PROPRIOCEPTIVE CONTRIBUTION TO DISTANCE ESTIMATION BY MOTION PARALLAX IN A PRAYING MANTID

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Summary

The behavioural experiments described here examined, in the praying mantis *Tenodera sinensis*, the manner in which the proprioceptive cervical hair plate sensilla are involved in the measurement of the distance to a jump target with the aid of motion parallax actively produced by translatory head motion. Various combinations of surgical deafferentation of the cervical hair plate sensilla had no influence on the linearisation of head motion. However, the measurement of relative and absolute distance and the jump frequency were impaired by these interventions. From the results, it is concluded that the cervical hair plate sensilla are involved in the distance measurement mechanism, probably by allowing the nervous system to compare retinal image motion with head motion.

Key words: praying mantis, mechanoreceptor, hair plate sensillum, distance estimation, motion parallax, vision, *Tenodera sinensis*.

Introduction

When an animal moves on a linear path, the image of an almost stationary object moves farther and faster on its eyes than does the image of a more distant object. It has, indeed, long been suggested that, in insects, side-to-side motion of the body (and thus of the eyes) might serve for estimating the distance to stationary target objects (Demoll, 1909; Baldus, 1926; for reviews, see Wehner, 1981, 1994). Wallace (1959) provided an early piece of direct evidence for this hypothesis in experiments on the so-called 'peering' behaviour of the desert locust (*Schistocerca gregaria*) by employing a simple trick. When the target object was shifted with or against the direction of the side-to-side motion of the head, the animal over- or underestimated the distance, so that its jumps to the object were too long or too short, respectively. The explanation that Wallace (1959) offered for this finding was that the motion of the object produced a smaller or greater image motion on the locust's eye than would be the case with a stationary object. The amount (speed) of image motion could thus convey information about the distance to the object. Sobel (1990) confirmed Wallace's results for *Schistocerca americana*. By employing modern video technology, he was able to demonstrate that locusts can estimate the jump distance by means of self-generated retinal image motion (see also Collett, 1978, 1996; Collett and Paterson, 1991).

Peering movements similar to those performed by the locust prior to jumping were also reported to occur in several species of mantids prior to reaching, with their foreleg, for a nearby object (Horridge, 1986, 1987). In a recent study, Walcher and Kral (1994) reported that, prior to jumping to a target, young larvae of the mantid *Tenodera sinensis* repeatedly executed spontaneous object-related movements of the type described above. When several objects were located at different distances in the visual surroundings of the animals, the animals were able to select the nearest object as a jump target with the aid of these head movements. In those experiments (Walcher and Kral, 1994), the range of the targets was outside the range of the stereoscopic vision of the mantid (Rossel, 1983; Collett, 1996; Kral, 1998), but it was not directly shown that image motion is involved in the distance estimation performance of the mantid.

To investigate this problem, Poteser and Kral (1995) examined the jumping behaviour of larval *T. sinensis* and *Polyspilota* sp. In contrast to the powerful leaps of locusts, mantid larvae jump only a few centimeters. Their jumps are thus linear rather than parabolic, and the probability of jumping beyond the object is small. Correspondingly, their estimation of distance seems primarily to provide information about the general reachability of an object, enabling the insect to determine which is the nearest object, and only secondarily establishing an appropriate jumping velocity (see Sobel, 1990). In fact, the animals can be deceived with respect to the reachability of an object. Jumps to an object lying within the optimum jump distance could be suppressed by moving the object simultaneously in the direction of the head motion of the animal. In contrast, by means of simultaneous contrary movement of the object, it was possible to trigger jumps

towards objects lying beyond the jump distance, which consequently failed. In the former case, it is the reduction in the amount (speed) of retinal image motion that gives the animal the impression of greater object distance whereas, in the latter case, an increase in the amount (speed) of image motion creates the illusion of a shorter distance to the object (see also Wallace, 1959; Sobel, 1990).

Poteser and Kral (1995) also addressed the question of the mechanism underlying the utilization of self-generated retinal image motion for distance estimation in mantids. They observed an increase in the average amplitude of head motion within a certain range of distances. However, it should be noted that this increase in the average amplitude was due to the increase in the minimum amplitude that more than offset the slight decrease in the maximum amplitude (see Kral and Poteser, 1997). Over this range of distances, the amount of image motion could be maintained above a critical level by increasing the minimal amplitude of head motion. The speed of head motion exhibited no such adjustments, but varied within certain limits. This distance-independence of the speed of head motion suggests that it could be the speed rather than the amount of image motion that is used to estimate the distance to the object. This presupposes, however, that the speed of head motion must be compared with the speed of image motion, which in turn would require a multisensory control system (a view already expressed by Horridge, 1986).

The aim of the present study is to clarify in *T. sinensis* the extent to which the cervical sensory hair plates, which are stimulated by the movements of the head described above, particularly in the yaw direction, are involved in the control of object-orientated swivel movements (i) to ensure that the head is displaced along a linear path, and (ii) to permit a comparison between the head motion and the image motion perceived when the animal peers at the target.

Materials and methods

We used young larval (second and third instars) praying mantids *Tenodera aridifolia sinensis* (Saussure) bred from eggs obtained from the Carolina Biological Supply Company, Burlington, USA (see Köck *et al.* 1993). The animals (body length approximately 1 cm) were kept under controlled laboratory conditions, with a daily cycle of light from 06:00 to 18:00 h, at 28 °C and at 70 % relative humidity.

Twenty-four hours before the behavioural experiments, after the animals had been anaesthetized with ethyl chloride, we performed surgery on the mechano-sensory sternocervical (SCH) and tergocervical (TCH) hair plate sensilla (Fig. 1) by severing the primary afferent nerves on one or both sides using micro-dissecting scissors. These interventions resulted in no discernible reduction in the freedom of movement of the joints or muscles in the region of the head or the limbs compared with those of intact animals.

For the experiment, we placed the animal on a round platform (2 cm in diameter) located in the middle of a uniformly illuminated (250 lx) white arena (22 cm across), surrounded by a white wall 20 cm in height (Fig. 2). The animal was presented with black, rectangular objects with a visual angle of 20 ° in width and 50 ° in height (measured from the centre of the platform), at distances of 30, 40 and 50 mm. The visual angle was held constant during the experiments, to rule out the possibility that the visual extension of the object could be used by the animals for distance measurement (see, for example, Cartwright and Collett, 1979; Lehrer and Collett, 1994). The height of the objects was adjusted so that the midpoint of the object was located at the average eye-level of the experimental animal. The angular distance between the objects was selected so that only one object at a time appeared in the visual field of the experimental animal. The animal usually turned towards each object and began to perform horizontal side-to-side movements of the head directed at its vertical edges (Fig. 3); it then chose the nearest object. This behaviour was recorded with a Sony video camera (DXC-151AP), displayed on a Sony PVM 144QM 14 inch colour monitor and recorded with a SVO9620P HiFi recorder. The data derived from the video analyses were evaluated with the aid of a graphics and statistics program by GraphPad Prism (San Diego, USA).

Results

How is the cervical proprioceptive system involved in the control of head motion?

Spatial relationship between head motion and the target object

Distance measurement with the aid of motion parallax presupposes a specific spatial relationship between the insect eye and the object. On the one hand, the visual distance must be held fairly constant during the entire measurement process; on the other hand, alterations in the visual angle between the object and the compound eye should be attributable as far as possible to parallax and not to any rotational movements of the animal. This can be achieved by exact linear steering of the head (and the compound eyes) in a horizontal plane ('linearisation') (Fig. 3).

The present findings show that this is, to a great extent, the case. As is evident from the relevant angle measurements, the head maintains its spatial orientation during the side-to-side movements by means of compensatory rotation about the yaw axis accompanied by simultaneous displacement of the entire body.

We now faced the question of whether, given the accuracy of movement coordination, simple control loops compare the angular positions of the prothorax and head, in which case the cervical sensory hair plates would be good candidates for providing the information needed.

To answer this question, we examined the positioning of the head during the side-to-side motion after unilaterally or bilaterally severing the primary afferent nerves of the SCH hair plates alone or of both the SCH and TCH hair plates (Fig. 1). The results are summarized in Fig. 4A–E. In both intact and deafferented animals, the magnitudes of the
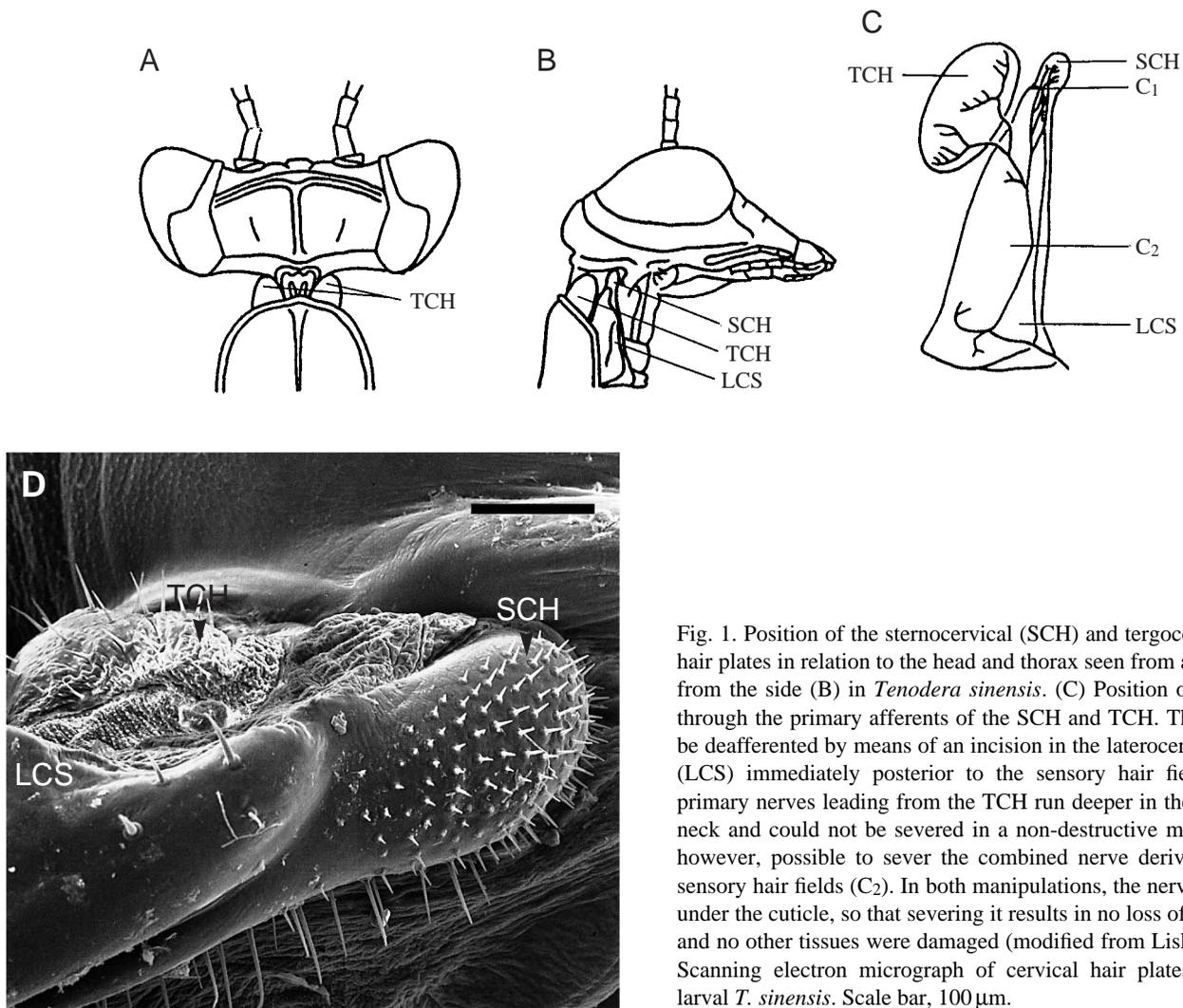
Fig. 1. Position of the sternocervical (SCH) and tergocervical (TCH) hair plates in relation to the head and thorax seen from above (A) and from the side (B) in *Tenodera sinensis*. (C) Position of the incision through the primary afferents of the SCH and TCH. The SCH could be deafferented by means of an incision in the laterocervical sclerites (LCS) immediately posterior to the sensory hair field (C_1). The primary nerves leading from the TCH run deeper in the tissue of the neck and could not be severed in a non-destructive manner. It was, however, possible to sever the combined nerve derived from both sensory hair fields (C_2). In both manipulations, the nerve lies directly under the cuticle, so that severing it results in no loss of haemolymph and no other tissues were damaged (modified from Liske, 1989). (D) Scanning electron micrograph of cervical hair plates in a young larval *T. sinensis*. Scale bar, 100 μm.

prothoracic angle ($\Delta\phi_p$) and the compensatory head rotation ($\Delta\phi_c=\Delta\phi_p\pm\Delta\phi_h$, with '+' denoting overcompensation) are strictly correlated. This finding suggests that the TCH and SCH hair plates provide little or no contribution to the linearisation of the head motion.

It remains to be investigated whether other mechanosensory sense organs (for example, stretch receptors on the cervical muscles or visual control) ensure the linearisation of head displacement (see Discussion).

Monitoring of head motion as an element in distance measurement

The variability of the magnitude of head motion during peering argues in favour of the idea that distance estimation by means of image motion requires information not only on the amount of image motion but, in addition, on the extent of head motion. In other words, because the amplitude as well as the speed of head motion (and therefore of image motion) during an individual peering movement are largely independent of the distance to the target, neither of these two parameters can provide reliable information about this distance unless head

motion is also measured and is compared with the perceived image motion.

The role that the cervical hair plate sensilla play in monitoring head motion was our next subject of inquiry. For this purpose, the deafferentations described above were carried out in various combinations in order to compare treated and intact animals with respect to their ability to reach a target object by means of an aimed jump.

The normal jump frequency does not alter substantially when only the SCH or both the SCH and TCH hair plates are eliminated on one side (Fig. 5). In the case of bilateral elimination of the SCH or of both types of hair plate, however, there is a dramatic and statistically highly significant drop in the jump frequency. In the case of bilateral deafferentation of the SCH and simultaneous unilateral deafferentation of the TCH, the jump frequency falls still further (Fig. 5). It is evident that the cause of this phenomenon is the additional asymmetry that results from the intervention. Assuming that willingness to jump to a target depends on whether the animal is able to estimate the distance to the target prior to jumping, these results suggest that
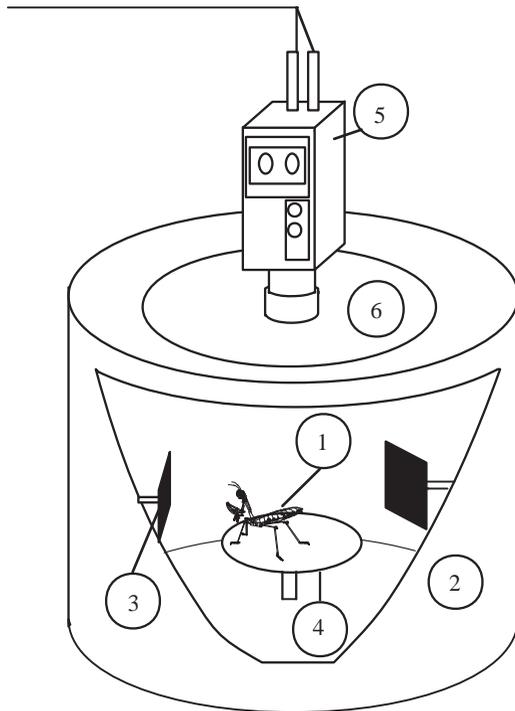
Fig. 2. Experimental arrangement (not to scale). A young larval *Tenodera sinensis* (1) was placed on a round platform (4) in the centre of a cylindrical arena (2) surrounded by a white wall 20 cm high. In each case, three black rectangular objects (3) were presented at fixed distances (30, 40 and 50 mm) from the edge of the platform. The experimental animal could reach the objects only by jumping, because the floor of the arena was covered with water. The experiments were recorded from above through a screen (6) by means of a video camera (5).

unilateral deafferentation does not impair distance estimation, whereas bilateral deafferentation does.

Comparing the accuracy of jumps under various conditions (Fig. 6), it emerges that, in the case of intact animals, more than 90 % of the jumps reach the target; after unilateral elimination of the SCH hair plates, the deviation from normal behaviour is not significant, and it is only weakly significant after bilateral elimination of the SCH. The relatively few jumps that miss the target are caused by landing too early so that the long legs just reach the edge of the target and the animal falls down. However, if both the SCH and the TCH hair plates are unilaterally or bilaterally destroyed, there is a dramatic and statistically highly significant increase in the proportion of missed jumps. The bilateral deafferentation of both hair plates gives rise to jumps that are on average 17±5.5 % (mean ± S.D.) (N=10 animals, n=15 jumps) too short, whereas in the case of the unilateral elimination of both hair plate afferents the jumps mostly miss the target to the side and they are on average 15±7 % (N=17 animals, n=57 jumps) greater than the target distance. The direction in which the animals miss the target depends on the site of the surgical intervention (Fig. 7). Animals with deafferentation of the left SCH and TCH hair plates jump to the right of the object,
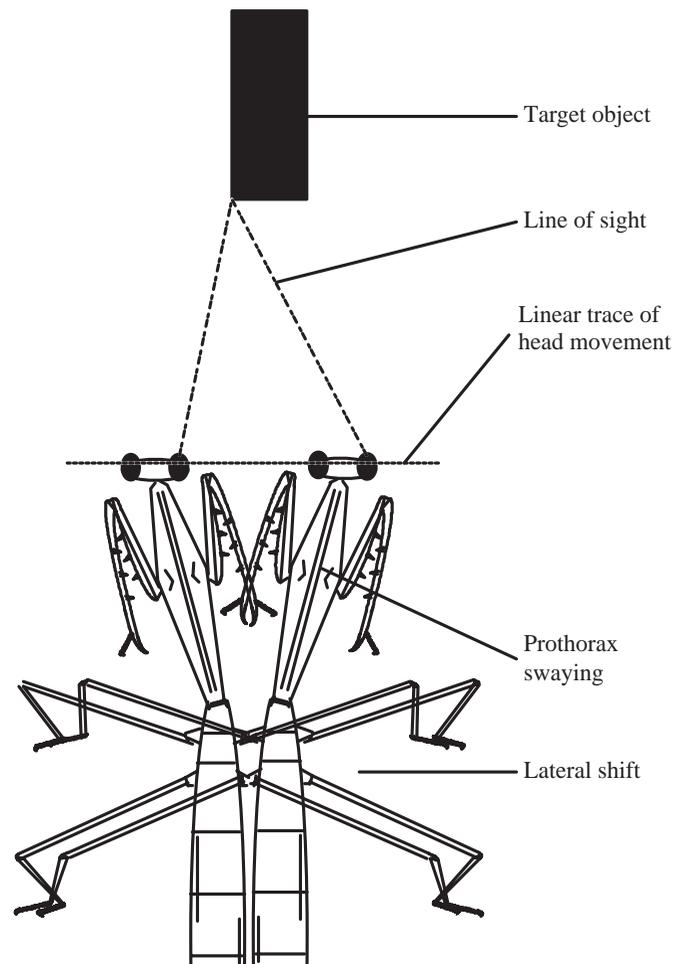

Fig. 3. Schematic representation of a typical peering motion of a praying mantis *Tenodera sinensis*. The distance travelled by the head between the starting point and the endpoint (or turning point) of its linear path is defined as the amplitude of the head motion. The deflection of the head is based on a lateral displacement of the body and, to a large extent, on a swinging motion of the prothorax. The linearisation of the head causes a change in the angle of incidence of the line of vision to the edge of a stationary object, the size of the change being dependent on the distance to the object. The magnitude measured by the underlying mechanism could be the speed at which the angle changes. In the event of variability of head motion, it would be necessary to monitor the speed of head motion to estimate distance.

whereas deafferentation on the right side results in jumps to the left of the target.

Apart from the experiments examining the capacity of the animals to estimate absolute distance (see above), we conducted a further series of experiments designed to examine their capacity to measure relative distance, e.g. to determine the nearest of three objects placed at different distances. The results are summarized in Fig. 8. In the case of three objects at different distances, more than 60 % of the decisions (twice as many as for each of the two more distant objects) are normally in favour of the nearest object. This value is not
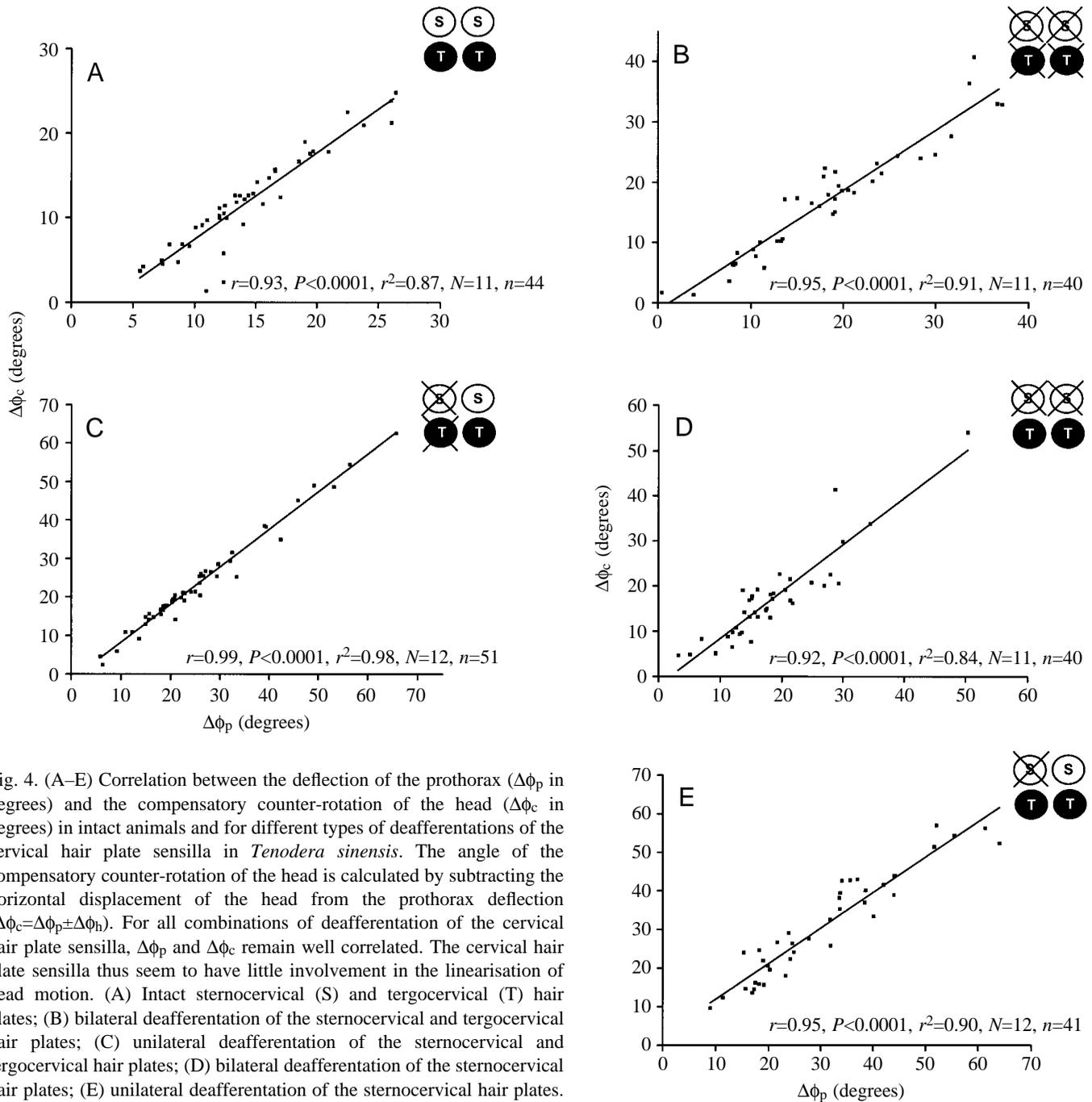
Fig. 4. (A–E) Correlation between the deflection of the prothorax ($\Delta\phi_p$ in degrees) and the compensatory counter-rotation of the head ($\Delta\phi_c$ in degrees) in intact animals and for different types of deafferentations of the cervical hair plate sensilla in *Tenodera sinensis*. The angle of the compensatory counter-rotation of the head is calculated by subtracting the horizontal displacement of the head from the prothorax deflection ($\Delta\phi_c = \Delta\phi_p \pm \Delta\phi_h$). For all combinations of deafferentation of the cervical hair plate sensilla, $\Delta\phi_p$ and $\Delta\phi_c$ remain well correlated. The cervical hair plate sensilla thus seem to have little involvement in the linearisation of head motion. (A) Intact sternocervical (S) and tergocervical (T) hair plates; (B) bilateral deafferentation of the sternocervical and tergocervical hair plates; (C) unilateral deafferentation of the sternocervical and tergocervical hair plates; (D) bilateral deafferentation of the sternocervical hair plates; (E) unilateral deafferentation of the sternocervical hair plates. It should be noted that the absolute magnitudes of the angles cannot be compared among the different types of intervention. The data do not originate from object-related head motions for objects at a uniform distance from the insect, but were collected using the standard experimental arrangement, with objects placed at three different distances to maximize the number of trials. The dependence of the amplitude of head motion on the particular type of intervention was examined separately. It was found that none of the types of intervention resulted in a significantly different amplitude of head motion from that observed in intact animals. *r*, Pearson correlation coefficient; *P*, significance against *r*=0; *r*^{2}, coefficient of determination; *N*, number of animals; *n*, number of events.

substantially altered by the loss of one or both of the SCH hair plates, or by the loss of the SCH and TCH hair plates on one side. However, when the functionality of all four hair plates is destroyed, distance discrimination breaks down. The inability to measure relative distance manifests itself in the fact that all three objects, regardless of their distance, are now chosen as jump targets with similar frequencies.

It should be noted that with uni- and bilateral deafferentation of the SCH hair plate an apparent, although not significant, improvement in the behavioural performance (both jump
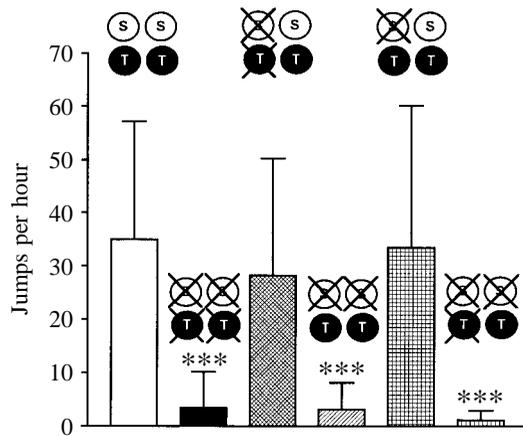
Fig. 5. Willingness to jump, in jumps per hour, of young larval *Tenodera sinensis* with intact neck hair plate sensilla or with various deafferentations of the hair plate sensilla. Bilateral deafferentation of the sternocervical (S) and tergocervical (T) hair plates or of the sternocervical hair plate results in a significant reduction in the willingness to jump, whereas unilateral interventions have no significant effect. $N=10–29$; $n=35–392$ (*t*-test). ***Significantly different from the value for intact animals, $P<0.0001$. Values are means ± S.D.
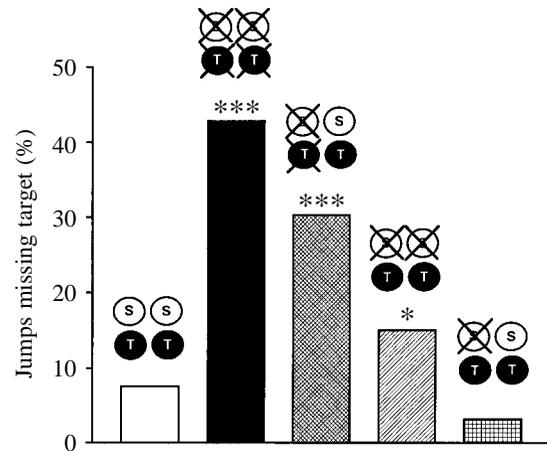

Fig. 6. Percentage of jumps that missed the target among young larval *Tenodera sinensis* with intact cervical hair plate sensilla and with various deafferentations. In the case of bilateral deafferentation of the sternocervical (S) and tergocervical (T) hair plates, the tendency to miss jumps increases to over 40 %, with jumps that are too short predominating. Unilateral deafferentation of the sternocervical and tergocervical hair plates also results in a significant increase in missed jumps. Here, however, jumps that miss laterally predominate. The direction of the deviation is dependent on the side on which the intervention occurred. Bilateral deafferentation of the sternocervical hair plates has a small but significant influence on the tendency to miss jumps; unilateral deafferentation has no effect. $N=10–29$; $n=35–392$ (Fisher exact test). Asterisks indicate a value that is significantly different from the value for intact animals, *$P<0.05$; ***$P<0.0001$. Values are means ± S.D.

quality and preference for the nearest object) is observed, compared with intact animals. This slight improvement may arise from a decrease in the tendency to jump that is induced by the surgical intervention. Prior to each jump, longer and more frequent head movements are performed by treated animals than is the case with intact animals. If the behavioural performance is otherwise unimpaired by the intervention, this could lead to a slightly improved performance.

Discussion

Control of the linearisation of head motion

From Fig. 4, it is clear that linearisation (i.e. compensatory rotation of the head in the yaw direction) remains well-coordinated with the deflection angle of the prothorax even after uni- or bilateral deafferentation of the SCH and TCH hair plates. Thus, the cervical hair plates play no role in the control of head rotation during peering. It is probably safe to rule out any role for the scattered hairs located beyond the hair plates or for the precoxal hair field, situated relatively far from the neck, which could be indirectly stimulated through a displacement of the laterocervical sclerites. In both cases, the small number of sensilla involved does not appear to be suited to allow such fine coordination of the positioning of the joints. However, a possible contribution from cervical muscle receptors cannot be ruled out (Weevers, 1966*a*,*b*; Shepheard, 1973; Heckele, 1994).

Another possibility to explain the lateral linearisation would be the visual control of head motion, as has been proposed for locusts by Collett (1978). According to this model, linearisation is achieved by moving the head along a path that produces no image motion in the lateral region of the
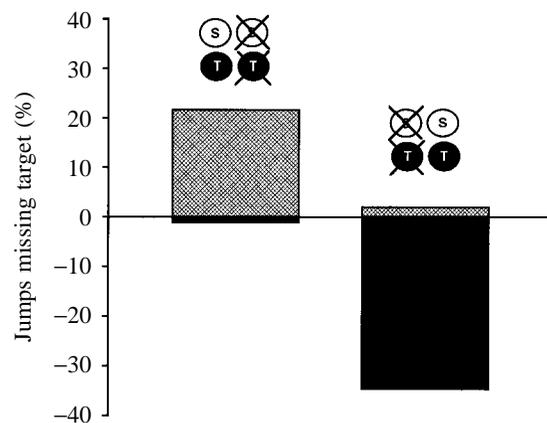

Fig. 7. Percentage of missed jumps by young larval *Tenodera sinensis* after unilateral deafferentation of the sternocervical (S) and tergocervical (T) hair plates. Positive values indicate jumps that missed to the left of the edge of the object, negative values those that missed to the right of the object. Elimination of the functionality of the afferents of the right-hand pair of sensory hair plates ($N=12$, $n=49$) results primarily in jumps that miss to the left of the object, and *vice versa* ($N=17$, $n=171$).

compound eye, i.e. the region oriented in the direction of head motion. In the praying mantis, the possibility of visual control is supported by the finding that the animal succeeds in adapting
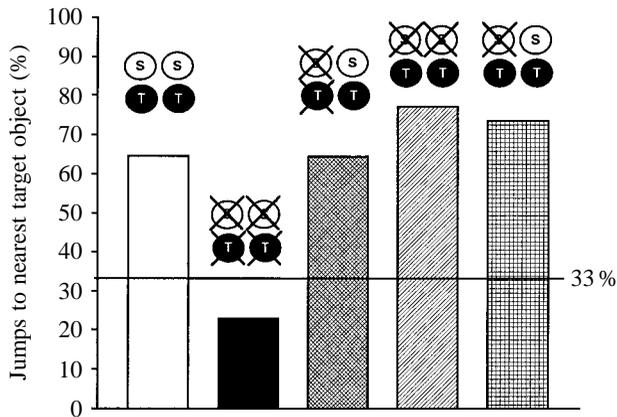
Fig. 8. Percentages of young larval *Tenodera sinensis*, some with intact hair plate sensilla and some with various deafferentations, preferring the nearest of three jump targets, located at different distances from the insect but having equal angular extents. An equal number of jumps, with no preference, is taken as the reference point (0=33.3% of the jumps). Only in the case of bilateral deafferentation of the sternocervical (S) and tergocervical (T) hair plates does the preference fall to a value of −10% (=23% of the jumps) compared with a value of 33% (=66% of the jumps) in controls and other deafferentation treatments. The tendency to prefer the nearest object is a very stable type of behaviour pattern for praying mantis larvae. The breakdown of this behaviour pattern strongly indicates that deafferentation affects the estimation of distance to the target. N=10–29; n=35–392 (Fisher exact test).

the way it moves to the peering situation. In the case of visual control, head movement can be regarded as the expression of a program for regulating lateral head motion, a program that would be substantially more flexible than one that simply coordinated the positioning of the body joints (see also Lehrer, 1994). However, at variance with the model proposed by Collett (1978) for locusts is the fact that mantids are clearly able to perform appropriate head movements in the absence of contrast boundaries in the lateral region of the compound eye or with laterally lacquered compound eyes (Walcher, 1994). An alternative would be a visual mechanism using the frontally situated object as a reference to achieve linearisation of the head. Such a mechanism would ensure linearisation by monitoring any alternation in the temporal activation pattern of neighbouring ommatidia resulting from deviations of the head movement from a linear path. In the case of the markedly forward-pointing compound eyes of the praying mantis, differences in the velocity profile brought about by rotation of the head (about the yaw axis) would be expected to be particularly emphasized by the foveal specialization of the frontal region of the eyes.

Monitoring head motion as an element in distance measurement

It has been shown that, with the aid of retinal image motion brought about by head motion, the praying mantis can measure relatively small differences in the distance to target objects

(Walcher and Kral, 1994; Poteser and Kral, 1995). This holds true even though the speed and amplitude of head motion are variable. Within the jumping range, the speed of head motion displays no dependence on the distance to the object and, although the average amplitude of head motion increases with the distance to the object, this increase is almost exclusively attributable to an increase in the minimum amplitude (Kral and Poteser, 1997). Despite the variability of head motion, the speed and/or amount of image motion seem to play a key role in the measurement of distance (Collett, 1978; Sobel, 1990; Poteser and Kral, 1995). The adaptation of the minimum amplitude of head motion suggests that the speed, rather than the amount, of image motion is the decisive parameter in distance measurement (Kral and Poteser, 1997). Whichever is the case, either parameter can be used for distance measurement only if head motion is also monitored.

The present study provides evidence for the importance of the proprioceptors in the neck region for estimating distance by head motion. Eliminating the functionality of all four cervical hair plates not only impairs the quality of the jumps dramatically (Fig. 6) but is also accompanied by an inability to determine the nearest target object (Fig. 8). It should be noted that the latter phenomenon cannot reflect any influence on the mechanical processes involved in jumping, and therefore it indicates an impairment in the system that controls peering motion. Moreover, the proprioceptive information from one side of the neck appears to be sufficient to allow an estimation of distance.

Although the importance of the proprioceptors in the neck region for measuring distance with the aid of head motion appears clear, the question remains as to which parameter is determined during head motion: amplitude, speed or both. Considering the possibility discussed above of the involvement of the speed of image motion, measurement of the speed of head motion appears probable.

In this context, the question arises as to whether the cervical hair plate sensilla are able to respond to the dynamic component of head motion. The cervical hair plate sensilla in the praying mantis, like most of the proprioceptors of this type investigated so far, represent static and dynamic stimulus magnitudes in their responses, and thus they constitute proportional and differential receptors (Mittelstaedt, 1957, 1962; Liske and Mohren, 1984; McIver, 1985; Liske, 1989). In addition, as has been discussed by some authors (Schwartzkopff, 1964; Spencer, 1974), information about the speed of head motion can presumably also be extracted from the chronological sequence of stimulation of the individual sensilla of one or more cervical hair plates.

Control of the direction of the jump

Although, in mantids, unilateral proprioceptive input monitoring the amount of head motion seems to suffice for accurate estimation of distance on the basis of the speed of image motion perceived relative to the target, bilateral information from at least the TCH hair plates seems to be necessary for a correct body alignment before the jump to a

target object. Such alignment of the body is required because, during head motion, the body axis may not be directed towards the object, and mantids only leap straight ahead. During the alignment movement, the head remains stable in its position, and the body is brought into line with it. Unilateral deafferentation leads to an asymmetry in this process, resulting in a jump that deviates in the direction of the untreated propriosensory side (Fig. 7). This effect has also been described in other bilaterally organized sensory control systems (Mittelstaedt, 1950; Schildberger and Kleindienst, 1989).

Interactions between visual and proprioceptive systems in the control of peering behaviour

We propose that the determination of the speed of the apparent image motion is based on visual input. It is not yet clear whether and in what manner visual information contributes to the linearisation of head motion (see above, Collett, 1978; Walcher and Kral, 1994). Considering the proprioceptive aspect, we propose that the sensilla of both cervical hair plates (SCH, TCH) contribute to the monitoring of head motion (speed). However, unilateral proprioceptive input seems to suffice for the estimation of distance. The individual functions of the sensory system may complement one another. The relationship is such that the linearisation of head motion enables the absolute distance to a target to be estimated on the basis of a comparison between image motion (speed) and head motion (speed). The TCH hair plates may also play a role in the control of jump direction.

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