular reference to the anatomically specialized dorsal rim area. *J. comp. Physiol. A* **155**, 289–296.
- MITTELSTAEDT, H. (1986). The subjective vertical as a function of visual and extraretinal cues. *Acta psychol.* **3**, 63–85.
- PREISS, R. AND GEWECKE, M. (1988). Visually-induced wind compensation in the migratory flight of the desert locust, *Schistocerca gregaria*. In *Sense Organs, Interfaces Between Environment and Behaviour*, Proceedings of the 16th Göttingen Neurobiology Conference (ed. N. Elsner and F. G. Barth), p. 144. Stuttgart: Thieme Verlag.
- RICHARD, D., PRETEUR, V., CAMPAN, R., BEUGNON, G. AND WILLIAMS, J. L. D. (1985). Visual interneurons of the neck connectives in *Gryllus bimaculatus*. *J. Insect Physiol.* **31**, 407–417.

- ROBERT, D. (1989). The ultrasound avoidance behaviour of flying locusts. In *Dynamics and Plasticity in Neuronal Systems*, Proceedings of the 17th Göttingen Neurobiology Conference, (ed. N. Elsner and W. Singer), p. 145. Stuttgart: Thieme Verlag.
- ROST, R. AND HONEGGER, H.-W. (1987). The timing of premating and mating behavior in a field population of the cricket *Gryllus campestris* L. *Behav. Ecol. Sociobiol.* **21**, 279–289.
- SCHILDBERGER, K. AND HÖRNER, M. (1988). The function of auditory neurons in cricket phonotaxis. I. Influence of hyperpolarization of identified neurons on sound localization. *J. comp. Physiol. A* **163**, 621–631.
- SCHILDBERGER, K. AND KLEINDIENST, H. U. (1989). Sound localization in intact and one-eared crickets. *J. comp. Physiol. A* **165**, 615–626.
- SCHMITZ, B. (1983). Analyse der akustischen Orientierung bei Grillenweibchen (*Gryllus campestris*). Inaugural-Dissertation, Universität zu Köln.
- STABEL, J. (1987). Der Mechanismus der Richtungsbestimmung und seine Beziehung zur Gesangserkennung bei der Phonotaxis der Grille (*Gryllus bimaculatus* De Geer). Inaugural-Dissertation, Universität zu Köln.
- STABEL, J., WENDLER, G. AND SCHARSTEIN, H. (1989). Cricket phonotaxis: Localization depends on recognition of the calling song pattern. *J. comp. Physiol. A* **165**, 165–177.
- STOUT, J. F., ATKINS, G., WEBER, T. AND HUBER, F. (1987). The effect of visual input on calling song attractiveness for female *Acheta domesticus* L. *Physiol. Ent.* **12**, 135–140.
- WEBER, T. (1990). Phonotaxis and visual orientation in *Gryllus campestris* L.: Behavioural experiments. In *Sensory Systems and Communication in Arthropods* (ed. F. G. Gribakin, K. Wiese and A. V. Popov), pp. 377–386. Basel, Boston, Berlin: Birkhäuser Verlag.
- WEBER, T., ATKINS, G., STOUT, J. F. AND HUBER, F. (1987). Female *Acheta domesticus* track acoustical and visual targets with different walking mode. *Physiol. Ent.* **12**, 141–147.
- WEBER, T. AND THORSON, J. (1989). Phonotactic behaviour of walking crickets. In *Cricket Behaviour and Neurobiology* (ed. F. Huber, T. E. Moore and W. Loher), pp. 310–339. Ithaca, London: Cornell University Press.
- WEBER, T., THORSON, J. AND HUBER, F. (1981). Auditory behavior of the cricket. I. Dynamics of compensated walking and discrimination paradigms on the Kramer treadmill. *J. comp. Physiol.* **141**, 215–232.
- WENDLER, G., DAMBACH, M., SCHMITZ, B. AND SCHARSTEIN, H. (1980). Analysis of the acoustic orientation behavior in crickets, *Gryllus campestris* L. *Naturwissenschaften* **67**, 99–100.
- WENDLER, G., HEINZEL, H.-G. AND SCHARSTEIN, H. (1984). Paired tread wheels as a tool for analysis of orientation behaviour in arthropods. In *Localization and Orientation in Biology and Engineering* (ed. D. Varjú and H. U. Schnitzler), pp. 170–172. Berlin, Heidelberg, New York, Tokyo: Springer Verlag.
- ZUFALL, F., SCHMITT, M. AND MENZEL, R. (1989). Spectral and polarized light sensitivity of photoreceptors in the compound eye of the cricket (*Gryllus bimaculatus*). *J. comp. Physiol. A* **164**, 597–608.