Gravity Reception in Crickets:
The Influence of Cercal and Antennal Afferences
on the Head Position*

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Summary. In the cricket, *Gryllus bimaculatus,* compensatory head movements are elicited by cercal and antennal receptors when the animals are rotated around their longitudinal axis. The cercal afferences originate in the club-shaped sensilla, whereas the antennal ones probably arise in receptors measuring displacements of the flagellum at the joint between scapus and pedicellus. The club-shaped cercal sensilla are true gravity receptors different from the proprioceptive gravity receptor systems characteristic of most insects.

Introduction

Most terrestrial walking insects obtain information on the direction of gravity from proprioceptors (Horn 1983), while it has been suggested that in crickets the club-shaped sensilla of the cerci are used for gravity reception. These sensilla are known to work like pendulums whose amplitudes of movement depend sinusoidally on the spatial position of the animal (Nicklaus 1968; Bischof 1974, 1975). Recordings from the giant interneurones of the last abdominal ganglion of the cockroach *Arenivaga* indicate that they receive input from the cerci whose strength depends on the strength of the gravitational stimulus (Hartman et al. 1979). The identification of gravity sense organs, however, is only possible using behavioural experiments. The necessary and sufficient condition for such identification is a situation in which elimination of a suggested gravity receptor causes the loss of the animal's normal response in relation to gravity. This condition was met in the experi-

ments on gravity reception in flies, *Calliphora erythrocephala,* in which bristles of the scapus (Horn and Kessler 1975) and leg proprioceptors (Horn and Lang 1978) were proved to be gravity sensitive.

In this paper, we describe the influence of cercal and antennal afferences on the position of the head when crickets are rotated in the field of gravity under conditions in which the gravitational stimulus cannot act on leg proprioceptors. The latter are responsible for gravity reception during geotactic orientation (Jander et al. 1970).

Materials and Methods

We used equal numbers of male and female crickets, *Gryllus bimaculatus,* which were obtained from a dealer and were 4 to 10 days old. The test situation is described in detail by Horn and Lang (1978). The crickets were supported at the thorax and were able to move a disc (2 cm wide and 8 cm in diameter) which was mounted on a spindle (fixed-ball-situation, see Horn and Lang 1978). This equipment eliminated any influence of gravity dependent leg afferences on the position of the head.

Under these conditions, crickets perform strong compensatory movements of the head when they are rolled around their longitudinal axis. This response occurs only if the cricket walks spontaneously or if it was caused to walk. The cricket, however, maintains its head in an abnormal position for many seconds after it stops walking. We elicited walking by pushing slightly the wings because crickets walk only reluctantly in the test-apparatus.

Movement of the abdomen relative to the thorax was eliminated by connecting both parts of the body to a piece of balsa wood. The illumination around the cricket's longitudinal axis was homogeneous.

Three different experiments were performed to elucidate the role of cercal receptors. In one group of crickets, we covered both cerci with fast-drying plastic. In a second group we shaved the club-shaped hairs with a sharp knife. Finally, for the third experiment, the cerci of this group were completely removed. The influence of antennal receptors was determined by cutting off the antennae at the middle of the scapus. This operation ensures the elimination of all receptors that measure movements of the antennae.
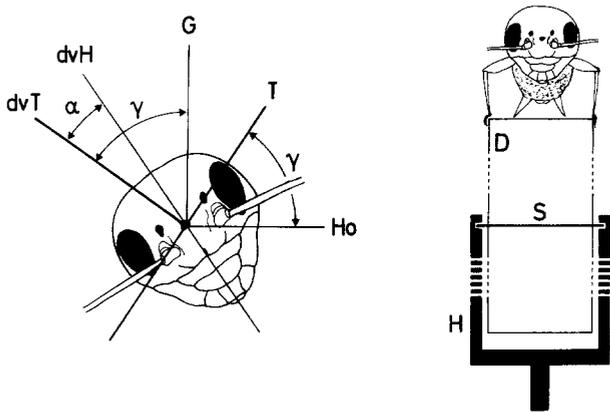
Fig. 1. Methods and definitions: *D* walking disc; *G* reference line of the gravitational field; *dvH* dorsoventral axis of the head; *dvT* dorsoventral axis of the thorax; *H* holder; *Ho* horizontal direction; *S* spindle; *T* transverse axis of the cricket; α head angle for rotation around the neck longitudinal axis; γ roll angle

The response characteristics of each animal were measured before and 1 h after experimental manipulation of cerci and antennae. Different results obtained from animals before and after the operation were not caused by fatigue. Control experiments demonstrated that the response characteristics of intact animals measured 1 h after the first measurement were identical.

Statistics. For each experiment we plotted the mean and its standard error (SEM). For statistical treatment, we used the paired value test from Wilcoxon (Sachs 1974), and always combined results obtained from males and females. Although there are some sex differences, this treatment is valid for two reasons: first, because the Wilcoxon test is a rank test; and second, because when angular changes occurred after an operation, they were all in the same direction.

Abbreviations. α angular position of the head = angle between the dorso-ventral axis of the head and the thorax; γ roll angle = angle between the transverse axis of the animal and the horizontal plane (Fig. 1); α (γ) response characteristic; for the description of the amputation effects we sometimes use the term A_{total} which is calculated by the difference between the angular positions α for $\gamma = 90°$ and $270°$.

Results

Intact crickets perform compensatory head movements even in the absence of leg afferences. When the cricket is rolled to the right side its head moves to the left side around the animal's longitudinal axis, and vice versa. The amplitudes of these compensatory movements depend sinusoidally on the roll angle γ. Maximal head deviations from the normal position are obtained if the dorsoventral axis of the thorax is placed perpendicular to the direction of gravity (Figs. 2–4). In intact animals the total amplitude difference A_{total} amounts to nearly 30°. However, there are significant differ-
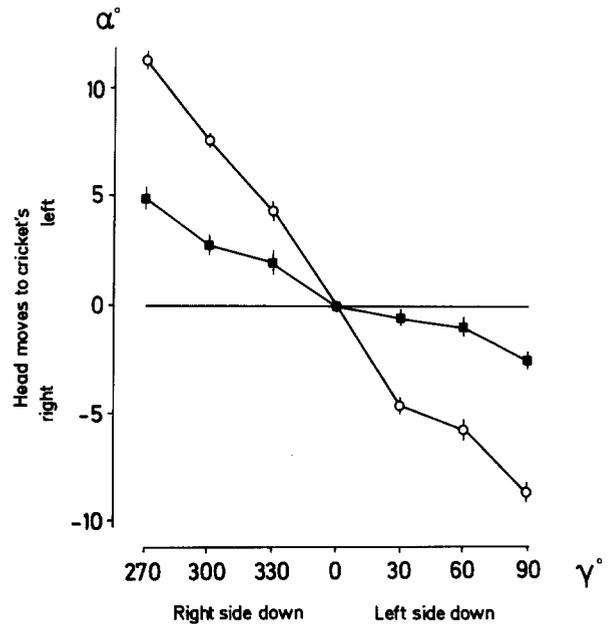
Fig. 2. Compensatory head movements of crickets during rotation around their longitudinal axis before (o) and after (■) immobilization of all sensilla of the cerci. α head angle for rotation around the neck longitudinal axis; γ roll angle; *vertical bars:* standard error of the mean (SEM). $n = 10$ crickets

ences ($P = 0.01$) between male and female animals; in males, A_{total} amounts to only 20° to 25°, while A_{total} of female crickets is greater than 30° (Figs. 3b, 4b).

Covering both cerci with fast-drying plastic causes a decrease of the head angles α for all inclinations γ, tested (Fig. 2). These differences are significant ($P < 0.01$) for crickets lying on the right or left side ($\gamma = 270$ and 90°). Detailed analysis demonstrates that elimination of the cercal club-shaped sensilla has the same significant effect; and complete amputation of both cerci causes no further decrease of the head angles α (Fig. 3 left).

The decrease of the amplitude of the response characteristic $\alpha(\gamma)$ after covering the cerci with fast-drying plastic or shaving the club-shaped hairs was found in every animal tested. However, the mean decrease of the head angle α is greater for female than for male crickets. In contrast to intact animals, the response characteristics $\alpha(\gamma)$ of male and female crickets without club-shaped sensilla are nearly identical (Fig. 3 right).

After amputation of both antennae, the mean head angles α decrease for all roll angles γ (Fig. 4 left). These differences are highly significant ($P < 0.01$) for $\gamma = 90°$ and $270°$ and adjacent roll angles. The total amplitude differences A_{total} of the response characteristics $\alpha(\gamma)$ of operated males was slightly smaller than that of the female crickets,
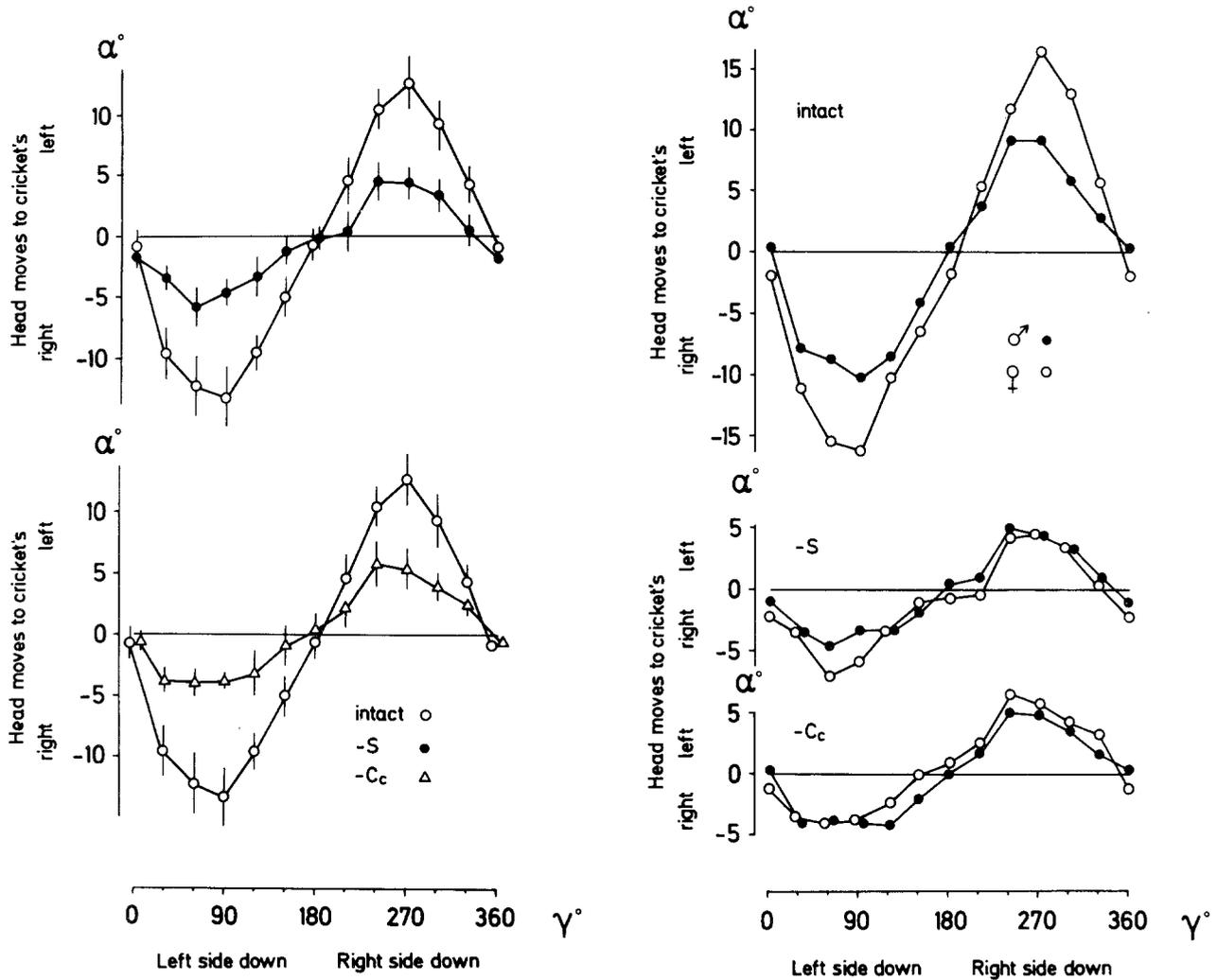
Fig. 3. Compensatory head movements of crickets during rotation around their longitudinal axis before (*intact*) and after shaving off the club-shaped sensilla ($-S$), and after additional amputation of the cerci ($-C_c$). α, γ see Fig. 2; *vertical bars:* SEM. $n=10$ crickets; 5 females and 5 males. – *On left side:* combined calculation for males and females; *on right side:* separate calculation of the mean response amplitudes α for males (●) and females (○). For intact males (females) the maximum value of SEM is $\pm 2.5°$ ($\pm 3.7°$), while in the operated groups, SEM never exceeds $\pm 1.6°$ ($\pm 1.5°$)

but this difference is not significant ($P>0.1$) (Fig. 4 right).

No significant difference was found between the response characteristics $\alpha(\gamma)$ of crickets after amputation of their antennae or shaving of their club-shaped hairs. In both groups, A_{total} amounts to $11°$ and $10°$, respectively (compare Figs. 3 left and 4 left).

After simultaneous amputation of both cerci and antennae, the compensatory head movements disappeared in all of the experimental animals (Fig. 5). The strong fluctuations of the head angles indicate a failure to perceive the gravitational stimulus.

The sex differences in the amplitude of the compensatory head movements of intact crickets

(Figs. 3 right, 4 right) are not caused by different numbers of the club-shaped sensilla. We counted their numbers for every 4 males and females and found a ratio of 108:117.

Discussion

The present investigation demonstrates that crickets, *Gryllus bimaculatus,* perform compensatory head movements when they are rolled around their longitudinal axis. These reflexes are elicited by cercal and antennal gravity receptors; but as with the fly, *Calliphora erythrocephala,* walking is a necessary condition that these responses occur. Horn (1982) suggested that in *Calliphora* this relation between walking and occurrence of head reflexes
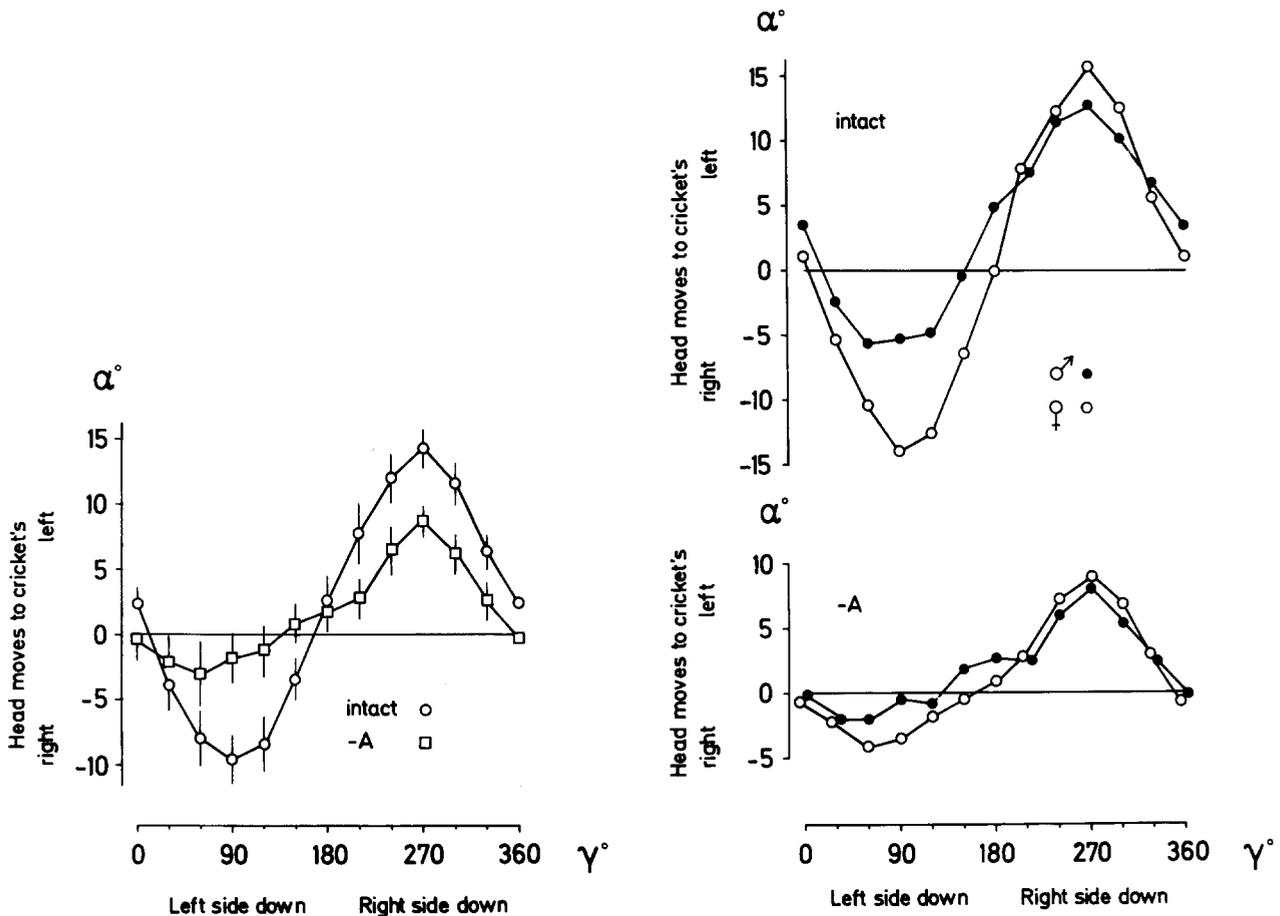
Fig. 4. Compensatory head movements of crickets during rotation around their longitudinal axis before (*intact*) and after amputation of both antennae (−*A*). α, γ see Fig. 2; *vertical bars:* SEM. *n* = 10; 5 male and 5 female crickets. − *On left side:* combined calculation of the mean response amplitudes; *on right side:* separate calculation of the mean response amplitudes for male (●) and female crickets (○). For intact males (females), the maximum value of SEM is ±2.9° (±3.9°), while in the operated groups SEM never exceeds ±1.4° (±1.8°)

is caused either by a specific linkage between peripheral proprioceptors controlling walking and gravity receptors, or by a facilitatory effect of central command neurones on interneurones of the reflex arc between the proprioceptive gravity receptor system of the legs and the motoneurones of the leg muscles. These neurones may also cause a general arousal. Similar mechanisms may also hold for the perception of gravity in crickets, but further experiments are necessary.

The compensatory head reflexes are elicited by two quite different types of gravity sense organs: first, the club-shaped sensilla of the cerci, and second, the antennae which, in contrast, to the first type, are probably a proprioceptive gravity receptor system. Both systems must be linked centrally, because they elicit the same reaction and their effects on the head movements are additive (Figs. 3 left, 4 left). The location of this connection is still unknown although there are hints that many neu-

rones in the mushroom-body area of the cricket (*Acheta domesticus*) brain are multimodal, with inputs originating in both the cerci and the antennae (Schildberger 1981).

The Cercal Gravity Receptors. The cercal gravity receptor system which is formed by the club-shaped sensilla differs considerably from all other gravity receptor systems known in terrestrial insects. While it is composed of cuticular sensilla, it is not a proprioceptive system like that found in many insect species (for references, see Horn 1983). As with statocyst-systems, the club-shaped sensilla are well-adapted for the reception of gravity. Bischof (1974, 1975) found that during the rotation of the animal the club-shaped sensilla are deflected from their normal position. The angle of this deflection depends sinusoidally on the animal's angle of inclination, as does the steady state response of single receptors. Hartman et al. (1979)
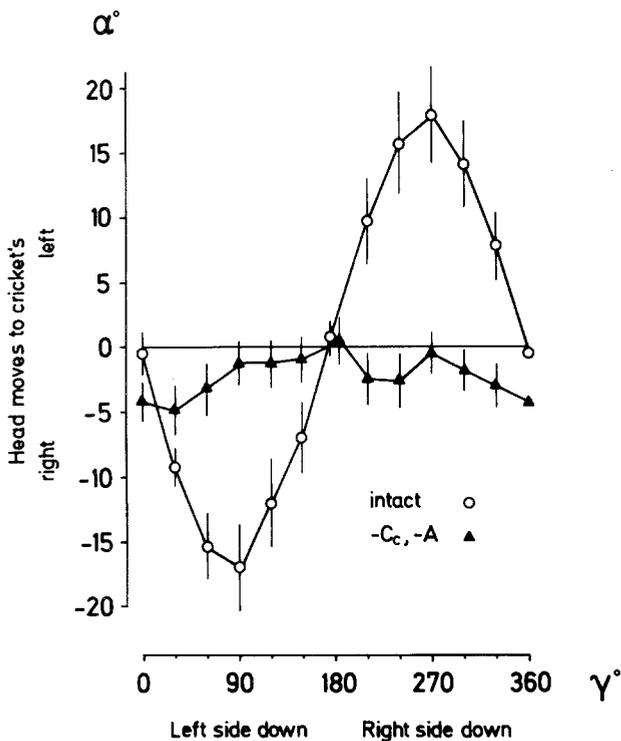
Fig. 5. Compensatory head movements of crickets during rotation around their longitudinal axis before (*intact*) and after simultaneous amputation of both cerci and antennae ($-C_c$, $-A$). α, γ see Fig. 2; *vertical bars:* SEM. $n = 13$; 5 male and 8 female crickets

described interneurones in the cockroach *Arenivaga* whose activity depends on the spatial position of the animal and which are driven by cercal sensilla. The advantage of this system is that it is less influenced by disturbances during walking which affect strongly the proprioceptive gravity receptor system in other insects. On the other hand, it appears that the club-shaped sensilla respond not only to static spatial positions but also to changes of position: these receptors have a strong phasic component at the beginning of a positional change (Bischof 1975). This means that the system may also function as a sense organ adapted to the perception of angular accelerations, and in this respect can be compared with the semicircular canals of vertebrates. Further behavioural experiments are necessary to elucidate this question.

The Antennal Gravity Receptor System. There is a large number of antennal receptors which influence behavioural reactions in the field of gravity. Certain receptors determine the sign of geotaxis (references, see Horn 1983), others distinguish only between up and down (Bässler 1971; Wendler 1965) or amplify response which are elicited by non-antennal gravity receptors (Horn and Lang 1978; Markl 1962). Finally, there are antennal gravity receptors as the scapus bristles of the fly, *Calliphora erythrocephala* (Horn and Kessler 1975) which elicit a response whose strength depends on the strength of the gravitational input.

We have found a second case of this type in the cricket, *Gryllus bimaculatus*. Crickets without cerci showed clear, albeit reduced compensatory head movements when they were rolled around their longitudinal axis, but this response disappeared after amputation of both antennae (Figs. 3, 5). We still do not know the location of the receptors. But supposing that passive deflections of the antennae caused by the field of gravity are responsible for the stimulation of gravity sense organs, those in the joint between scapus and pedicellus would seem to be suitable candidates. According to Honegger (1981), movements of the antennae in the animal's horizontal plane originate mainly in the joint between scapus and pedicellus, while movements in the animal's vertical plane originate in the joint between head and scapus. For rotations around the animal's longitudinal axis, passive deflections of the antennae from their normal position are only directly proportional to the roll angle γ of the animal, if measurement of the movements in the joint between scapus and pedicellus are taken into consideration.

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