HIDING RESPONSES OF LOCUSTS TO APPROACHING OBJECTS

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Summary

Locusts, *Locusta migratoria*, sitting on a plant stem hide from dark moving or expanding shapes in their environment. The fore- and middle legs perform this avoidance response by making lateral tilting movements, while the hindlegs slide laterally and guide rotation of the posterior body over the stem. During larger turns, the legs take lateral steps when lateral tilting is limited by the joints. Slow hiding movements of less than $300\,°\,s^{-1}$ of angular velocity are induced by slowly changing (looming) shapes, and interposed stops or slowing of the movement can delay the progress of this hiding manoeuvre. Fast hiding movements with angular velocities between $120\,°\,s^{-1}$ and $860\,°\,s^{-1}$ proceed continuously and rapidly in response to rapidly expanding stimuli. Hiding responses to expanding shapes occur only after the expanding image has exceeded a threshold visual angle of $8–9.5\,°$. Hiding response latencies range between $220\,ms$ and $1.2\,s$ for fast hiding and are approximately $1.2\,s$ for most slow hiding responses. Predator-avoidance responses such as freezing, jerking, crouching, walking backwards, dropping or jumping can be used instead of or in conjunction with hiding behaviour. We conclude that the fast hiding behaviour of locusts is a specific goal-directed type of optomotor behaviour requiring positional information from small-field detectors of shape expansion in the interneurone layers of the locust eye.

Key words: hiding, behaviour, locust, *Locusta migratoria*, looming, moving stimulus, optomotor reaction, leg coordination.

Introduction

Avoidance behaviour of locusts in response to sensory stimuli has been described for several sensory modalities. Tactile hair receptors on different regions of the body can elicit specific avoidance responses ranging from simple retraction of a leg to active defence (Pflüger, 1980; Siegler and Burrows, 1986; v. Rekowski and Hustert, 1991; Matheson, 1998). Chemical cues from leg contact chemoreceptors elicit avoidance by setting the tarsus into a new position (White and Chapman, 1990). Heat or infrared radiation are avoided by flying locusts (Robertson et al., 1996). Auditory input from ultrasound sources also induces avoidance steering, which has been interpreted as a reaction to bat calls (Robertson, 1989). Visual cues reliably initiate the aversive reactions of collision avoidance in flying locusts (Robertson and Reye, 1992). Expanding shapes elicit steering responses that have been interpreted as collision-avoidance strategies in different flight situations (Robertson and Johnson, 1993). Several large visual interneurones descending from the brain react to expanding shapes and may therefore contribute to these visually elicited avoidance responses (for a review, see Rind and Simmons, 1992).

The aversive reactions of locusts range from stereotyped small movements of the appendages to ballistic movements such as kicking or jumping. These movements are usually oriented towards or away from the molesting or dangerous stimulus. The precision of such aversive reactions is demonstrated by the hiding response of locusts, a method of predator avoidance (Chopard, 1938; Jacobs, 1953; Uvarov, 1977). This response is a 'positioning' behaviour that ranges between the extremes of escape and active defence (Kevan et al., 1983). We have studied this behaviour in detail.

Locusts and other grasshoppers sitting on branches, leaves or grass tend to hide from an approaching observer by moving behind the object. Thereafter, they sit still, peer from behind the stem, climb down to safer ground or jump away from the observer (B. Hassenstein and R. Hustert, personal observations). Using these responses to expanding shapes, sitting or walking insects try to avoid being captured by a curious scientist or being eaten by a predator.

In the laboratory, the hiding responses of locusts and other insects behind a rod may be elicited readily when either a dark disk is moved towards the animal or a dark disk is enlarged progressively on a nearby computer screen, both stimuli simulating the approach of an object towards the animal (Hassenstein and Hustert, 1995). We have studied the hiding responses of locusts sitting on vertical rods, the essential features of stimuli evoking the response and the relationships between stimulus parameters and the variability of the hiding movements.

A preliminary account of the results has been given previously (Hassenstein and Hustert, 1995).

Materials and methods

Male and female fifth larval instars of *Locusta migratoria* were taken from a laboratory culture. In exploratory trials, the manually controlled approach of black disks (on a transparent rod) induced late larval instars to display hiding responses most reliably when they sat at the end of a vertical rod 8 mm in diameter. We observed regular hiding responses in third-instar to adult locusts sitting on rods or leaves with different shapes and inclinations from vertical to horizontal. For more controlled stimulation and movement recordings, locusts were placed in the centre of a drum 30 cm in diameter and lined with white paper. Two different devices were used to record hiding movements.

First, restrained locusts were mounted vertically on a holder inside the drum (Fig. 1A). The holder, glued dorsally to the pronotum, was extended by a pin that could rotate and move horizontally in a small tube and thereby allow the animal to control, using its legs, its dorso-ventral distance from a vertical rod (8 mm diameter balsawood) that could be rotated about its long axis.

An opto-electronic device monitored the rotation of the rod continuously (Fig. 1B). The rod was dark at its base with a triangle of reflecting foil glued around the perimeter. A small sector of the triangle was illuminated by a light-emitting diode (LED) through a vertical slit. The amount of light reflected through the slit, which was proportional to the position of the rod, was recorded by a light sensor (reset at $0°=360°$).

The stationary locust was stimulated visually under diffuse illumination from above by a black disk (5 cm in diameter), moved using a step motor (Megatron 630/R, single steps of $0.12°$), around the outside of the drum at a radius of 16 cm. The disk was visible to the locust above the upper rim of the drum. A second stimulus type was used to test the latency of the response in restrained locusts and to elicit hiding reactions

Fig. 1. The recording apparatus used for examining the hiding responses of locusts on a vertical rod in a uniform visual environment provided by a white drum. (A) The locust is held stationary and can move a rotatable rod with its legs. The visual stimulus is a black cardboard disk that can be moved radially. Movements of the rod and stimulus are recorded synchronously. The recordings represented in Figs 3 and 4 were obtained using this type of stimulus. (B) The apparatus used for recording the position or rotation of the rod consists of the rotating shaft (RS) on a needle bearing (NB). The lower shaft has an arrowhead-shaped piece of reflective foil (RF) on its perimeter that reflects light from a light-emitting diode (LED). The light passes through a vertical slit in the blind (Bl) to a light intensity sensor (LCRI). The recorded intensity is proportional to the angular position of the shaft. A separate reflective sensor (Rt) records the transition between the base and tip of the reflective foil. (C) Freely moving locusts sitting near the top of a rod can observe stimuli presented on a computer screen. Hiding responses are elicited by black disks expanding radially on the computer screen against a bright background. The movements of animal and the stimuli are recorded by a video camera centred over the drum. A frame counter displays the numbers of consecutive video frames. The rod can be turned by hand to position sitting locusts at 90° with respect to the stimulus display.
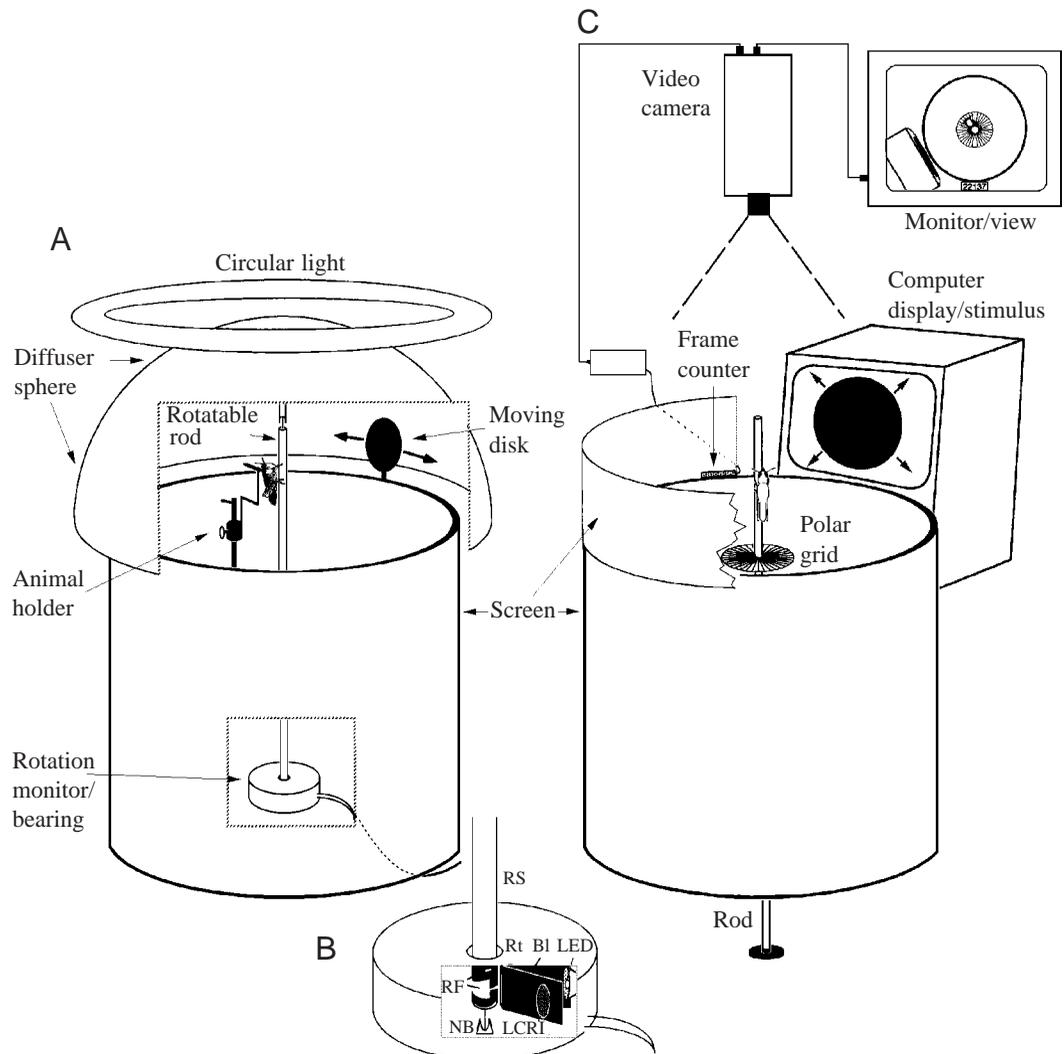
in freely moving insects from field catches: the approach of a black disk (5 cm in diameter, mounted on a 40 cm balsawood lever). The lever was moved towards the sitting animal from 14 to 4 cm by a step motor (Megatron, steps 0.12 °).

Second, in the 'unrestrained locust set-up', a vertical 8 mm rod was positioned in the centre of the drum, and a video system recorded, from above, the visual stimuli and the turning movements of the locust around the rod (Fig. 1C). Expanding shapes were displayed on a computer monitor (Macintosh SE30, refresh rate 60.1 Hz; Hypercard) located 18 cm from the drum. Results from experiments relating certain stimulus expansion velocities to response latency were rejected because the locusts obviously responded to a jerky build-up of the stimulus on the screen. This was noted in frame-by-frame video sequences and is due to interference between the refresh rate and certain velocities of shape expansion. These stimulus velocities were not included in the data presented below.

The locust could see the entire screen when it sat near the top of the rod. Before each visual stimulus, the rod with the motionless locust was rotated so that the computer screen was within the lateral visual field of one eye. The attention of experimental animals was raised 20 s before every visual stimulus by an acoustic signal (a computer beep, noise mixture of 1–10 kHz).

The different shapes and expansion velocities of dark figures (1.1 lx) were displayed against a white (170 lx) background, resulting in a contrast of 0.9845. A standard black disk was expanded radially (from 0 to 35 ° visual angle) from an initial black dot to a radius of 5.75 cm by linearly increasing the radius. At this range, the radial increase of the disk was almost directly proportional to the resulting visual angle covered by the disk (subtense) in the locust visual field. The movements of the locust around the rod were recorded with reference to a radial grating below the rod and analysed frame by frame (single frame duration 20 ms) with an angular precision of 2.5 °. Some recordings included the lateral view of the animal obtained using a small mirror positioned at 45 ° to the animal. The anterior faces of the legs were painted with bright lines of Tipp-Ex to improve the optical contrast in the video frames.

Experiments were usually performed at 20–24 °C using animals that had previously shown hiding reactions rather than jumping off the rod upon visual stimulation (approximately two-thirds of the animals tested). The best hiding reactions were achieved between 15:30 and 20:00 h. After each stimulus, pauses of at least 2 min and maximally 4 min elapsed. The readiness of a locust to hide was tested using the most effective standard stimulus of 1.2 cm s^{-1} (7.6 ° s^{-1}) disk expansion. Animals showing no responses to the 1.2 cm s^{-1} stimulus were released, the test series was finished and their last negative responses were omitted from the data.

The occurrence of hiding behaviour in other grasshopper species and other insect species (see below for details) was observed in open grassland between Goettingen and Kassel in Northern Germany. The visual stimulus in the field was the approach of an observer's hand, head or camera; under laboratory conditions, it was the approach of a black disk.

Results

Movement characteristics

Hiding movements by locusts sitting on a vertical rod are mainly lateral body turns, which are distinct from any other type of locomotion. The major features of the hiding behaviour are specific: (i) turning behind a rod is performed by lateral tilting of the body and by stepping movements when the limit of bending or extension of the leg joints is reached, (ii) the longitudinal orientation of the body axis parallel to the rod is maintained, (iii) the movement is 'quadrupedal' since, during turns, the hindlegs provide guidance with the tibia and proximal tarsomeres only when sliding around the rod, (iv) in larger turns that include lateral stepping, the leading legs swing with a much wider trajectory than the trailing legs, (v) slow hiding movements (often not continuous) are distinct from continuous rapid hiding or 'dodging' (Uvarov, 1977).

The detailed temporal sequence of stages of visually elicited hiding movements was observed from the front and from a lateral aspect (Fig. 2). A locust resting on a vertical rod uses all its legs for support. The forelegs are held forward, clasped
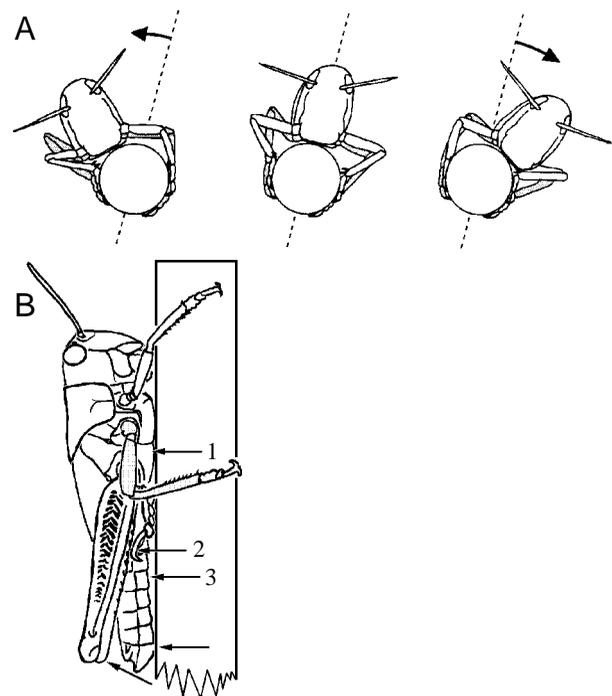

Fig. 2. (A) Frontal aspects of the positions of a locust larva on a rod 8 mm in diameter before (centre) and after hiding in opposite directions without stepping (arrows to left and right indicate movement with respect to the initial position, which is marked by a broken line). From the initial leg positions (middle legs shaded, hindlegs omitted), the small target angles of left and right hiding movements require no lateral steps. The right middle leg and the left foreleg nearly reach their limit of flexion of the femoro-tibial joints. (B) Lateral view of a locust prepared for hiding. The thorax and mouthparts touch the rod (1), the hindleg claws are lifted (2), the middle part of the abdomen moves away from the rod (3), the tip of the abdomen touches the rod (4) and the hindleg femora move dorsally.
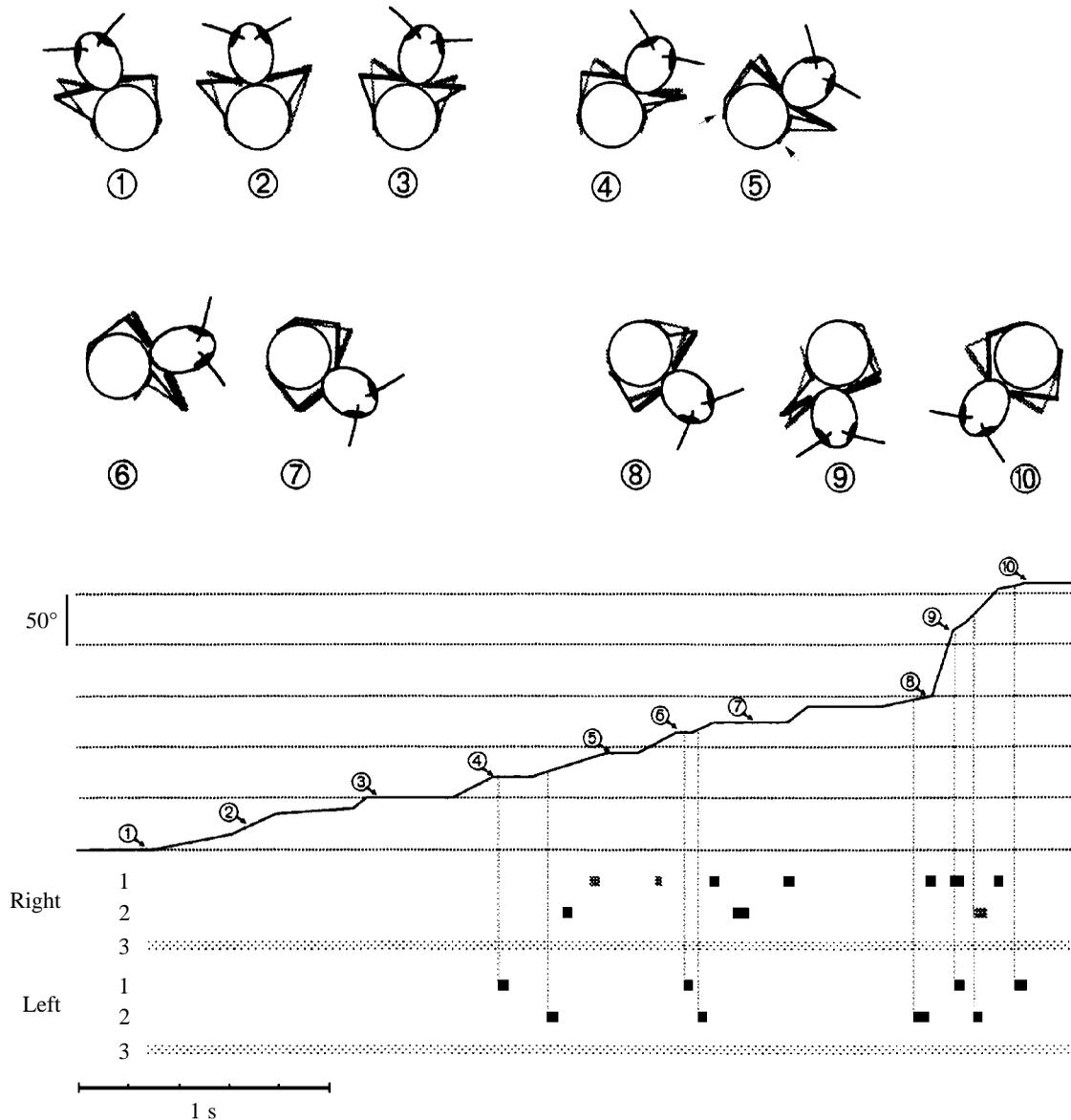
Fig. 3. Stages of successive slow hiding movements of a locust larva on a rotatable rod. The upper frontal views of leg positioning are numbered (adjusted as if the rod were stationary). Arrows indicate the first time that the legs are repositioned. The animal is held stationary and the rod rotates beneath its legs, as recorded continuously in the middle trace. The numbers correspond to the relative animal-to-rod position of the frontal views given above. The scale bar corresponds to a turning angle of 50°. The lower part of the diagram indicates swing phases (black rectangles) during which the tarsi have no contact with the rod during the movements. Right 1–3 and left 1–3 indicate the right and left fore-, middle and hindlegs, respectively. Vertical dotted lines indicate that legs can step during still and turning periods of the body.

around the rod at an angle of approximately 45° to the long axis of the body. The middle legs are held backwards, with the tibiae and tarsi clasping the rod approximately horizontally. The hindlegs are held down and parallel, and the tibia is flexed very close to the femur, which lies parallel to the abdomen. The tarsi hold on to the rod. In this situation, the ventral thorax and abdomen rarely touch the rod.

A locust preparing for hiding (Fig. 2B) lifts the tarsal claws of the hindleg slightly off the rod while flexing the femur–tibia joint completely and moving the whole leg slightly dorsally. Further contact of the body with the rod is made by the

mouthparts, the thoracic sternites, the legs and the tip of the abdomen.

Hiding movements start with a lateral shift of the whole body either from a symmetrical or from a laterally tilted posture. The joints of the fore- and middle legs ipsilateral to the hiding direction are flexed, while the contralateral legs (on the side of the visual stimulus) are extended as far as their joints allow, but still maintaining a stable grip on the rod (Fig. 2A).

When the locust turns through a larger angle, lateral steps around the rod are required whenever the joints of an
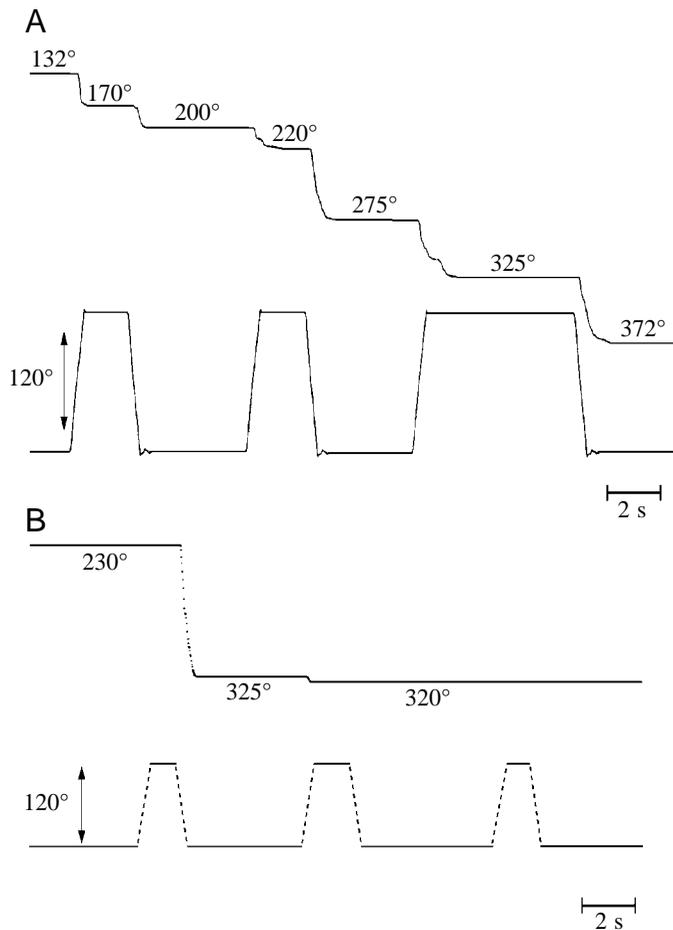
Hiding responses of locusts 1705

Fig. 4. Differences in velocities and amplitudes (in degrees of rotation) of hiding movements (upper traces) in response to sequences of similar ramp-and-hold amplitude. Stimuli consisted of lateral angular displacements of a black disk (lower traces) presented to stationary locusts sitting on a rotatable rod as in Fig. 1A. (A) Increasing responsiveness. (B) Adapting responsiveness in a different animal.

individual leg reach their extreme flexion or extension position. From symmetrical sitting positions, a fifth-instar larva on a rod 8 mm in diameter can turn through approximately 45–50° just by moving its leg joints. The widest steps of a single leg cover approximately 60° (or 8.4 mm on the circumference) on the 'standard' 8 mm rod. After hiding, the animal repositions its legs symmetrically except when jumping off the rod is the next behaviour.

A continuous recording of a restrained locust shows the principal hiding manoeuvres in response to different stimuli (Fig. 3). In hiding responses observed in the field, the basic movement patterns are similar and all animals maintain their elevation on the rod.

The following two basic types of hiding can be distinguished. (i) Slow hiding (1–7 in Fig. 3), which presumably leaves time for the visual system to observe the stimulus continuously during the movement. This could be utilised for a closed-loop hiding manoeuvre based on visual feedback. When lateral steps of one or more legs are required,

the flow of the whole movement is jerky. (ii) Rapid hiding (8–10 in Fig. 3) follows almost the same 'rules' of leg coordination as slow hiding, but the locust reaches its final position in one continuous movement (possibly an open-loop manoeuvre). The target position is on the opposite side of the rod to the approaching or moving visual threat. When locusts start a large hiding manoeuvre from a symmetrical resting position, they often do not use the remaining flexion or extension reserve of their leg joints first. Instead, they rapidly swing a fore- or middle leg laterally into the hiding direction as if 'anticipating' the need for wide stepping and release of tarsal contact during the subsequent turning manoeuvre.

Stimulus specificity of the hiding response

Hiding responses occur only upon visual stimulation, but other modalities may have some influence. Locusts never showed hiding responses to noises or when exposed only to red light (660 nm wavelength), which they cannot see (Bennett et al., 1967). However, noises preceding the presentation of a visual stimulus can raise the locust's attention and may increase its readiness to hide (see Materials and methods). In some animals, even the slightest dynamic visual stimulus, either lateral or expansion movements of dark shapes, can elicit hiding. No hiding was elicited (i) by the sudden appearance of a large dark circular disk in the visual field of the locust, (ii) by a constant-shape grey disk that darkened continuously into black within 2 s, or (iii) by an enlarging black ring with a constant annulus, 8 mm wide (extending over approximately 5.1° of the visual field at small angles).

The shape of the dark expanding object is not crucial. Expanding rectangles of different horizontal or vertical aspect can elicit hiding equally as well as the expanding disks that we used in this study.

An alternative behavioural reaction to hiding in response an expanding stimulus is jerking, which consists of short, sometimes slightly lateral, crouching movements in the initial position.

The sensitivity to stimuli repeated at intervals of at least 3 s can vary considerably. Increases in turning angles of subsequent hiding response in some animals contrast with decreases in others (Fig. 4).

Stimulus size threshold

Most reactions to an expanding disk occur only after the disk surface has expanded above a threshold value of approximately 7 cm^2 (9.5° of visual angle). In only six out of 150 cases did animals respond to disks with a smaller radius. Of these, a 3.4 cm^2 disk surface (6.6° visual angle) was the smallest. Therefore, especially when measuring response latencies, the time a stimulus takes to reach this critical threshold must be taken into consideration.

Stimulus location in the visual field

The lateral visual fields of locusts proved to be most sensitive to expanding shapes that elicit hiding responses: unrestrained locust larvae (N=6; three trials per animal) sitting
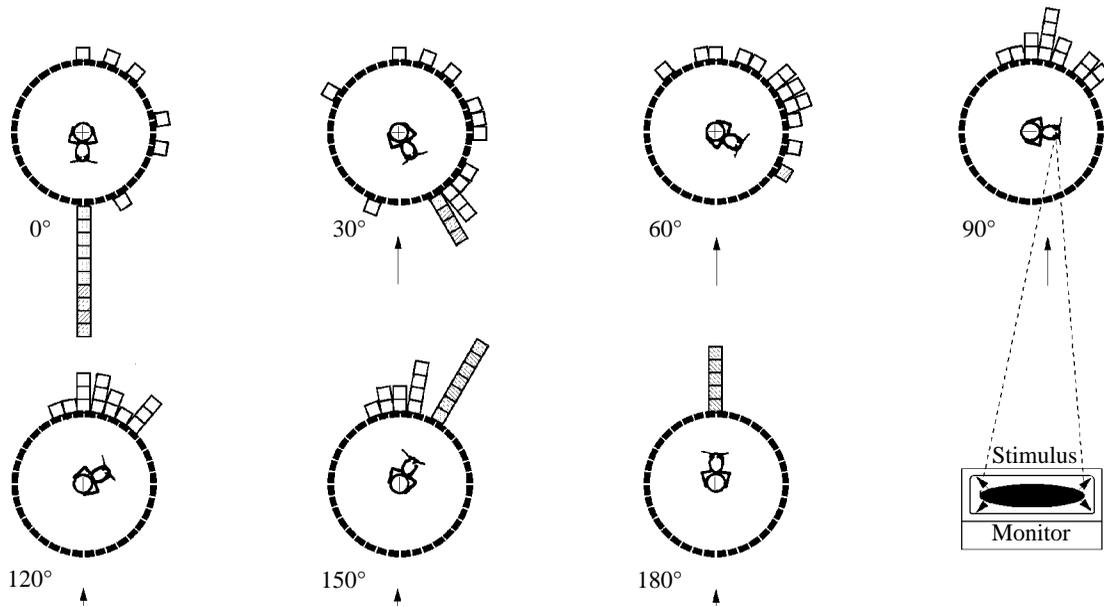
Fig. 5. 'Target' positions of hiding responses for one fifth-instar larva when stimulated from different angles (arrows) relative to its dorso-ventral axis. The diagrams represent responses to a black disk expanding radially at 1.2 cm s^{-1} on a computer screen (example far right) at a level horizontal with the eyes. The empty boxes represent hiding responses and the 'target' positions, the stippled boxes represent jerking and the hatched boxes represent no response.

on a vertical rod were exposed to the standard expanding stimulus on the computer screen (a black disk expanding radially at 1.2 cm s^{-1}). This stimulus had proved to elicit the slow type of hiding movements most reliably (Figs 5, 6). Stimuli were presented to the locust eyes at different angles (on a plane perpendicular to the body length axis) and the responses included (i) none, (ii) jerking without locomotion, (iii) incomplete hiding and (iv) complete hiding (Figs 5, 6).

Stimuli from above or from below rarely cause hiding reactions. Hiding was elicited most reliably at stimulus angles between 50 and 120°. Many animals stop before they reach the perfect 180° 'target' angle opposite the centre of the stimulus so that they can still observe the stimulus from behind the supporting rod using the ipsilateral eye. Later, they often peer around the contralateral rim of the rod.

Stimulus velocities and response characteristics

The velocity of turning manoeuvres during the hiding response varies from a few degrees to 860° s^{-1} (at 28 °C). The velocity is influenced by the angular expansion of the stimulus, by the position of the stimulus in the visual field and by the ambient temperature (Fig. 7). At a temperature of approximately 20 °C, the maximal turning velocity is 300° s^{-1} angular rotation, while at 26 °C rotational velocities of up to 700° s^{-1} were recorded. A particular range of turning velocities is rarely used for the hiding responses, especially at higher temperatures, as indicated by the 'steps' in Fig. 7. It could not be determined whether all turning velocities below such steps belonged to the 'slow' type of hiding and all those above such steps to the fast type only.

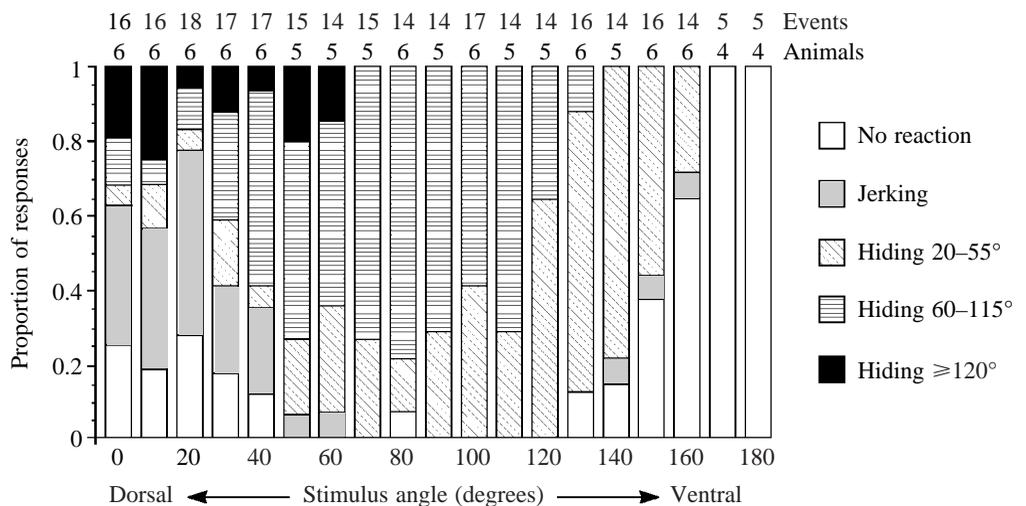Response characteristics in relation to different expansion

Fig. 6. Responses of fifth-instar locust larvae when stimulated from different angles (ordinate) relative to the dorso-ventral axis. The diagrams represent responses to a black disk expanding radially at 1.2 cm s^{-1} on a computer screen (an example is shown on the far right in Fig. 5) at a level horizontal with the eyes. The proportions (abscissa) of the different response types (column types are explained on the right side) are given for the different stimulus angles.
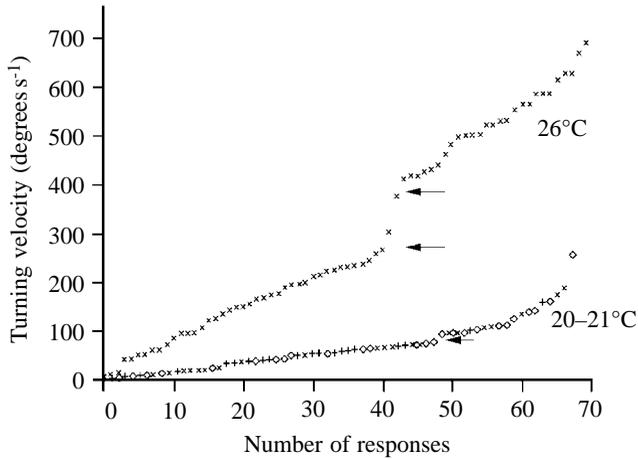
Fig. 7. Composite diagram demonstrating the turning velocities measured for all hiding responses of three freely moving fifth-instar larvae at two different ambient temperatures (70 responses of one larva at 26 °C represented by crosses, and 70 responses of two further larvae at 21 °C represented by plus signs and diamonds). The recorded velocities are arranged in order of ascending angular velocity. The arrows indicate the ranges of turning velocities rarely used.

velocities were tested for freely moving animals under video observation (Fig. 8). The locusts (N=4–10, with 3–5 trials per animal for each stimulus type) werw stimulated with stationary disks enlarging at different radial velocities at a lateral angle (90 °). Under these conditions, the best responses (with the largest hiding turns of more than 60 °) were obtained to radial expansion velocities of 0.3–1.2 cm s^{-1}.

The angular velocity of turning in hiding responses is influenced by the rate of stimulus expansion, although variability was very high (Fig. 9). The rapid hiding type (faster than 120 ° s^{-1} at approximately 24 °C) requires radial disk enlargements of at least 6 cm s^{-1}. In rapid disk expansions that induce 'just' slow-type hiding, all velocities of turning lie above 30 ° s^{-1}.

Hiding response latencies

Mean latencies in response to a rapidly approaching object

(the approach of a motor-driven 5 cm diameter black disk) are 220 ms at an ambient temperature of 26 °C. A further increase in the rate of stimulus expansion using faster approaches results in no significantly shorter response latencies.

The latency of the responses is approximately proportional to the expansion velocity of the disk (Fig. 10). Locusts respond very reliably to the most rapid expansions of 2.9–41 cm s^{-1} (18.3–133 ° s^{-1}). In response to this type of stimulus, the latencies approach a minimal value near 220 ms, and no further reaction can be elicited at higher ('flashlike') expansion values.

Hiding of other grasshoppers and other insects

In the following European grasshopper species (determined according to Bellmann, 1984), active hiding responses of freely moving adults were observed in meadows: (Acrididae) *Chorthippus albomarginatus*, *Chorthippus biguttulus*, *Chorthippus brunneus*, *Chorthippus mollis*, *Chorthippus montanus*, *Chorthippus parallelus*, *Gomphocerus rufus*, *Mecostethus grossus*, *Myrmeleotettix maculatus* and *Omocestus viridulus*; (Tetrigidae) *Tetrix undulata*; (Tettigoniidae) *Conocephalus discolor*, *Conocephalus dorsalis*, *Metriptera brachyptera*, *Metriptera roeseli*, *Pholidoptera griseoaptera* and *Tettigonia viridissima*; (Gryllidae) *Nemobius sylvestris*.

In the wild, African desert locusts *Schistocerca gregaria* sitting on the stems of their major food plant *Schouwia thebaica* show a distance-dependent reaction to the approach of a human observer (H. Wilps, personal communication): in the afternoon and evening, the animals hide at distances of less than 5 m, and at less than 1 m they jump, fly away or drop to the ground.

Other adult insects (determined according to Bromer, 1984) showing hiding responses are cicadas (*Cicadellidae*) and bugs of the Families Pentatomidae, Alydidae, Coreidae, Miridae and Lygeidae; phasmid insects of the species *Carausius morosus* and *Extatosoma tiaratum* do not show hiding responses.

Discussion

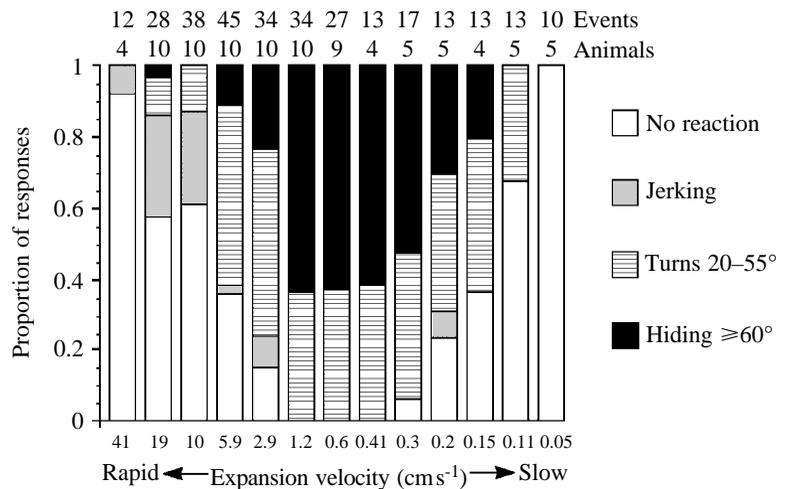Hiding is a specific optomotor reaction by a locust or

Fig. 8. Responses of a locust on a vertical rod to stimuli expanding at different radial velocities presented laterally to one eye (corresponding to the 90 ° stimulus angle in Fig. 5).
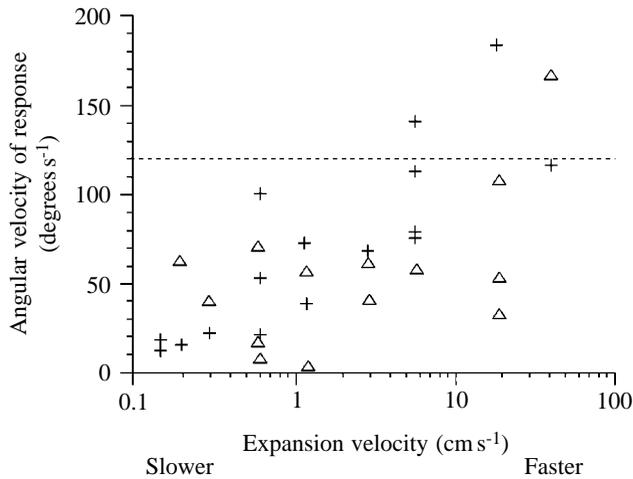
Fig. 9. The angular velocity of hiding responses to expanding stimuli at different radial velocities (presented from 90° laterally) for two individuals at 21 °C. Turns of the fast response type are never slower than 120° s⁻¹ (broken line).

grasshopper sitting in an elevated position on a stem in response to looming or moving visual stimuli. It can be used in rapid succession with other behaviours, for example escape jumping, dropping from the stem or climbing down or peering from behind the stem (Lahmann, 1996). The rotational shift of the long axis of the locust parallel with the stem during hiding distinguishes this behaviour from other forms of locomotion, including walking, which are characterised by forward and backward stepping or turning

about the locust's vertical axis. The two types of hiding, slow and fast, differ not only in their speed but also in their trajectory (interrupted *versus* smooth) and leg coordination (stationary leg grip as long as possible *versus* early 'anticipatory' lateral stepping).

Fast hiding is the locust emergency reaction. It usually follows strong visual stimuli, specifically the rapid approach of an object that is equivalent to imminent danger or an attack by a predator. 'Dodging' (Uvarov, 1977) may be an appropriate term for fast hiding. Dropping to the ground or subsequently jumping can further diminish the danger. A preparatory phase for a potential jump, the complete femoro-tibial flexion of both hindlegs, often occurs before, during and after the hiding manoeuvre. Lahmann (1996) observed preparation for jumps by locust larvae during the turning movement and jump initiation during the last phase of hiding. Nevertheless, hiding is not simply a preparation for possible jumps in a favourable direction, because sitting motionless or other behaviour patterns may follow hiding.

H. Wilps (personal communication) described a diurnal pattern of preferred avoidance behaviours: during the day, the desert locust *Schistocerca gregaria* in its natural habitat jumps immediately after it has noted a distant moving visual stimulus, especially when it sits above structured terrain. Towards the evening, locusts rely more upon hiding in response to the same type of stimulus. The maximal velocity of hiding increases with increasing temperature (Fig. 7), but it is not known whether temperature affects preferences for other avoidance reactions to approaching objects.

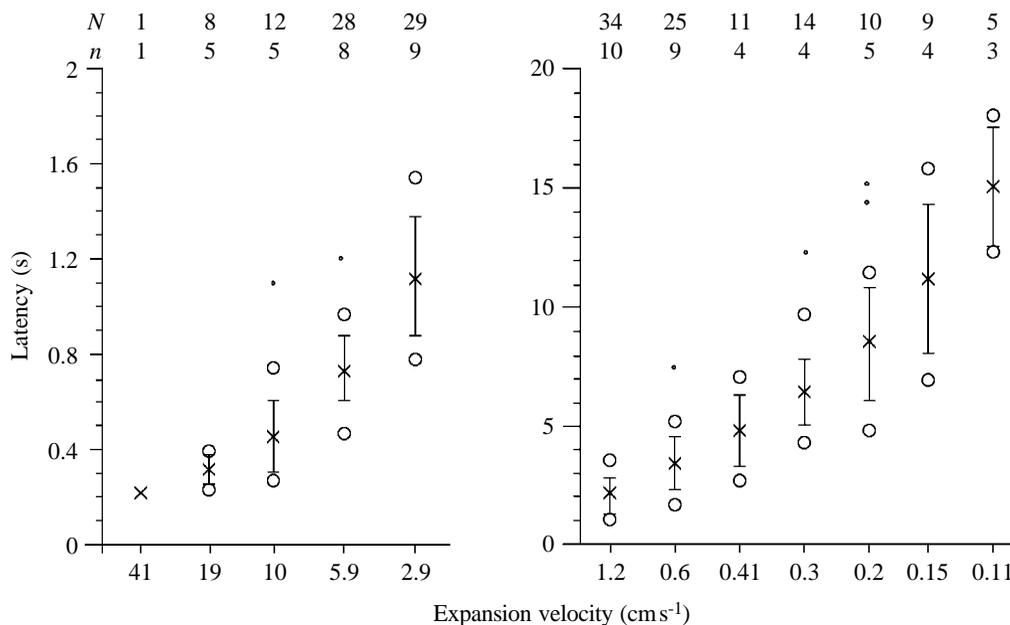Slow hiding is the response to slight and moderately strong

Fig. 10. Latencies of all hiding responses in relation to the expansion velocity of the stimulus. The mean values (×), the standard deviation (bars) and the minimal/maximal values (○) are indicated. Outliers are indicated by a dot and were excluded from calculations of standard deviations. For better discrimination of short latencies after rapid disk expansions, the graph is divided into two separate parts, with the left-hand plot on a larger scale than the right-hand plot, which shows the longer latencies in response to slow disk expansion. The number of responses (N) and the number of animals (n) are given above each velocity.

stimuli such as slowly moving or distant objects detected by an early warning system (see Edmunds, 1974). This may serve to avoid the attention of a distant predator that might see the protruding shape of the locust. These slow movements are hard for a predator to see from afar. For the locust eye during hiding, an object expanding ipsilaterally changes its position ventrally in the ipsilateral visual field, because of the locust's own body movements. In contrast, when locusts are held stationary with a movable foothold (Fig. 1A), the stimulus does not shift in its visual field, yet the slow and fast hiding movements still appear normal. Therefore, the progression of the stimulus over the visual field during active body movements does not seem to be a prerequisite for continued hiding movements. This may indicate that a lateral shift of the stimulus is not the essential parameter for visual feedback that could be used to control movement during the slow hiding manoeuvre.

Stimulus characteristics

The disk on the computer screen expanding at a linear radial velocity does not simulate precisely the natural stimulus of an approaching object, which increases slowly in size when at a distance and covers the visual field rapidly only during the final approach (for details, see Rind and Simmons, 1992; Hatsopoulos et al., 1995) (Birds with long tapering beaks may circumvent this effect when they seek for grasshoppers because the wider head remains rather distant.) Experimentally, hiding responses were elicited most reliably by dark round shapes expanding from at least 8–9.5 ° of visual angle (300–700 mm^2 at 18 cm distance). This threshold angle exceeds by approximately sixfold the acceptance angle of approximately 1.5 ° of a light-adapted ommatidium of the locust compound eye (Wilson, 1975). Therefore, hiding responses are elicited only after shading of at least a strip of 5–6 ommatidia on the lateral visual field of the compound eye. A similar minimal stimulus size (approximately 10 °) within the visual field was observed for flying locusts in their collision avoidance response (Robertson and Reye, 1992; Robertson and Johnson, 1993).

Apparently it is neither simply the contrast of the expanding edge nor the sum of the responses of several more distributed ommatidia shaded simultaneously that releases the response, since showing a black disk suddenly or an expanding dark ring of 5.1 ° angular width (8 mm at 18 cm distance) never elicits hiding. We cannot determine by observations of hiding behaviour whether specific local networks within the locust optic lobes and brain can detect the smaller expanding stimulus prior to the behavioural threshold for hiding.

The well-aimed fast hiding responses of locusts imply that the position of the looming stimulus is used for these goal-directed movements. Therefore, in the compound eye, local sensitivity to small expanding shapes must be distributed over the whole visual field. This implies that, in the optic neuropiles of locusts, many adjacent and/or overlapping subsets of small-field visual integration neurones for small-field dark shape expansion must be the primary integrators and analysers.

Processing of the spatial information could be achieved by higher-order neurones that code the position of the previously coded expansion information in the visual field. Positional information is required to assemble complete motor programmes for the leg trajectories and target positions of the hiding movement, especially when a target position must be reached with just one rapid turning manoeuvre during fast hiding. The target information, for example, could not be relayed to the thoracic motor control centres by a large-field integration interneurone such as the DCMD neurone, for these neurones do not specify positional information. But they could code for other parameters such as stimulus velocity or time to collision (for a review, see Rind and Simmons, 1992) or mediate an early alert (60–80 ms delay) that may prepare the thoracic motor control systems for any of the responses to approaching objects described here.

Motor organisation and sensory cues

Hiding movements by locusts on a vertical stem can start from various different combinations of leg and joint positions, although most locusts attempt to arrange their legs symmetrically to hold onto a stem before they settle. Proprioceptive control of the hiding manoeuvre should take into account (i) the initial load distribution and joint positions (of the four participating legs and the 'guiding' hindlegs), (ii) the planned and actual trajectories of the legs, (iii) the distribution of load changes on leg segments, (iv) the need for interposed lateral steps, and (v) the organisation of stopping all movements behind the rod. Hiding is one of the few locust behaviours in which extreme bending of the fore- and middle leg joints occurs voluntarily (for grooming, see Berkowitz and Laurent, 1996). The 'emergency proprioceptors' that record strain, specifically the campaniform sensilla and the hair rows that record extreme bending of leg joints (Pflüger et al., 1981; Laurent and Hustert, 1988; Mücke, 1991), must be involved in signalling the need to start new steps.

Decisions and motor command characteristics

The decision of a locust to hide must prevail for some time after the stimulus has subsided. During that time, the brain and the posterior central nervous system must (i) define the target of the hiding movement, (ii) trigger hiding and (iii) simultaneously determine, for the thoracic motor neurones, the temporal pattern required for movements in each joint, all of which result in the intended trajectory of the whole body.

We still have to determine where and how decisions to hide or to behave differently, to turn on a rod gradually or rapidly with a predetermined target angle are made in the locust central nervous system, and also where the 'drive' for the performance of a target-oriented behaviour resides until the movement is completed.

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