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The regulation of distance to dummy flowers during hovering flight in the hawk moth *Macroglossum stellatarum*

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Abstract. 1. While collecting nectar in hovering flight the European hawk moth *Macroglossum stellatarum* efficiently regulates its distance relative to flowers that are shaken by wind. This can be demonstrated in laboratory experiments by moving dummy flowers (blue cardboard disks) towards and away from the feeding animal (Fig. 1).

2. Distance regulation is predominantly mediated by visual cues. Mechanoreceptors on the proboscis appear to contribute little to the response.

3. Movements of dummy flowers can be simulated by expanding and contracting a pattern projected onto a screen. With this technique we investigated the dynamical properties of the servo mechanism underlying distance regulation. The system behaves as a bandpass filter with corner frequencies of 0.15 and 5 Hz (Figs.2,3).

4. When a high-speed ramp-like movement of the flower is simulated, there is an asymmetry in the response. During simulated approach the reaction is phasic-tonic with a pronounced overshoot at the beginning, during simulated retraction it remains tonic (Fig.5B,C).

5. During distance regulation the animals compensate for the speed of the edge of the projected pattern. Distance regulation improves substantially when the number of stimulated elementary movement detectors is increased through increasing the number of contour lines by projecting concentric rings instead of a homogeneous disk (Figs.7, 8).

Key words: Hawk moth – Hovering flight – Distance re gulation – Speed compensation

Introduction

Foraging hawk moths (*Macroglossum stellatarum*) collect nectar while hovering in front of flowers. Due to the high energy demand, they have to visit daily about 1000–1500 flowers (Pfaff 1991). In the field the animals can be observed to switch very quickly from flower to flower, where they come to a stop just in the right distance in order to reach the nectarium with the proboscis. In previous laboratory experiments evidence was obtained that during their approach to a feeder hawk moths are likely to perceive distance by means of binocular stereopsis (Pfaff and Varjú 1991). Due to the low spatial resolution of their compound eyes and to the short interocular distance stereoscopic depth perception only works at short range in insects (Burkhardt et al. 1973). Nevertheless, the praying mantis has clearly been shown to use stereoscopic cues in distance estimation (Maldonado and Rodriguez 1972; Rossel 1983).

Depth perception by means of motion parallax appears to be, on the other hand, rather common in insects (Collett 1978; Erikson 1980; Lehrer et al. 1988; Sobel 1990; Collett and Paterson 1991), and there is evidence that under certain circumstances also *Macroglossum* makes use of it (Pfaff and Varjú 1991).

Since hawk moths do not land on the flowers, they have to regulate their spatial position relative to the blossom whenever it is shaken by wind. In laboratory experiments we investigated how well *Macroglossum* performs when a (dummy) flower is moved towards and away from the animal. Since in this situation the animals have to control distance, we asked what cues are involved. Beyond stereopsis and motion parallax the task can visually be performed by keeping the angular size of the flower constant such as male hoverflies do while chasing a female (Collett and Land 1975) or by compensating for the angular speed of its border line or other contour lines on its surface. Our main question was which of these visual cues are involved in distance regulation and what are the properties of the underlying control circuit.

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Along with vision, mechanoreceptors on the proboscis might provide sensory input. The proboscis of the animals carries sensory structures, some of which are very likely mechanoreceptors (Zhou 1991). They might be stimulated by friction and signal that the flower is moved towards or away from the animal. We shall deal briefly also with this question.

The results have in part been published previously in a preliminary form (Varjú and Farina 1993).

Material and methods

The European hawk moth *Macroglossum stellatarum* (Sphingidae, Lepidoptera) inhabits the southern parts of the continent, predominantly the regions around the Mediterranean. The larvae feed exclusively on bedstraw (*Galium* sp.). During the summer the moths migrate to the north of Europe. We succeeded in breeding them in the laboratory. Adults live up to 6 months. Since bedstraw is available during the entire year in our region, and since the animals have no diapause, they reproduce in our laboratory culture also during the winter. The day-active animals are, thus, available at any time during the year. To avoid inbred animals, we restart the colony from time to time with animals caught in the field. The animals are kept in flight cages measuring around 2.5 x 2 x 2.2 m, illuminated during the day from above and from the side by fluorescent tubes. They are fed on a 20–25% weight to weight honey or sucrose solution. At this concentration the compensatory response has its maximum (Farina and Josens 1993).

The experiments were carried out either in the flight cages or in smaller cages measuring 0.8 x 0.8 x 0.8 m. The moths accept almost any object as source of nectar, but they prefer blue disks with diameters ranging from 0.6 to 6 cm. (Regarding the preference of *Macroglossum* for shape and color of flowers see also Knoll 1922): In the center of the dummies an unlimited flow of honey solution is provided through a tube (inner diameter 2 mm). In contrary to natural food sources which are emptied within a few seconds, the animals sometimes keep feeding for over 1 min at the dummies.

In one set of experiments we used cardboard dummies which could be moved towards or away from the animal, that is disk and tube, either by hand or by means of a X–Y-recorder. It was also possible to move only the disk, while the tube remained stationary. In a second set of experiments we projected a blue disk or concentric rings onto a screen with a zoom lens. A tube with unlimited honey solution opened in the center of the projected pattern. The animals accepted these projected disks as dummy flowers. Movements towards and away from the animal were simulated by expanding and contracting the pattern by moving the zoom with an electromotor. This technique allows one to simulate periodic movements of a flower at high frequencies. It should be noted that zooming not only changes the size of the pattern but also its brightness. Control experiments revealed, however, that there is no systematic response of the animals to variation of the brightness of the projected patterns.

During the experiments the animals were videotaped from below with a properly aligned camera. The distance of their base of the proboscis to the screen was evaluated with 20 to 160 ms sampling rate and stored in a PC for further processing. Some additional remarks on methods, especially regarding data evaluation, will be given when presenting the results.

Results

The efficiency of distance regulation

We tested the efficiency of distance regulation by moving the cardboard disk together with the artificial nectarium in a ramp-like fashion towards and away from the animal. The speed of the dummy was about 3 cm/s, and the peak to peak amplitude varied between 0.5 and 3.5 cm. Figure 1A shows a sample record of the dummy position and that of the base of the proboscis over time. It demonstrates that the animal follows the movement of the dummy quite accurately. The small-amplitude oscillations of the animal's position is not a part of the response. This kind of positional jitter is always observed in hovering *Macroglossum* (Pfaff 1991; Zhou 1991).

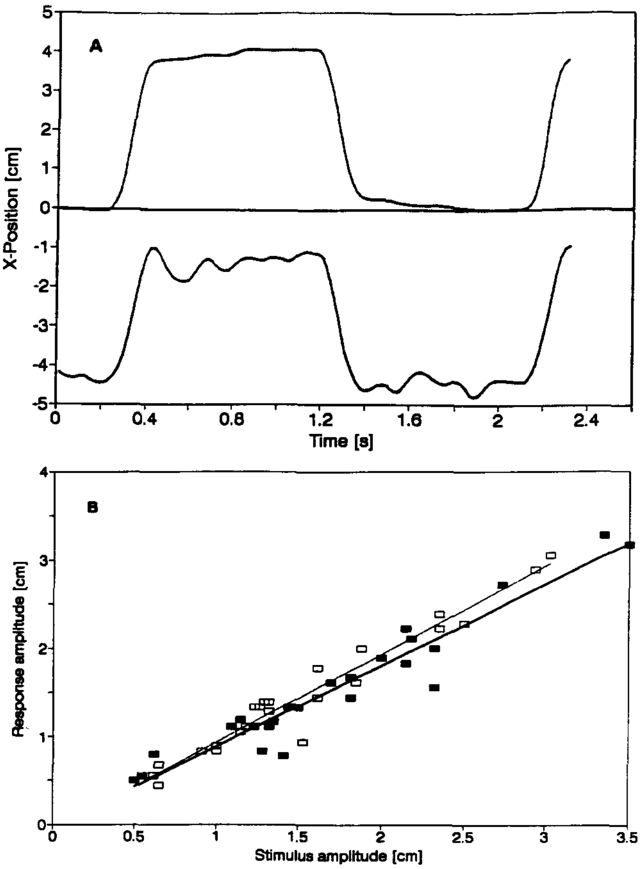

Fig. 1. A Sample record of the response of a hawk moth to ramp-like movements of a dummy flower, a blue cardboard disk. Position of the dummy (*top trace*) and that of the base of the proboscis (*bottom trace*) versus time. The small amplitude oscillation is not part of the response (cf text). **B** Response amplitude plotted over the stimulus amplitude for dummy movements towards (*empty rectangles, thin line*) and away from the animal (*filled rectangles, thick line*). The gain is constant within a considerable amplitude range. The slopes of the regression lines differ slightly, but the difference is statistically not significant

Response versus stimulus amplitudes for dummy movements towards (empty rectangles, thin line) and away from the animal (filled rectangles, thick line) are plotted in Fig. 1B. The relations are linear, which means that the underlying feedback servo mechanism has a constant closed loop gain, defined as the ratio of response to stimulus amplitude. There is, however, a slight asymmetry in the response. The gain is 0.999 when the dummy is moved towards, and 0.920 when it is moved away from the animal. The difference is, however, statistically not significant (Fs = 0.0865, df = 48, slope comparison test: NS). The correlation coefficients are 0.98 ($P<0.001$) and 0.96 ($P<0.001$), respectively.

When we moved only the cardboard disk and kept the nectar tube stationary, the reponse was only slightly weaker. The relations are again linear, and the closed loop amplification is indeed reduced, but only to 0.920 during movements of the dummy towards and to 0.839 during movements of the dummy away from the animal. The correlation coefficients are 0.97 ($P<0.001$) and 0.96 ($P<0.001$), respectively. In this situation the visual input and possible mechanosensory messages from the proboscis contradict each other. If mechanoreceptors were playing a significant role, we would expect the response to the movement of the disk to be substantially reduced. These experiments were carried out within the amplitude range of 1 to 4.5 mm. We conclude that mechanosensors on the proboscis play a negligible role in distance regulation.

The dynamical properties of distance regulation

To investigate the dynamics of the distance regulation we projected blue disks onto a screen and sinusoidally varied their diameter. Figure 2 shows 3 sample records obtained with different stimulus frequencies. Especially at higher stimulus frequencies the response curve frequently drifts or jumps and its amplitude can vary substantially from cycle to cycle (Fig. 2B)

In the Bode-plots in Fig. 3 average gain values are presented together with the standard errors of the means, for 4 to 6 animals. The gain was calculated as the ratio of the response amplitude along a line perpendicular to the screen during one stimulus cycle to the amplitude of calculated displacement which would have been needed to keep the apparent size of the dummy constant.

The gain has a broad plateau between about 0.15 and 5 Hz (Fig. 3A) and a steep drop-off at high, and a shallow one at low frequencies. In the plateau region the gain amounts to about 0.7, a value which is considerably lower than that obtained with cardboard discs moved in a ramp-like fashion (Fig. 1B).

The reduction of gain at both high and low frequencies indicates that the closed-loop feed-back circuit has band-pass properties. The true high frequency response of the postulated band pass filter is distorted by a further behavioural component. When confronted with cardboard disks a considerable number of animals leaves whenever the dummy starts to oscillate with a frequency of 4.5 Hz or more (Zhou 1991). In our experiments with projected patterns several moths continued feeding at pattern oscillation up to 10 Hz. However, they do not respond to every cycle of the simulated flower movement at these frequencies (Fig. 2C). The dropout increases with increasing frequency (Table 1), which makes the calculation of average response amplitudes and phase shift problematic. We used only complete response cycles, indicated by horizontal lines in Fig. 2C, to calculate these values.

In the low frequency range there is another kind of problem. At 0.05 Hz, for example, one period lasts for 20 s, and the animals continue drinking only in exceptional cases for 2 or 3 periods, making data acquisition tedious. It is, therefore, unknown, whether the gain would continue to drop at untested lower frequencies as one would expect in the case of a true band-pass response, or whether it remains constant indicating a proportional response component.

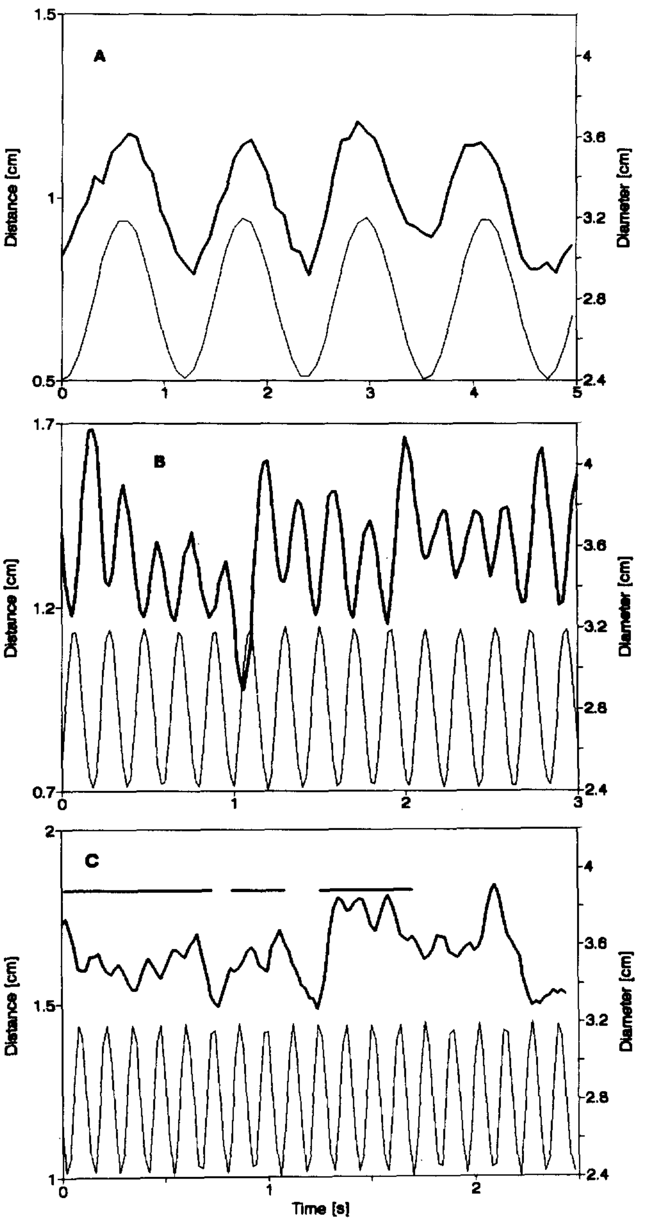

Fig. 2. Sample records obtained with 3 animals (**A–C**) demonstrate that the movement of a flower towards and away from the animal can be simulated by expanding and contracting a projected blue disk. *Lower* (*thin*) *trace*: Diameter of the projected disk (range of variation 2.4 to 3.2 cm). *Upper* (*thick*) *trace*: The distance of the base of the proboscis to the projection screen. *Frequencies*: **A** 1 Hz; **B** 5 Hz, **C** 8 Hz. Note that at high oscillation frequencies the animals do not respond to every stimulus cycle (**C**, response cycles indicated by *horizontal lines*)

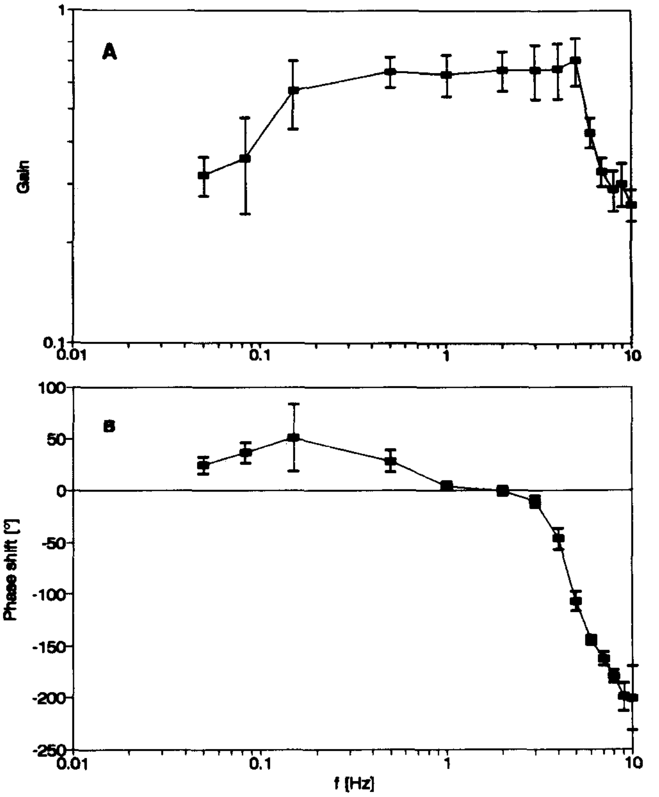

Fig. 3A, B. Bode plot of the animal's response to expanding and contracting projected discs. Average gain ±SE (**A**) and average phase shift (**B**) versus stimulus frequency. The disk diameter varied from 2.4 to 3.2 cm. Data obtained with 4 to 6 animals

Table 1. The number of response periods in percentage (% P) of the stimulus periods as a function of the stimulus frequency f[Hz]. %P is 100 from 0.05 Hz to 4.0 Hz and decreases thereafter as shown

f[Hz]:	5	6	7	8	9	10
%P:	87.5	67.9	56.5	35.0	31.8	23.8

The results presented in Fig. 1B indicate that there might be differences in the responses to approaching and retracting flowers, even if the deviation of both slopes is statistically not significant. Such differences became apparent when we increased the velocity of ramp-like stimuli, as documented in Figs. 4 and 5. The response to simulated approaches becomes more and more phasic-tonic with increasing speed. There is a pronounced overshoot at the beginning of expansion, whereas the response to simulated retraction remains tonic. Frequently these properties are masked by a drift, usually toward the disk, as in Fig. 4B. We, therefore, first eliminated drift before calculating average values for the curves shown in Fig. 5. Moreover, since we wanted to document the time course of the responses, we shifted the data along the ordinate so that their average values coincided during the period to simulated retractions. This procedure does not influence the overall average values (thick lines in Fig. 5), but leads to a more informative standard error with respect to the time course of the responses.

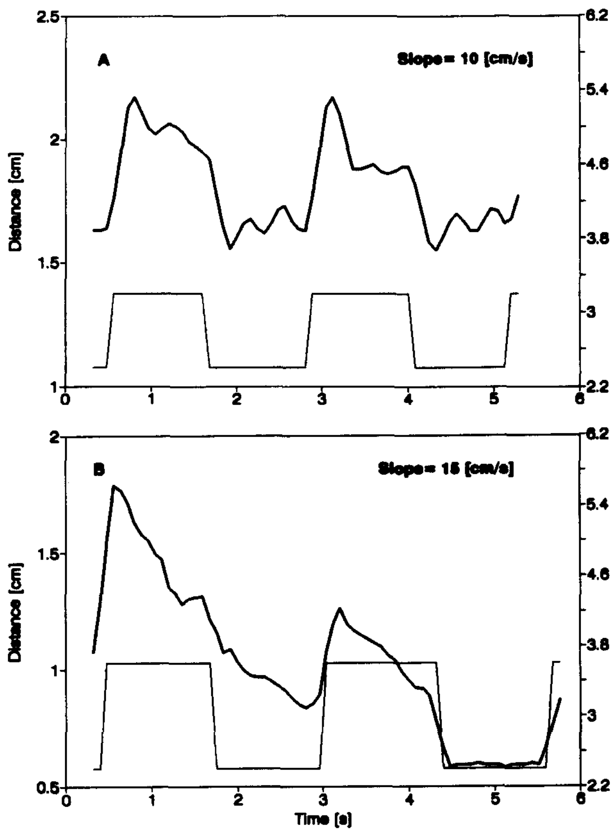

Fig. 4A, B. Sample responses to ramp-like expansion and contraction of projected disks with relatively high speed (cf Fig. 1). *Thin lines*: diameter of the projected disk; *thick lines*: position of the base of the proboscis. As the slope of the ramp becomes steeper, there is an overshoot in the reaction to the expansion (**A**). Frequently there is also a considerable drift, as a rule towards the projection screen (**B**)

The influence of the angular size of the pattern

If the animals used stereoscopic cues for distance regulation one would not expect the gain to increase with increasing size of the pattern. On the contrary, with increasing diameter of the projected disk the border comes to lie outside the binocular visual field and, consequently, stereoscopic distance perception becomes impossible. To test this we varied the mean diameter of the projected disc and kept the stimulus amplitude constant at 0.6 cm (peak to peak). The results are shown in Fig. 6. They demonstrate that the gain increases considerably, when the mean diameter of the pattern is increased from 1.1 through 1.9 to 2.7 cm.

Structured versus homogeneous patterns

We interpret the finding presented in the preceding section as indicating that more elementary motion detectors (EMDs) are stimulated during the oscillation of a large disc than during that of a small one. According to this hypothesis the response would be the result of spatially integrating the outputs of the EMDs to produce a motor

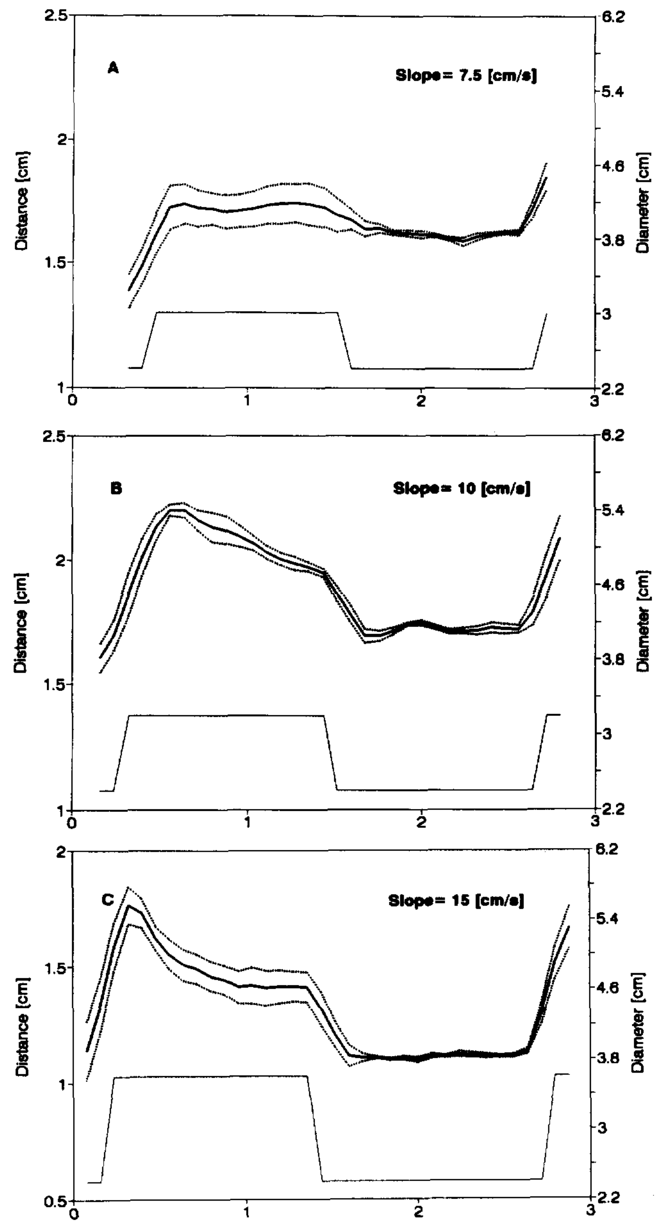

Fig. 5. Same as in Fig. 4, but averaged over 6 (**A**), respectively 5 periods (**B**, **C**). *Thick lines* represent the average response, *dotted lines* the standard error, and the *thin lines* stimulus. The overshoot in the response is the more prominent the higher the speed of expansion

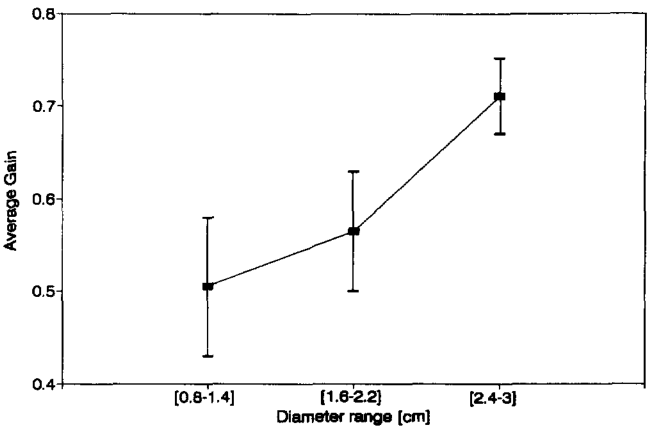

Fig. 6. Average gain SE ± versus mean diameter of the projected disk. Oscillation amplitude 0.6 cm (peak to peak), frequency 2 Hz. Data obtained with 4 to 6 animals

command. The number of stimulated EMDs can also be increased by increasing the number of contour lines in the pattern. We therefore replaced the homogeneous disk by concentric rings within the same surface area. The sample records in Fig. 7 demonstrate how the response amplitude increases when the number of border lines is changed from 1 to 8. We varied the number of rings from 1 to 32, thus offering 2 to 64 contour lines. In Fig. 8 the gain is plotted over the number of border lines for 2 stimulus frequencies. As expected, the closed loop gain indead increases up to 8 border lines and actually reaches values at or even slightly over 1 around 2 Hz oscillation frequency. The gain decreases with patterns that contain more contours, presumably due to the limited spatial resolution of the eyes.

Discussion

The effectivity of distance regulation and the role of mechanoreceptors

Our results reveal that *Macroglossum* regulates its distance towards moving dummy flowers very efficiently, predominantly by means of visual cues. Mechanosensors on the proboscis contributed only little to the response in our experiments. When only the cardboard disk was moved and the artificial nectarium was kept stationary, the gain was reduced by just 6%. This finding has to be interpreted cautiously however. We know little about the surface properties of natural nectaria, where the friction between wall and proboscis might be quite different from that in our plastic tube. Pilot experiments in which the surface quality of the material contacted by the proboscis was varied, however, gave no clear-cut results (Zhou 1991). Similarly the viscosity of nectar in natural sources might differ from that of our honey solution and play a role during distance regulation. Farina and Josens (1993) have demonstrated that the gain of the closed loop indeed depends on the profitability of the source.

The visual cues

As far as visual cues for distance regulation are concerned we think that our results rule out the following ones: 1. Binocular stereopsis. 2. Motion parallax. 3. Angular size. The arguments against the involvement of these cues are:

1. If hawk moths were to use stereoscopic cues we would not expect the gain to depend on the size of the pattern and on the number of border lines contained in it. One could, of course, object that the change of absolute

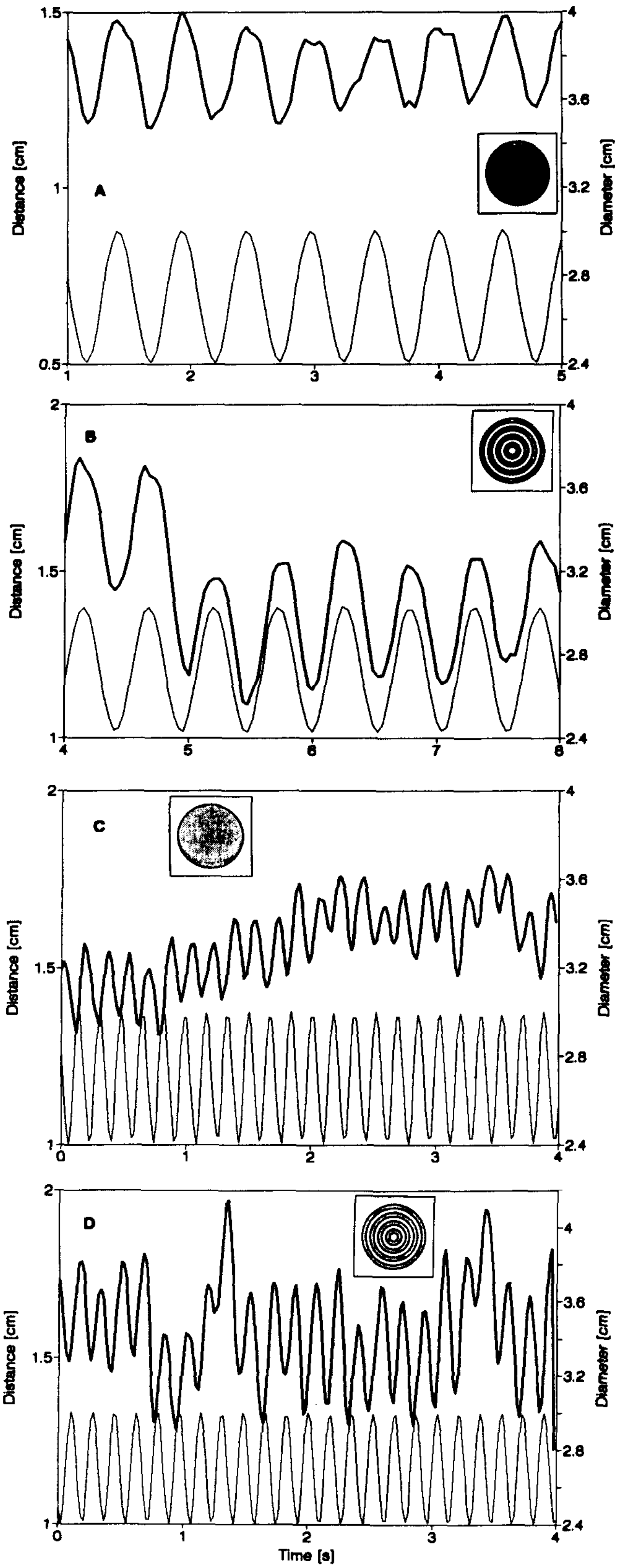

Fig. 7. Sample records obtained with four animals demonstrate how the response amplitude increases when the number of contour lines is increased from 1 (**A**, **C**) to 8 (**B**, **D**). Disk diameter oscillated between 2.4 and 3 cm. Frequency: 2 Hz in **A** and **B**, 6 Hz in **C** and **D**

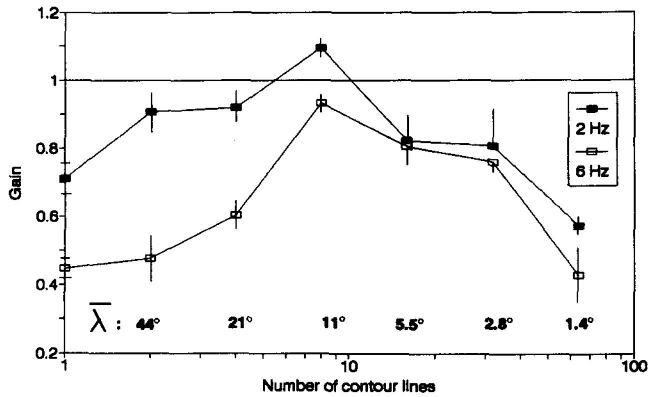

Fig. 8. Average gain versus number of border lines in experiments with projected concentric bright and dark rings. Lambda is the average spatial wavelength of the pattern

distance can be detected more reliably when numerous ommatidia are involved. But stereopsis is only possible within the binocular field of vision. In *Macroglossum* the extent of the binocular field is 25° at about 60° below the eye equator (Frantsevich and Pichka 1976). Recently, Bartsch and Warrant (personal communication) found a binocular overlap of 30° at elevations of 30° to 50° below the eye equator. The dummy is seen by feeding animals at an elevation of 30° or more below the eye equator, since their longitudinal body axis is slanted by 30° relative to the horizontal during hovering flight. However, at a mean distance of 1.4 cm borders only provide binocular cues if they are separated by 0.6 to 0.8 cm. The borders of most of the patterns we used were well outside of this range. With further increasing dummy diameter less and less receptors will be stimulated in the binocular visual field. The gain, however, increases (Fig. 6).

Increasing the number of border lines by projecting concentric rings instead of a homogeneous disk might lead to an increased gain because border lines come to lie within the binocular visual field. This is, however, the case only with two rings (4 border lines). In this case the angular extent of the innermost border line is 27°. But the gain considerably increases when the homogeneous disk is replaced by a single ring, the inner border of which is outside the binocular field of vision.

2. We can rule out motion parallax at the border of dummies as a cue to distance perception since we used projected disks. We can, of course, not exclude that under natural conditions motion parallax contributes to the response. This would at least partially explain, why the highest gain obtained with real disks is larger (0.999, Fig. 1B) than that obtained with projected disks (0.7, Fig. 3). The animals saw the cardboard disk against plenty of background contours. There is still the possibility, however, that animals perceive the relative motion produced by their own movement. In addition to the spontaneous and periodic distance modulation (Fig. 1) the animals also move up and down, and occasionally pivote around a vertical axis. There is evidence that under certain conditions the animals do, in fact, utilize motion parallax. In a simulated patch of flowers in front of a structured background, the animals prefer those dum-

mies that are further away from the background (Pfaff and Varjú 1991).

3. Our arguments against angular size as a cue to distance are, admittedly, rather indirect. They are partially based on the dynamics of the response. For a start, it would be hard to explain, why the gain drastically decreases after lowering the oscillation frequency for example from 0.2 to 0.1 Hz. Further evidence against the constant angular size hypothesis has been presented by Pfaff (1991). He used the stop of a photographic camera as a projected disk, the diameter of which could be changed rapidly by a trigger mechanism. It changed at a speed of 40 cm/s. This was more than 2.5 times faster than our highest ramp speed (Fig. 5C). These high-speed changes of the dummy diameter never elicited a compensatory response. The constant size hypothesis would predict at least some delayed reaction.

We conclude, therefore, that *Macroglossum* controls distance via the apparent speed of the contour lines of a pattern. This would also explain the dynamical properties of the system, which we consider next.

The dynamical properties of the system

The retinal speed of the contour lines is most likely perceived by elementary movement detectors (EMDs) of the correlation type (Hassenstein and Reichardt 1956; Reichardt and Varjú 1959; Varjú 1959; Egelhaaf and Borst 1993). If EMDs are involved, the drop of gain at both high and low frequencies would be due to the fact that their output has a maximum at a certain contrast frequency. Especially the decrease of the gain at low frequencies needs no further explanation. On the other hand it would be hard to understand if one of the other three mechanisms would be assumed to play a role. The very steep high-frequency cut-off could, of course, be influenced by other factors. The animals might not be able to reverse flight direction rapidly enough. This might be the reason, why the percentage of response periods decreases with increasing frequency (Table 1, Fig. 2C). Moreover, it cannot be excluded that the animal's own rhythmic movements interfere with the response to periodic stimuli. The frequency of the animals' spontaneous movements range from 5 to 12 Hz, its average amplitude is 0.5 mm. Note that the lowest frequency at which the animals fail to respond to each period is also 5 Hz. However, the broad plateau of the gain-frequency curve cannot be accounted for solely by the properties of the EMD's, since their velocity characteristic has a distinct optimum, as shown in open loop behavioural experiments and through model calculations (see for example Hassenstein and Reichardt 1956; Reichardt and Varjú 1959). We are left with the following possibilities. (i) There might be classes of EMDs tuned to different velocities or frequencies, respectively. (ii) Our experiments have been conducted under closed loop conditions. Closing the feed back loop might lead to the obtained results. Model calculations have shown that the closed loop velocity characteristic tends to have a broad plateau during stationary stimulation, provided that the open loop amplification is high enough (Fig. 7 in Varjú 1973).

The asymmetry of the response

As indicated in Fig. 2B and documented convincingly in Figs. 4 and 5, there is a pronounced difference in the responses to the simulated approach and retraction of flowers, which becomes more and more apparent with increasing pattern velocity. This is, on the one hand, not particularly surprising, since differences in the response to progressive (front to back) and regressive (back to front) movements of the panorama in standard optomotor experiments have already been demonstrated in flies (Wehrhahn and Hausen 1980) and in beetles (Varjú 1987). Moreover, there are indications that the response of velocity sensitive neurons in the fly's lobula plate to high speed stimuli is distorted in a way similar to our response curves (Egelhaaf and Borst 1993). One has to ask, of course, why the differences in the response to simulated approach and retraction do not manifest themselves during sinusoidal stimulation, at least in the high frequency range, where the maximum speed was 12.6 cm/s (Fig. 2B) and 15.1 cm/s (Fig. 7C,D) respectively. Most likely, the limited time resolution of our customary video cameras do not allow us to demonstrate the differences.

At present we can only speculate on the possible biological significance of the asymmetry in the response. It might be that a sudden approach of a flower triggers a kind of escape response in order to avoid collision. The frequently observed drift towards the flower could, on the other hand, reflect the need of hawk moths not to loose contact with an oscillating food source.

During long-lasting bouts of drinking the oscillation of the pattern was occasionally terminated before the moth left. The behaviour of the animal thereafter depended on the distance to the pattern. When the moth was close to the pattern, it maintained its distance. When the distance to flower was large, the animal moved towards the pattern. We believe that this close-up and possibly also the drift toward the pattern during sinusoidal or ramp-like stimulation is mediated by mechano- and/or chemosensory receptors on the proboscis.

Structured versus homogeneous patterns

We have demonstrated that the gain first increases and then decreases again with increasing contour lines in the pattern (Figs. 7,8). We interpreted the increase as indicating that a larger number of contour lines stimulate more EMDs. This is in accordance with the finding that increasing the size of a homogeneous disk has the same effect (Fig. 6). There is a likely explanation for the decrease of the gain, when the number of border lines in the pattern becomes more than 8. Increasing the number of rings reduces the average radial spatial wavelength of the pattern, as indicated in Fig. 8. As estimated by Pfaff (1991) the interommatidial angle in the fronto-ventral part of the eye is about 1.6 to 2°. It is usually assumed that the acceptance angle has about the same value as the interommatidial angle. This means that at a wavelength of 5.5° (16 border lines), about 30% of a period is covered by one ommatidium, which leads to a considerable contrast reduction. This, in turn, reduces the output of the EMDs (cf Varjú 1959). The effect will be more and more pronounced as the spatial wavelength becomes still shorter.

The movement of flowers in wind

It would be interesting to know whether the frequency range of distance compensation matches the requirements in the field. The question is a subtle one, since *Macroglossum* forages on a variety of flowers, and little is known about how they move in the wind. We analyzed the movements of *Phlox*, one of the food sources favoured by *Macroglossum* in our region. A bunch of flowers shaken by wind was videotaped from the side. Sample records are presented in Fig. 9A,B. They show the horizontal (thick lines) and vertical position (thin lines) of two neighbouring flowers versus time. The movements are irregular, but they have a pronounced basic frequency. The similarities but also the differences in the movements of the two flowers are noticeable. In the third example (Fig. 9C) the speed of the wind (Fig. 9D) had been registered during recording. When wind speed starts to increase, the flower is strongly deflected (1 to 5 s), but returns to its previous position, when the wind speed remains high but does not fluctuate (5 to 8 s). Moreover, small amplitude oscillations persist even if the wind speed is constant and low (after 9 s). The basic oscillation frequency has been evaluated in experiments in which the stem of flowers has been pulled sideways and then suddently released. The flower was videotaped from one side. The oscillation frequency varies between 0.97 and 1.56 Hz, and lies, therefore, within the plateau of the gain - frequency characteristics (Fig. 3A). *Geranium*, another food plant favoured by *Macroglossum*, has similar basic oscillation frequencies. It should also be noted that in the field a nectarium is emptied within about 1 to 2 seconds. Thus, the animal has to compensate for movements only during a few periods.

A flower shaken by wind does not move in one plane. Seen from above it moves along ellipsoid paths, the size and excentricity of which steadily change. This is especially pronounced, if the stem of the flower is not perfectly cylindrical, as it is in *Phlox*. The animals, thus, have to compensate for movements along all three body axes simultaneously. Zhou (1991) has shown that *Macroglossum* compensates also for movements of flowers in the frontal plane.

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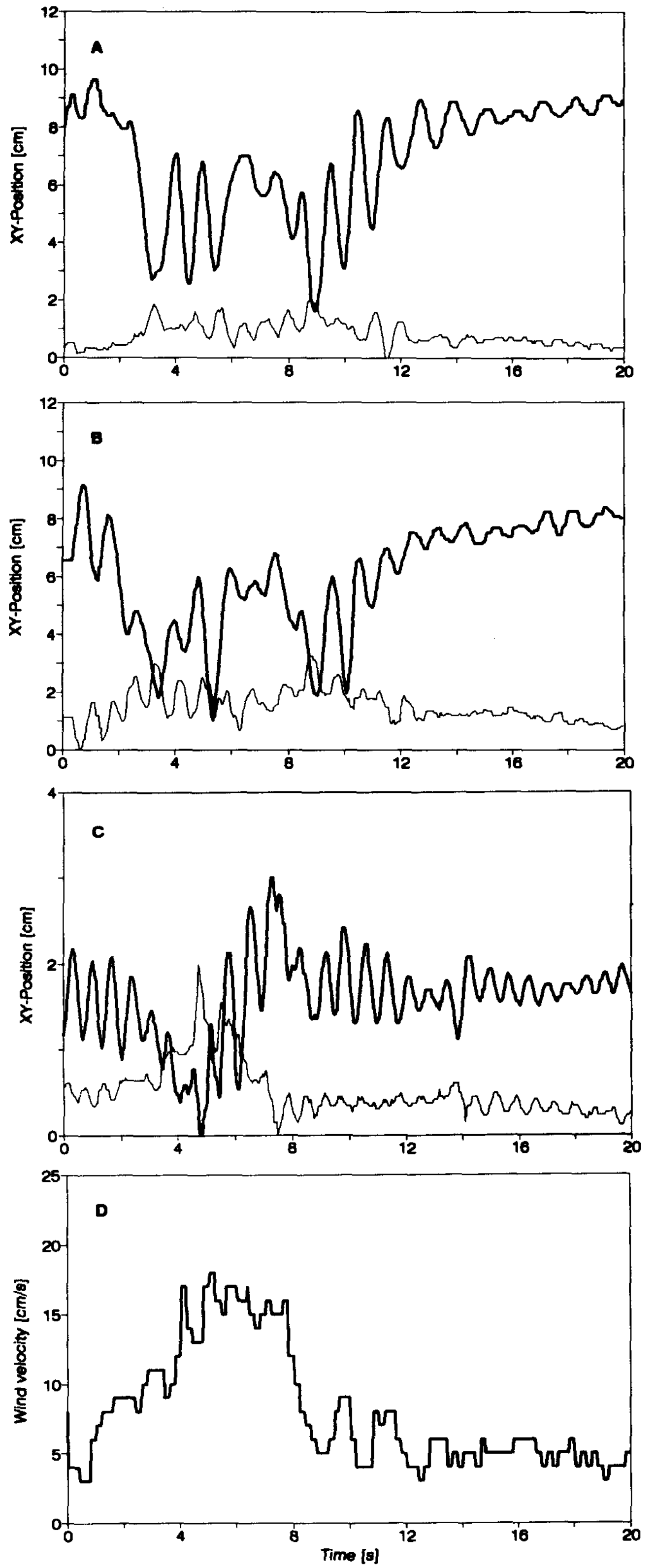

Fig. 9A–D. Horizontal (*thick lines*) and vertical position (*thin lines*) versus time of flowers (*Phlox*) shaken by wind. **A**, **B** Two nearby flowers; **C** Movement of a third flower; **D** wind speed during the sequence shown in **C**

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