Modification of the courtship song by visual stimuli in the grasshopper *Gomphocerus rufus* (Acrididae)

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ABSTRACT. Males of *Gomphocerus rufus* L. perform a courtship song consisting of repetitive units, each of which is composed of three subunits (S1, S2, S3). S1 is characterized mainly by slow and fast head rolling; S2 and S3 are distinguished by different types of leg-stridulation. These movements and the associated sounds were recorded during presentation of visual stimuli, either linear displacement of a living female or optomotor stimuli generated by a striped drum. Females moved artificially through the binocular visual field of a courting male with a velocity of 1 cm/s or more are mounted by the male from any subunit S1, S2 or S3, although under natural conditions mounting occurs only from S2. Thus above a critical velocity the courtship programme can be modified. Rotation of a striped drum about the yaw axis of the male during the slow S1 induces asymmetrical leg position, following movements of the head, and prolongation of S1. During S2 the male is especially sensitive to optomotor stimuli and responds with marked changes in body position. In S3 the intensity of the song is reduced, and its duration shortened. Fast drum movements interrupt the courtship programme. Rotation of the drum about the roll axis elicits optomotor head turning that interferes with the head rolling of S1. The fast phase of S1 and the frequency of head-rolling during S1 cannot be modified by optomotor stimulation. The results can be interpreted by assuming certain interactions between three central nervous elements: a calling-song generator, a head-rolling generator, and an optomotor centre.

Key words. Acrididae, *Gomphocerus rufus*, grasshopper courtship song, visual stimuli, optomotor reactions.

Introduction

Males of *Gomphocerus rufus* L. perform a courtship song comprising both visual and acoustic elements (Jacobs, 1950; Elsner, 1968). The courtship song is subdivided into courtship units which are repeated for many minutes. Each

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courtship unit consists of three subunits (S1, S2, S3). S1 is expressed by head-rolling movements with a frequency of about 0.5 Hz (slow S1) which rises to about 1 Hz at the end of the subunit (fast S1). Head rolling is accompanied by palp movements and small amplitude hindleg movements in the same rhythm. In S2 both antennae are rapidly swung backwards twice, while the hindlegs produce a sharp sound by jerking up

and down. In S3 the typical gomphocerine song is produced by rhythmical up- and downstrokes of the hindlegs. This display is considered a prime example of a fixed action pattern (Jacobs, 1950; Loher & Huber, 1964; Elsner, 1968). A courtship song is terminated either by the male mounting the female at the end of S2, or by the female walking away. In the latter case, the male does not interrupt the ongoing subunit, but continued until the next S2, or even the one after that, before it stops and searches for the female, producing pursuit sounds (Jacobs, 1950). This continuation of the courtship song is far more conspicuous in blinded males, which perform up to ten courtship units after the females departure (Riede, 1978).

Since males with intact vision do not react to the departure of a female, at least during S1 and S3, it was hypothesized that the courting male does not evaluate visual information. To test this hypothesis, a courting male was stimulated by an artificially moved female.

In a second set of experiments, optomotor stimuli were presented during courtship song. This situation is particularly relevant to the head-rolling of S1, a motor pattern that might be influenced by visual reafference; evidence for such an influence has been given by Loher & Huber (1966) and Elsner & Huber (1969) who firmly fixed the head to thorax. The normal head rolling of S1 was thus prevented, and was substituted by a slow side-to-side swinging movement of the body, similar to the 'peering' movements of locusts described by Wallace (1959) and Collett (1978). Optomotor stimulation about the roll axis during the head-rolling of S1 confronts the freely moving male with an unexpected reafference. The modifications of S1 provoked by this type of stimulation provide some insight into the interaction between the 'optomotor centre' and the fixed action pattern of courtship song..

Material and Methods

Insects

Adult *Gomphocerus rufus* were caught in the vicinity of the institute. Males were kept individually in small cages, females remained in groups. For the experiments, only consistent singers were used.

Recording of head movements and sounds

To monitor head-rolling in S1, a 1 mm² piece of a reflecting foil (high gain, 3M & Nordic GmbH) was glued to the male's head so that it did not interfere with head movements. The freely moving male was placed in an arena, as illustrated in Fig. 1. It usually stayed within a light-spot 5 cm in diameter, generated by a DC-lamp. An image of the entire area, including the male, was projected onto a photoresistor (LDR03) by a half-silvered mirror. The effective area of the reflecting surface depends on its angle to the incoming light and hence varies with head-roll movements. This modulation of light intensity provides sufficient information about the frequency of head-rolling (Fig. 2a, lower trace).

The sounds produced by leg stridulation in S2 and S3 were recorded with a condenser microphone (Brüel & Kjaer 1 inch type 4145). The signal was rectified and low-pass filtered so that the time-course and intensity of sounds were represented (Fig. 2a, upper trace).

Artificial movement of the female

A living female was fixed ventrally on one end of a balsa rod: The other end was connected to the writing head of an x,y plotter (Fig. 1). The electric signals monitoring the courting male triggered a signal generator that drove the x,y plotter and hence moved the female. The system could be adjusted to produce movements of different amplitudes and velocities during preselected subunits. The female was not moved until the male had performed a series of at least ten courtship units. The head movement and stridulation were recorded together with the female movement on a four-channel strip-chart recorder.

Optomotor stimulation

The central element in the arrangement was an aluminium plate, 25 cm in diameter, fixed rigidly to a stand. Below the aluminium plate was a plastic disc slightly larger in diameter, which held the striped drum and could be rotated by a DC motor with a traction drive. The velocity of rotation was measured by a tachometer at the edge of the ring. Its output voltage was compared with the velocity signals produced
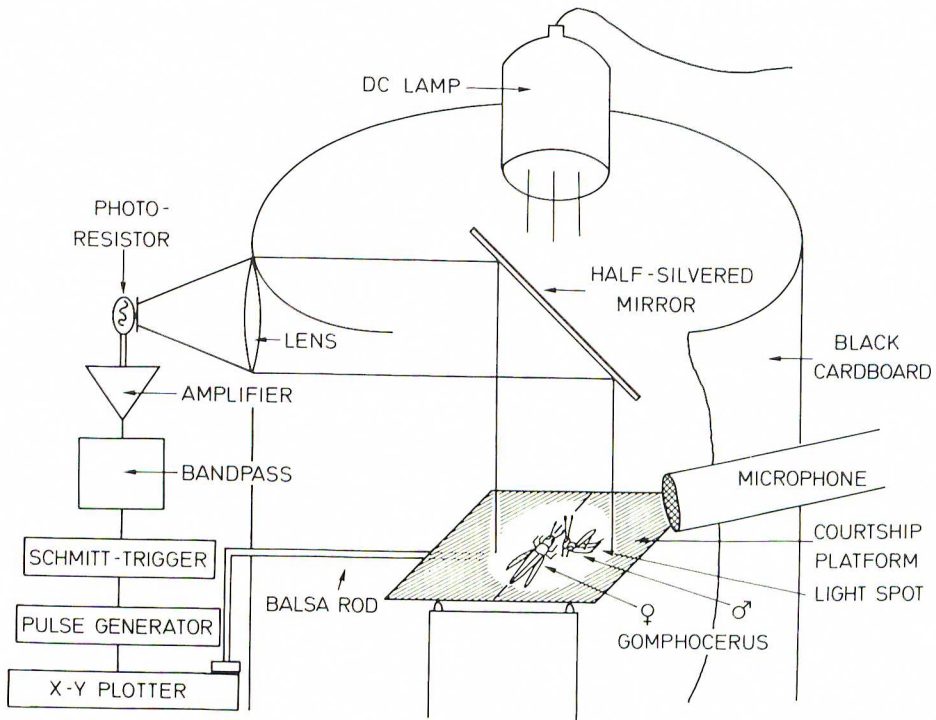
FIG. 1. Arena and apparatus for programmed stimulation of the male by linear movement of the female. The male is free to move within the light spot produced by the DC lamp. The arena is divided in the middle by a slit 1 cm wide, along which the female is moved. She is glued by her ventral side to a balsa rod, leaving her legs free to move. The male's head-rolling during S1 is monitored by an opto-electronic system, and the sound produced during S2 and S3, by a microphone. These signals can be used to trigger the artificial movement of the female by activation of the x,y plotter which displaces the balsa rod at a speed set by the pulse generator.

by a function generator which served as the reference input to the control system for cylinder movement.

The drum consisted of a cylinder of transparent plastic with stripes of black cardboard glued to its outside. In all cases the drum pattern consisted of thirty-six alternating black and white stripes 10° wide. It was illuminated almost homogeneously by three annular fluorescent tubes. To reduce the 100 Hz flicker, the three lamps were driven by different current phases. Two layers of tracing paper diffused the light.

A video system (Grundig 1 inch videorecorder BK 401) recorded part of the striped pattern with one camera and the courting male with another. A microphone recorded the stridulatory sounds. The output voltage of the tachometer measuring drum movements was converted to a tone and recorded on the second sound channel.

Two kinds of drum movements were produced by the function generator: step stimuli (unidirectional rotation) of variable duration and velocity, and oscillating movements at various frequencies and amplitudes. Each stimulus began after the male had started to court the restrained female with a stable sequence of courtship units. Because the duration of subunits varied from male to male and with temperature, quantitative comparisons were based on the response of single individuals which courted for up to 2 h within the striped drum.

For optomotor stimulation about the yaw axis, the female was mounted on a cardboard platform *c.* 2 cm high. A light-spot (5 cm in diameter) illuminated this region. Female and light-spot attracted the freely moving male. As soon as he began to court, the light-spot was turned off and the drum illumination turned on,
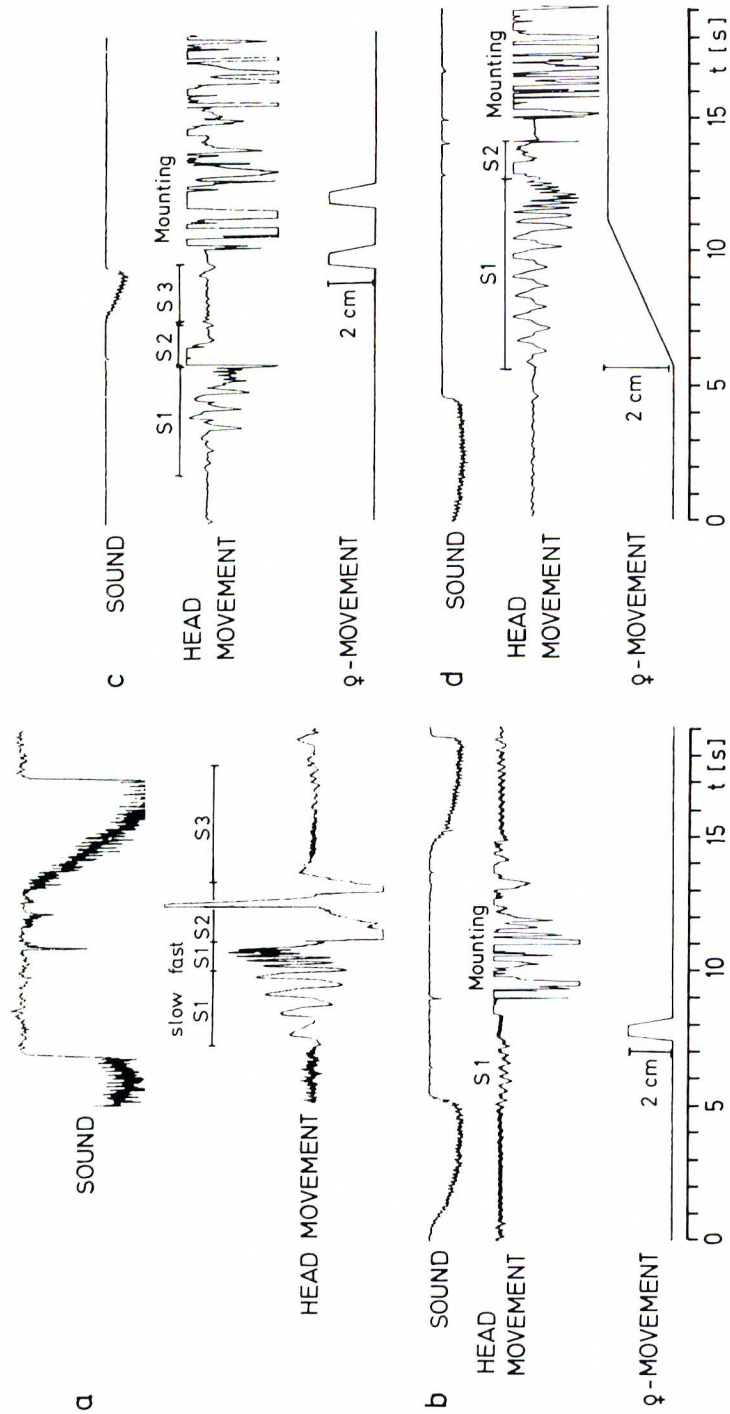
FIG. 2 Recordings of sound and head movements during courtship. (a) Undisturbed courtship unit. Sound of S2 and S3 is rectified and low-pass filtered, head-movements of S1 and movement of body axis in S2 are recorded by an opto-electronic system. These signals could be used to trigger female movement. (b) Rapid female movement (10 cm/s) in S1 elicits unsuccessful mounting. (c) Elicitation of mounting from S3, by the same stimulus. (d) Slow movement (0.4 cm/s) during S1 elicits mounting only after completion of S2.
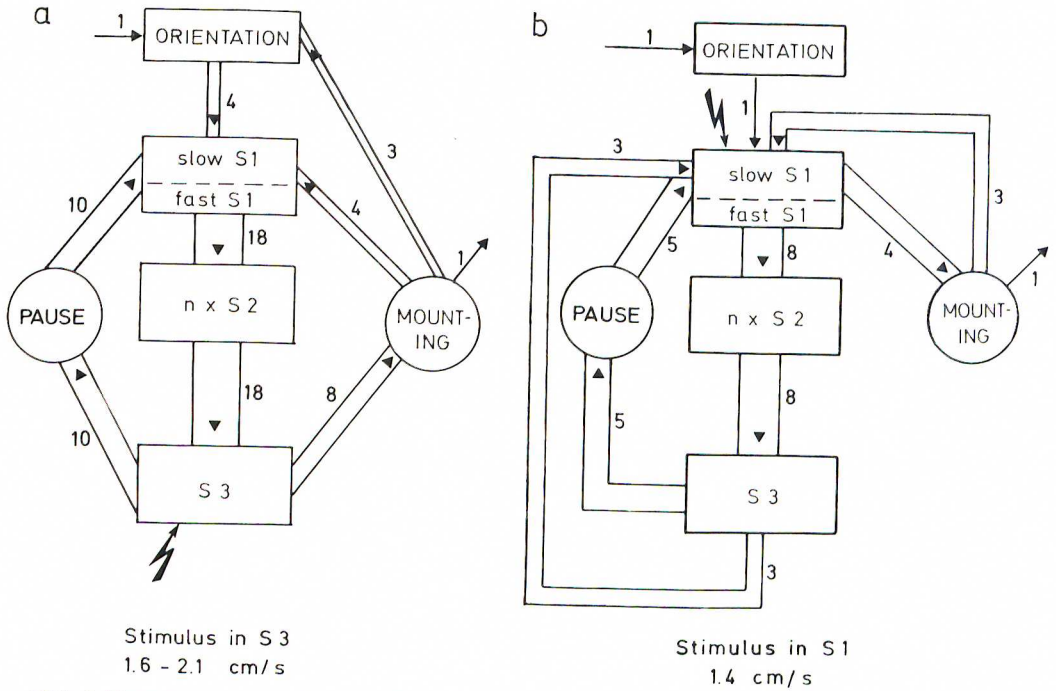
FIG. 3. Flow charts representing the effects of artificial female movement (symbolized by the jagged arrow) in S3 and slow S1. Each flow chart summarizes the events occurring during one courtship song of one male, beginning with orientation and ending after successful mounting. The frequency of transition between different behavioural states is symbolized by the width of the bars, the numbers beside them represent the actual number of transitions. S2 can be repeated up to three times ($n \times S2$). (a) Movement stimulus in S3 causes either pausing or mounting. (b) Movement stimulus in slow S1 causes mounting, but if the stimulus is presented right after S3, at the supposed beginning of S1, there is a pause for the duration of the stimulus before S1 starts.

and after a few courtship units the stimulus programme was started.

For optomotor stimulation about the roll axis, a plastic coated wire was placed vertically in the middle of the drum. A female was glued to its bent upper end. The male courted on this wire and was stimulated around the roll axis. The video recording showed the male's head frontally, so that head-rolling and palp movements could be registered. Furthermore, the entire system could be tilted over 90°, so that the orientation of the male with respect to gravity was the same as during stimulation about the yaw axis.

Analysis

To analyse the response to stimulation about the yaw axis, the change in the male's position was measured by photographing it from the video monitor before and after the optomotor stimulus. The time-course of drum movement, the song and the signal triggering the camera shutter were recorded on a four-channel strip-chart recorder. The photographed video frames were aligned with the corresponding sections of the record (Figs. 4 and 5).

To analyse the effect of stimulation around the roll axis, the position of head and palps was

TABLE 1. Effect of female movement on the duration of S3. Female movement amplitude: 1 cm, velocity: 1.67 cm/s.

	Stimulus onset in S3 (s)					
	2.1	2.4	2.5	2.9	3.1	3.2
S3 duration (s)	2.3	2.8	3.0	3.0	3.9	3.6

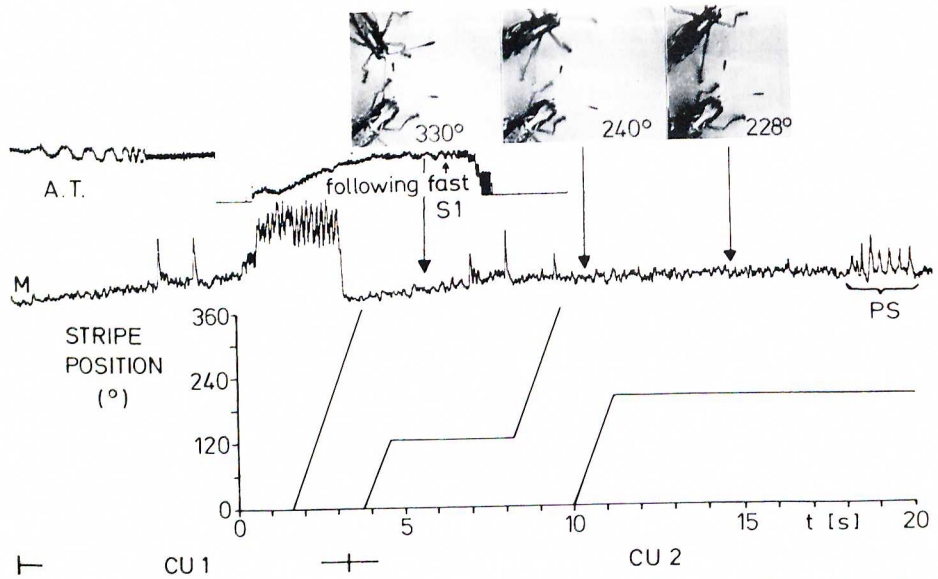Mean song duration of undisturbed S3: 4.1 s, $t=29°C$.

FIG. 4. Effect of optomotor stimuli about the yaw axis. The stridulatory sounds made by the male (microphone signal M) and the drum movement (position of a selected stripe) were recorded simultaneously by a pen-recorder, together with markers showing the times at which the screen was photographed. These photographs were then mounted above the associated sections of the records, indicated by the arrows. Subunits S2 and S3 are clearly identifiable in the acoustic record. The angles given are those of the long axis of the male relative to the left edge of the screen. The antennal movement is represented by a tracking curve (A.T.). Stimulus velocity 180°/s. CU 1: An undisturbed S1 is identifiable in the antennal movement (A.T.). Onset of the stimulus during S3 elicites a following movement of the head. CU 2: The stimulus continued, and instead of the head-rolling characteristic of slow S1 the animal continues the optomotor movement begun in the preceding S3, but only moving the head and the body, thus producing an asymmetrical leg position. When the stimulus stops, fast S1 appears. Renewed stimulation in S2 causes the male to change position (330° to 240°) by optomotor following movements. S3 is omitted, and instead the male searches for the female while making pursuit sounds (PS).

determined using a video tracking system (Hirzinger & Landzettel, 1979; Landzettel, 1980), capable of measuring precisely the x,y coordinates of selectable, contrasting structures, in this case head and palps. The analogue signals representing the movement coordinates were digitized and fed into a computer (PDP 11–40). To study the synchronization of head and palps two passes of tracking were required. The head-rolling and palp-movement data were realigned in the computer and plotted (Fig. 7). By this procedure the structure of S1 could be represented in detail revealing disturbances produced by optomotor stimuli.

Results

Modification of courtship by artificial movement of the female

It was impossible to initiate courtship behaviour by presenting a female dummy, even if it was moved in the visual field of the male. However, if a live female was replaced by the dummy while the male was already courting, he continued the courtship song. Moreover, he mounted the model either spontaneously or in response to its movement.

The following experiments were therefore performed with living females. Three kinds of

TABLE 2. Number of position changes after various optomotor stimuli in subunits 1, 2 and 3.

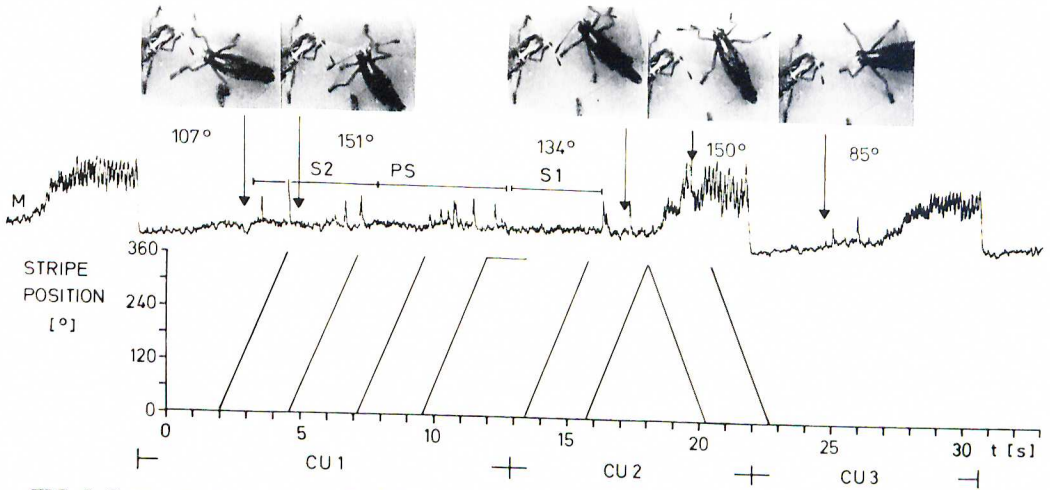| | Angular difference (°) of the male's long axis before and after stimulation | | | | | | | | | | | | | |
	4°	8°	12°	16°	20°	24°	28°	32°	36°	40°	44°	48°	52°	54°	>58°
S1	26	10	12	4	3	1	0	0	0	1	1	0	1	0	0
S2	10	3	4	6	8	1	7	1	0	2	2	3	1	2	9
S3	27	10	7	3	7	3	1	1	0	0	0	0	0	0	0

FIG. 5. Optomotor stimulation at 140°/s applied during fast S1, S2 and S3 of consecutive CUs. CU 1: Onset of the stimulus in fast S1 leads to a position change after S2 (107° to 151°). The ongoing stimulus leads to omission of S3, and instead the male produces pursuit sounds (PS). After the stimulus stopped, courtship was resumed with S1 of CU2. A second stimulus again causes a change in position (134° to 150°). A reversal of the drum movement disturbs the song of CU 2 and leads to a position of 85°, characterized by an asymmetrical leg position.

responses to artificial movement could be distinguished: (i) continuation of the courtship unit and interruption of the next S2, as would happen in normal courtship; (ii) interruption of the ongoing subunit by a pause until female movement stopped, whereupon either the subunit was resumed where it had been interrupted or the male reorientated himself and then began anew with S1. These modification can also be observed in natural courtship. (iii) Mounting of the female following interruption of S1, S2 or S3, where mounting from S1 or S3 are new variants not seen in nature. These modifications are therefore described in more detail.

Fig. 2(b) shows the record of a mounting response that occurred during slow S1 with a female moved faster than natural, with a velocity of 10 cm/s. The mounting attempt failed and the male omitted fast S1 and S2, resuming the courtship unit with S3. Mounting from the fast S1 was never observed, though the number of movement stimuli was the same as for the slow S1. Fig. 2(c) demonstrates that mounting elicited by rapid female movement can interrupt S3, so that its duration is determined by the onset of female movement (Table 1).

These modifications are clearly inconsistent with the natural course of courtship behaviour, during which the male responds only in S2 to female movements. However, the movements used as stimuli were far more rapid than a female's natural walking speed which does not exceed 0.5 cm/s. Therefore slow movement stimuli were tested to simulate the natural situation.

At speeds of *c*. 0.5 cm/s the male interrupted courtship only after S2, in accordance with natural behaviour (Fig. 2d). For twenty-eight males studied, the threshold for mounting from S1 or S3 was found at velocities between 1 and 1.5 cm/s, 2–3 times faster than the natural walking speed.

All the modifications of a single male in response to artificial female movements are summarized in the flow-charts of Fig. 3. Because mounting can be elicited from all subunits, the male must perceive visual stimuli during the entire courtship programme, except in fast S1.

Effects of optomotor stimuli on the courtship song

As the courting male is capable of reacting to movement stimuli, one would expect optomotor stimuli to interfere with courtship as well. The following experiments shows that optomotor stimuli can effect all the subunits of a courtship unit except the fast S1. Courtship can be modified by superposition where the male performs the courtship unit and an optomotor response at the same time, or by interruption
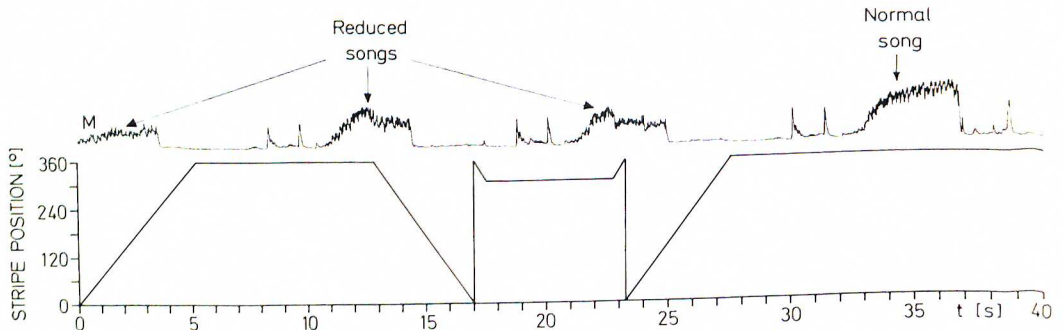
FIG. 6. Reduction in song intensity by optomotor stimulation. Top trace, acoustic signal; bottom trace, drum movement.

where he substitutes courting by the optomotor response.

Stimulation about the yaw axis. The following modifications of S1 were observed: (i) An asymmetrical leg position is induced, in that the male follows the optomotor stimulus with the body without moving the legs ('following', in Fig. 4). This position is retained until mounting movements occur. (ii) The head-rolling in S1 is replaced by optomotor head turning until the stimulus ends or fast S1 starts ('following', in Fig. 4). The antennae-movement record clearly marks the transition from head-rolling to head-turning. Fast S1 then starts, without execution of slow S1. (iii) Slow S1 is replaced by an optomotor response and the male orients anew after the end of the stimulus, thus breaking off the ongoing courtship unit. S2 continues together with strong optomotor reactions, which indicates a high stability of this subunit with respect to visual perturbations (Table 2).

S3 is modified according to stimulus velocity: at pattern velocities less than $40°/s$ the song intensity is reduced (Fig. 6); at rapid pattern velocities ($120°/s$ or even more), the male breaks off S3 and terminates the ongoing courtship unit, showing optomotor responses and pursuit sounds (cf. Figs. 4 and 5). In a series of stimulations, S3 durations are reduced to 2.8 s (SD 1.6, $n=73$), whereas undisturbed songs last 4.0 s (SD 1.6, $n=79$).

Table 2 summarizes the effects of optomotor stimuli on position for the different subunits. S2 is compatible with large positional changes, while S1 and S3 are interrupted.

Stimulation about the roll axis. The distinctive difference from stimulation about the yaw axis is that optomotor induced head rolling interferes with head-rolling during S1.

In a preliminary experiment, an attempt was made to stimulate a quietly sitting male by a drum motion so as to elicit optomotor head-rolling similar to that exhibited in S1. Though rhythmical head-turning movements could be elicited over minutes, the male never started S1. This clearly demonstrates that the performance of head-rolling alone cannot initiate courtship.

Optomotor stimuli about the roll axis modified S1 as follows: the amplitude of head-rolling was damped or replaced by optomotor responses (Fig. 7b, c); S1 continued undisturbed, in spite of strong optomotor stimuli (Fig. 7b); head-rolling and associated palp movements were separated (Fig. 7c). Here the stimulus pattern mimicked the exafference produced by head-rolling. After a short initial following reaction, head-rolling ceased completely, while the palps continued to perform the typical 'square wave' movements of S1. After about 20 s the fast S1 started in spite of the continuation of the optomotor stimulus. The duration of slow S1 was extended.

On the whole, then, the influence of optomotor stimuli about the roll axis is extremely variable. For a given moment, a particular individual can fail to respond at one time, and make following movements immediately thereafter (Fig. 7b). Thus, the role of visual afference during S1 could not be clarified. However, the modifications obtained show that during slow S1 the visual system is accessible to optomotor input and palp movements characteristic of S1 can occur independently of head-rolling. Again it was impossible to disturb the fast S1.

With respect to S2 and S3, the effects are similar to those obtained during yaw stimulation.
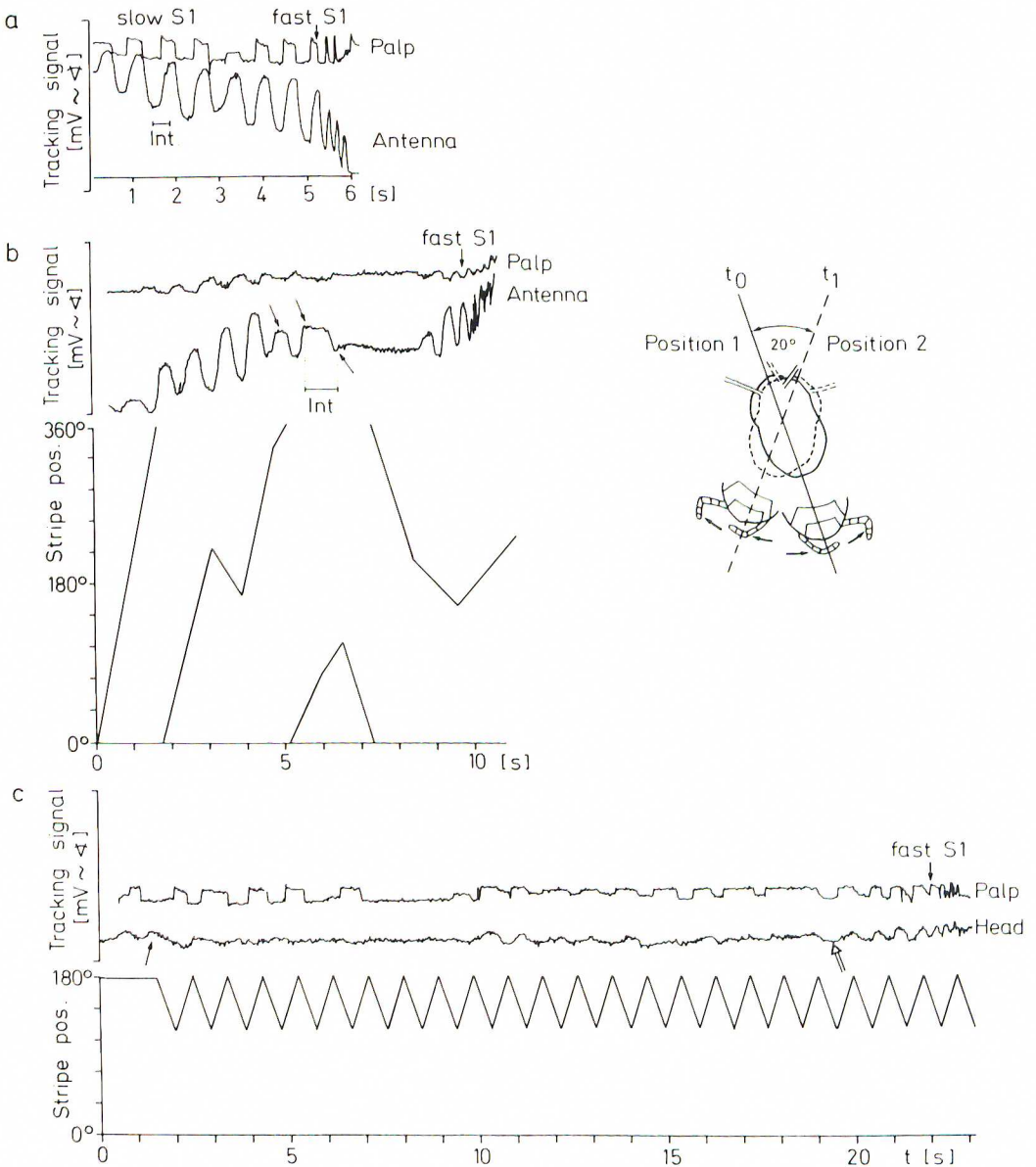
FIG. 7. Videotracking curves of head and palp movement. Inset: The two extreme positions of the head, at times t_0 and t_1. For clarity, the associated movements of the maxillary palps are diagrammed below. Note the active change of palp position relative to the head. (a) Undisturbed movement of antenna and palp during S1. Note the close synchronization of the two movements. Because the antennae move together with the head during S1, the curve also represents the head movement. The frequency of head-rolling in the fast S1 is twice that of slow S1. Int. is the head-rolling interval, the time between two extreme positions of the head (i.e. t_1, t_0 of inset.) (b) Effects of optomotor stimulation on slow S1. Stimulation at $216°/s$ up to 5 s, thereafter $90°/s$. At ↘ the head movement is truncated, and from then on both head and palp movements cease. Despite continuation of the stimulus, however, slow S1 is resumed and followed by fast S1; the net result is prolongation of slow S1. (c) Separation of head and palp movements in S1 due to optomotor stimuli. Drum oscillated at 0.91 Hz ($120°/s$); after the onset of drum movement there is a short following movement (↗) after which the head stops moving while the palps continue to move as in S1. This phase is greatly prolonged; only after ↖ is the head movement of slow S1 resumed. The animal proceeds to the fast S1, while the drum movement continues.

Quantitative relations between optomotor responses and head-rolling intervals

Analysis of the head-rolling intervals ('Int.', in Fig. 7a, b) in perturbed slow S1 can specify more exactly the influence of optomotor stimuli on this phase. For this purpose the optomotor responses in S1 were evaluated, as were the self-generated head-rolling movements by measuring the intervals between consecutive extreme positions (Fig. 7b). A comparison of the histograms of head-rolling intervals with and without detectable optomotor movements. Fig. 8(a) shows a clear difference, in that the mean is increased by the presence of extremely long intervals in S1 perturbed by optomotor stimuli. These long intervals occurred when optomotor head-movements were interspersed with S1. Disregarding these extreme values, the main peaks of both distributions lie between 320 and 400 ms. This indicates that the oscillating process generating head-rolling is not influenced by optomotor stimuli and is thus independent of visual reafference.

By taking the sequential position of head-rolling intervals within the slow S1 into account, and averaging the first, second, third, etc., intervals in a series of S1s modified by optomotor following reactions, the resulting curves show a progressive decrease in the mean duration of head-rolling intervals (Fig. 8b). This shows that S1 is more easily perturbed near its onset.

The incorporation of optomotor responses lengthens S1 (8.1 s mean, SD, 3.18, as compared with 5.2 s mean, SD 0.72, in undisturbed S1). However, many S1s are not extended in the presence of optomotor responses, the modes of the two distributions lie both between 5.25 and 6.8 s. Neither the number of S2s nor their duration can be modified by optomotor reactions. While optomotor reactions cause prolongation of S1, they shorten S3, as already shown above. When the duration of a subunit is changed, the following unstimulated subunits are of normal duration. That is, when S1 is prolonged, no compensatory shortening was found for S3 to keep the overall duration of the courtship unit constant. A shortening of S3 never provoked a prolongation of the following S1.

Partial blinding

Blinded males can start courtship if they hear the conspecific female song (Loher & Huber, 1964) or touch a female or male accidentally (Riede, 1978). Therefore it was of interest to study the effects of partial blinding, as separate eye regions may be involved in female fixation and optomotor reactions. With the lateral parts of the compound eyes covered with black paint (Finodur), leaving free the binocular visual field, the male continues to orientate normally to the female and to court her (Riede *et al.*, 1979). It is no longer possible, however, to induce optomotor responses by drum rotation: the male neither exhibits turning responses nor breaks off courtship. Though preliminary, this experiment shows that optomotor responses are controlled mainly by the lateral, monocular parts of the eyes, whereas the frontal, binocular eye regions suffice to mediate orientation towards the female.

Discussion

This paper provides evidence that during courtship visual input, and therefore visual reafference, have access to those structures in the nervous system that generate the courtship programme.

Artificial fast movements of the female (velocity greater than 1 cm/s) can interrupt S1 and S3, and the male can mount the female; a situation never observed in nature.

Rapid movements do occur in natural interactions, for instance, defensive females make kicking movements or jump away, receptive females sing. All these movements contain high velocity elements. Nevertheless, they do not elicit mounting from S1 or S3. Jumping away is probably too rapid to elicit mounting, and furthermore the female disappears from view immediately. But why is mounting elicited by rapid female movements in the experimental situation? Rapid artificial displacements of a female stimulate a large region of the male's eye. Evidently they serve as highly efficient movement stimuli, sufficient to produce the observed perturbations in courtship. These do not have any function in the natural course of behaviour, but tell that the male can take visual information into account during S1 and S3.

Courtship is preceded by an orientation phase, during which the male finds his correct position with respect to the female by means of visual cues (Jacobs, 1950; Riede *et al.*, 1979). It is impossible to elicit courtship by a motionless
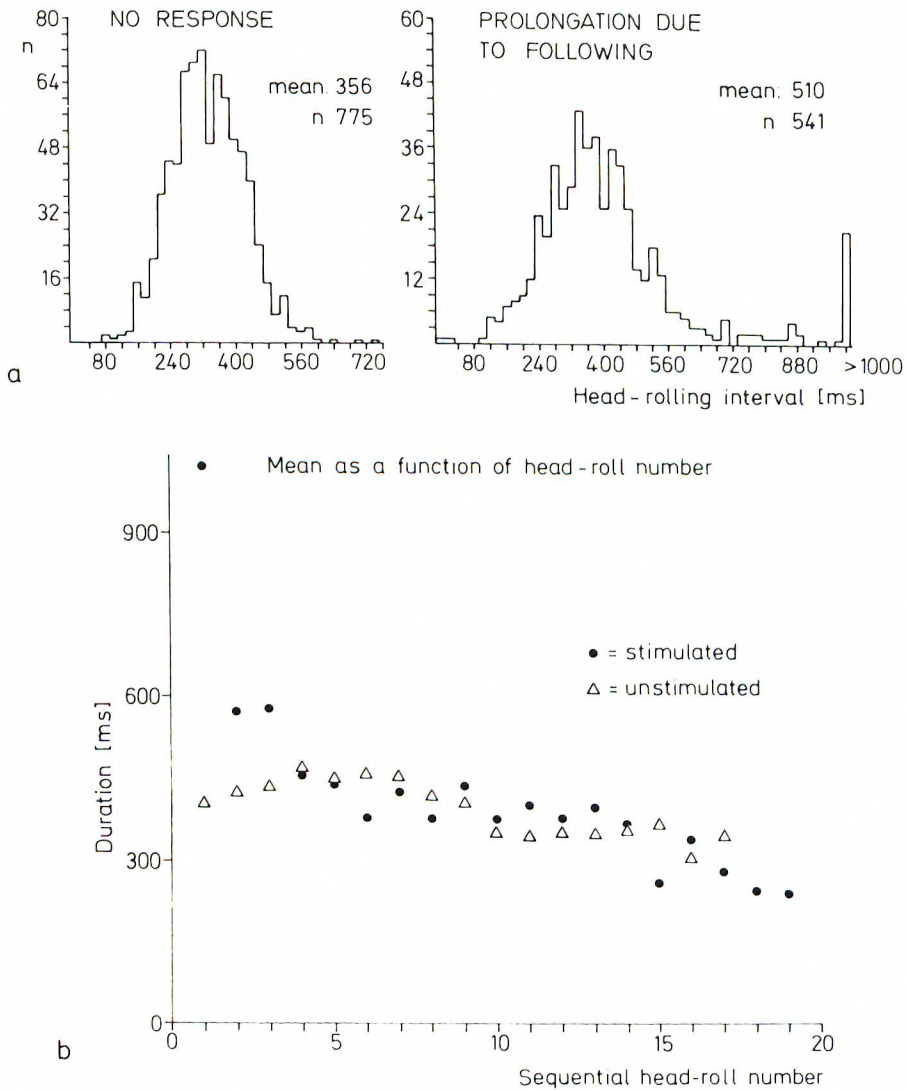
FIG. 8. (a) Effects of optomotor stimulation on head-rolling interval in slow S1. The histograms at the top represent cases in which the optomotor stimulus had no discernible effect (no response) and those in which following movements were elicited, as a result of which the slow phase of S1 was prolonged (prolongation due to following). (b) Means of the first, second, third, etc., head-rolling intervals in thirty-nine S1s. For the 'stimulated' curve, the optomotor stimulus lasted throughout S1. Head-rolling movements at the beginning of S1 have a stronger tendency to be replaced by following movements (higher means at the left of the curve).

dummy, but once courtship has started, the live female can be replaced by the dummy without interrupting courtship. These observations indicate that during the orientation phase more and perhaps more complex features of the female are taken into account than after the orientation has been completed. When the courtship programme is in progress, simpler 'perceptions' suffice. It is conceivable that correct positioning with respect to the female and the mounting movements are controlled by edge fixation (cf. Varjú, 1976), because *Drosophila*, is known to continue courtship when the female is replaced by an edge (R. Cook, personal communication).

The interference of optomotor reactions with courtship implies that both have sensory, central nervous and motor substrates which can interact on several levels. A hypothetical scheme of
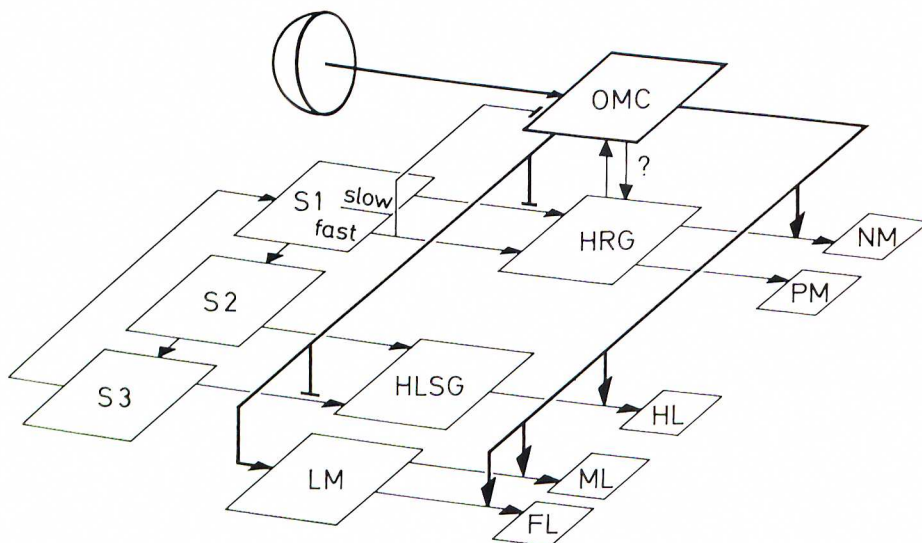
FIG. 9. Scheme illustrating the relations between optomotor centre (OMC) and courtship. A generator produces the succession from S1 to S3. S1 is connected to the head-roll generator (HRG) which generates the motor programme for neck and palp muscles (NM, PM). A hindleg-stridulation generator (HLSG) produces the stridulatory sounds, characteristic for S2 and S3. The optomotor centre (OMC) receives input from the eye and sends commands to the neck muscles (NM) and the leg musculature (LM), to middle and front legs (ML, FL). There has to be some interaction between HRG and OMC to avoid self-stimulation of the OMC by head-rolling. These interactions are marked with a question mark. Inhibitory interactions are symbolized by $\perp$. Connections of S1 to S3 which are not discussed here are left out (f.i., faint sounds are produced during S1, so that there would be a connection between S1 and HLSG). Also the connections of S1 to the antennae are left out. Further explanation in text.

interplay of these systems is presented in Fig. 9, on which the following discussion is based.

A 'courtship generator' is assumed to produce the sequence of subunits S1, S2 and S3. Various 'subroutines' are involved in the production of the characteristic motor patterns of each sub-unit: a head-roll generator (HRG) for the production of head and palp movements during S1, and a hindleg-stridulation generator (HLSG) to produce singing in S3. More motor programmes are involved in the production of the complex courtship movements (for instance, antennal movements), they are not considered here.

Evidence for a centrally localized 'courtship generator' that controls the succession of the subunits S1 to S3 has been given by the experiments of Elsner & Huber (1969) and Loher & Huber (1966). They showed that in spite of amputation or fixation of hindlegs, the succession of subunits S1 and S2 was normal: the song was replaced by a pause of equal length. The same holds for animals with the connectives anterior to the metathoracic ganglion cut (Elsner & Huber, 1969). This demonstrates that at least for S3 the composition and succession of subunits are generated independently of their

execution; a feedback from the effectors performing the respective subunit is not necessary to keep the 'courtship generator' going.

The assumption of 'subroutines' called up by a courtship generator, is justified by the following evidence: elements of courtship can be elicited by brain stimulation (Wadepuhl, 1983) independently of each other, which indicates that substrates responsible for production of subroutines were stimulated, and not the courtship generator; subunits can blend into each other. Head-rolling can start while the male is singing. That is the courtship generator has already proceeded from S3 to S1, but the HLSG still operates in parallel and independently, finishing the song once it has been triggered.

The interactions with the optomotor centre can be interpreted as effects on a more central and a more peripheral effector level. On the effector side the optomotor centre is connected partially to the same subset of muscles involved in courtship. These are the neck muscles (NM), responsible for optomotor head-turning as well as S1 head-rolling, and the hindlegs (HL), involved in optomotor turning reactions and hindleg-stridulation of S3.

Another subset of muscles works independently for courtship and optomotor reactions respectively: these are the palp muscles (PM), involved in S1, and the leg musculature (LM) of the middle- and front-legs (ML, FL), which are involved in optomotor reactions. The following effects can be interpreted in terms of interference on this peripheral level: damping of head-rolling in S1 as a result of superposition of head-roll and optomotor commands acting on the neck musculatur (NM); separation of palp and head movement. The ongoing palp movement during absence of head-rolling shows that the head-roll generator (HRG) still operates, but the optomotor centre (OMC) and HRG effects on the neck muscles cancel each other so that the head stands still. The splitting of head and palp movement shows that there must be a parallel output from the HRG to neck and palp muscles.

In S3, the reduction of song intensity can be explained by the interaction of OMC and HLSG commands on the hindleg musculature. Even small changes in the position of the hindlegs change the angle between wings and legs, thus influencing the sound intensity. It is impossible to tell from the above behavioural experiments, on which level these interactions take place.

A more central interaction of the optomotor centre with courtship subroutines must be postulated to explain the other observed effects. Optomotor reactions sometimes replace S1, so that both head-rolling and palp movements cease. Therefore there must be an inhibitory relation between optomotor centre and head-roll generator. Though one does not observe head and palp movements, the courtship generator goes on, and even leads to fast S1.

S1 itself is sensitive to peripheral influence: disturbed S1s are prolonged, showing that this subunit is restarted after disturbance. As the mechanisms for this 'reset' is unclear, it is not symbolized in the scheme. The sensitivity of S1 to disturbance is greater at its beginning and susceptibility vanishes completely in fast S1.

The absence of any optomotor response during fast S1 is remarkable because the only difference from the motor events of slow S1 is that the frequency of head-rolling is doubled. This 'immunity' of fast S1 to optomotor stimuli is symbolized by an inhibitory arrow between fast and S1 and the OMC. This inhibition of visual input might operate like a 'saccadic suppression' (Zaretsky & Rowell, 1979; Zaretsky, 1982).

Another possible explanation is that in the fast S1, the activation of the neck muscles by the HRG dominates in such a way as to override optomotor inputs.

While S1 is prolonged by disturbance, quite the contrary is the case for S3. The song can only be shortened or broken off altogether, symbolized by an inhibitory arrow from OMC to HLSG. This leads to a new start with S1, but never to a reset of S3: only shortening of S3 is possible.

Pure superposition of movements associated with S2 (antennae, palp, hindleg) and optomotor responses (turning of the head, rotation of the body) shows that in this subunit the two programmes have no disturbing effect on each other. Under natural conditions, the male quite frequently changes position with respect to the female between two subsequent S2s, partly because S2 is carried out rather vigorously and nearly moves the whole body. Thus, body movements during S2 can be considered as a part of the overall courtship display, where they evidently serve to correct the male's position with respect to the female. Because this orientation is visual (Riede *et al.*, 1979) the male's high sensitivity to visual and optomotor stimuli during S2 becomes understandable.

An interesting aspect of courtship is the significance of visual reafference during S1, the only subunit during which the male moves his head and produces relative movements of the surroundings. As the animal is accessible to visual input during this phase, there is presumably some mechanism by which the reafference caused by the animal's own movement can be distinguished from the exafference. One possibility is a peripheral–central interaction as formulated in the reafference principle (von Holst & Mittelstaedt, 1950, and revised by Mittelstaedt, 1971). In addition, it could well be that not only visual reafferences, but also hair field afferences from the neck region (Goodman, 1959; Kien & Land, 1978) are used to control head-rolling. Unfortunately, the irregular responses observed in S1 make it impossible at present to envisage the mechanism. A set-point shift in the optomotor control circuit (feed-forward; Collett, 1980) can be ruled out, because it would be expected to produce regular interference between head-rolling and pattern motion when the pattern is moved.

As the preliminary results of partial blinding indicate, the lateral eye regions contribute to

optomotor responses, and the frontal regions to fixation of the female (cf. Rossel, 1980; Kien, 1974). Therefore the diversity of reactions observed in S1 could result from the way the visual inputs from the lateral and frontal eye regions are weighted. That the insect nervous system is capable of 'selective attention' has been shown by Heisenberg & Wolf (1984) in *Drosophila*, and by Srinivasan & Bernard (1977) in their analysis of pursuit and optomotor responses in house flies. In the experiments here, the female is fixated by the courting male, and evidently his readiness to respond to optomotor stimuli fluctuates.

Acknowledgments

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