

PREY CAPTURE IN THE PRAYING MANTIS *TENODERA ARIDIFOLIA SINENSIS*: COORDINATION OF THE CAPTURE SEQUENCE AND STRIKE MOVEMENTS

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Summary

Coordination of the complete capture sequence of the praying mantis has been studied in detail using several specially developed photographic techniques.

The mantis was able to attack prey throughout a large three-dimensional capture zone by changing body orientation relative to its perch. This orientation centred prey on the median plane and brought it within an attack zone relative to the prothorax. Alignment with the median plane simplifies the attack since the prey can then be localized using only two dimensions. The attack comprised several stereotyped components which together formed a single movement sequence of all six legs. Although too rapid for visual feedback, a simple mechanism permits steering of these movements to capture prey at particular locations within the attack zone.

These findings are contrasted with those from studies of mantis visual behaviour and a simple mechanism is suggested for how prey location is encoded to produce steering of the attack.

Introduction

Praying mantids capture their prey, mainly insects, by rapid movements of their specialized forelegs. Recognition of prey by the mantis is predominantly visual (Rilling *et al.* 1959) and makes use of rapid saccades of the movable head (Mittelstaedt, 1957; Lea and Mueller, 1977; Rossel, 1980). Head saccades centre an image of the prey binocularly within specialized frontal regions of the large compound eyes (Levin and Maldonado, 1970; Rossel, 1980) and permit estimation of distance by binocular triangulation (Rossel, 1983, 1986). Movements of the

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body occur with head saccades and orient the mantis relative to the prey prior to release of the attack (Rilling *et al.* 1959).

The attack is brought about by rapid movements of the forelegs, known as the 'strike' (Roeder, 1959), and of the middle and hindlegs, termed the 'lunge' (Maldonado *et al.* 1967). The strike is supplemented after a brief delay by the lunge which propels the body of the mantis in the direction of the prey (Copeland, 1975). Both magnitude and direction of the lunge vary qualitatively depending on the three-dimensional location of the prey (Copeland and Carlson, 1979). Analysis of muscle output suggests that the strike is a direct result of muscle action and that no specializations for prior energy storage are present (Gray and Mill, 1983).

Release of the attack is extremely unpredictable (Roeder, 1960), making high-speed photography of this behaviour difficult and expensive. Therefore, only a small number of high-speed films have been analysed in previous papers (Roeder, 1960; Copeland, 1975; Gray, 1981; Gray and Mill, 1983). Furthermore, in most experiments mantids have been tethered, which prevents normal orientation and the lunge.

In the investigation described here, several techniques were used to obtain detailed photographic records from a large number of prey captures, by both unrestrained and restrained mantids, in which prey location was systematically varied. These photographs were analysed to provide a description of the natural coordination of orientation, strike and lunge during capture of prey.

Materials and methods

Animals

Adult females of the praying mantis *Tenodera aridifolia sinensis* Saussure were obtained from laboratory culture (for culture methods see Corrette, 1980). Each mantis was starved for 3–5 days prior to an experiment. Live blowflies (*Sarcophaga bullata*) of uniform size and with wings removed served as prey.

Measurement of positions of the mantis and the prey

Foreleg position and 'relative' prey location

The predatory foreleg of the mantis consists of an elongated coxa, a nearly fused trochanter and femur, a tibia (Fig. 1A) and a tarsus (shown on the foreleg in Fig. 1B). The tarsus is used during locomotion, but is retracted during prey capture and was therefore not taken into account. The femur can rotate slightly medially on the trochanter, but these two segments move as a unit relative to the sagittal plane and the coxa during prey capture, and in describing foreleg movements are referred to together as the 'trochanter–femur'.

The length of an adult foreleg (excluding the tarsus) varies from 36 to 56 mm depending on the animal's body size. The relative length of individual segments and of other structures associated with prey capture, however, remains nearly constant (Corrette, 1980). To compensate for size, the length of the foreleg of

experimental animals was measured from photographs, and all linear measurements were converted to percent foreleg length (%*fl*).

Position of the foreleg segments projected onto the saggital plane is described by three angles (Fig. 1A): α , the angle of the coxa, measured between a line parallel to the median carina of the prothorax passing through the coxifer (the main articulation between coxa and prothorax: Levereault, 1936) and the line connecting the coxifer and the coxo-trochanteral joint; β , the angle of the trochanter-femur, measured between the long axis of the coxa and a line joining the coxo-trochanteral and femoro-tibial joints; and γ , the angle of the tibia, measured between lines formed by the bases of the lateral spines on the femur and by the tips of the proximal spines on the tibia. These joint angles are maximal when the foreleg is fully stretched in front of the mantis and minimal when the foreleg is tightly folded against the prothorax.

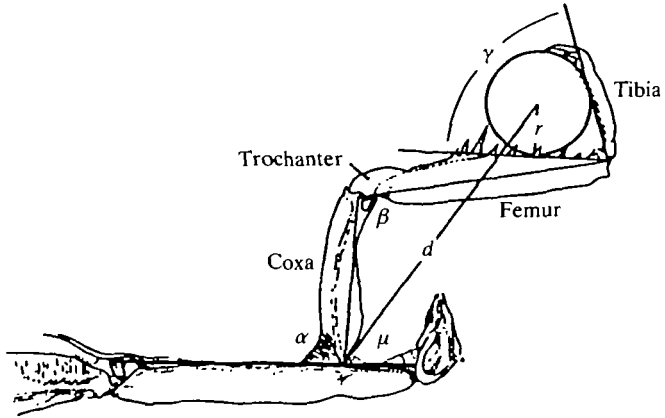
Mantids attack prey by means of a rapid strike of the forelegs combined with a slightly delayed lunge of the body. These movements bring the femoral spines into contact with the prey and enable it to be grasped with opposable spines on the tibiae (Fig. 1A). Whether the prey can be contacted by the femoral spines depends on its position relative to the prothorax. This 'relative' prey location was measured as the distance (d in %*fl*) from the coxifer to the prey centre, and the angle (μ) formed between the line joining the coxifer with the prey centre and a line parallel to the median carina of the prothorax (Fig. 1A).

Position of the prothorax changes both during the lunge and during orienting movements which precede it. To separate the effects of these two movements, relative prey location was measured at the beginning of the lunge (d , μ) and at the instant of foreleg contact with the prey (d_c , μ_c). Orienting movements slow down or stop before the strike is released, and changes that occur during the brief delay between strike and lunge can be neglected. Relative prey location at the beginning of the lunge (d , μ) is thus assumed to be the starting position of the prothorax for both the strike and the lunge. The contribution of the lunge to the position of the prothorax when contact with the prey occurs was evaluated by comparing d , μ with d_c , μ_c .

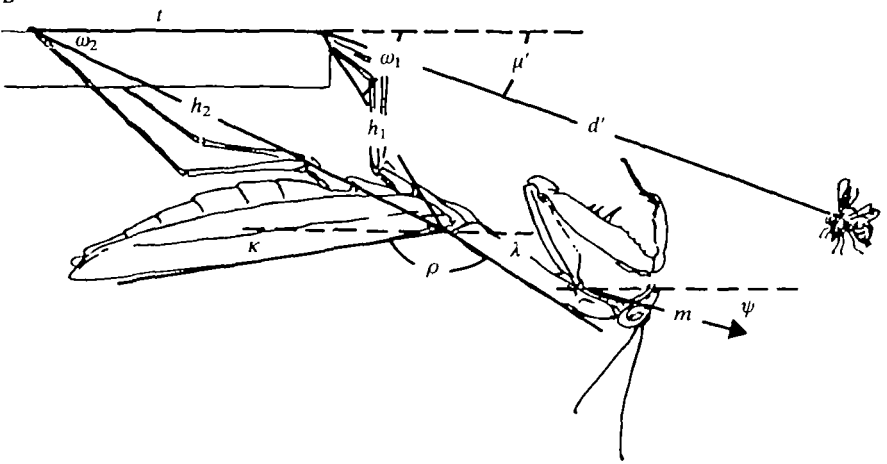
Body position and 'absolute' prey location

To determine how the position of the prothorax is adjusted before release of the attack, the positions of the mantid body and of the prey within the vertical plane of the perch were measured (Fig. 1B). Since the mantids did not always grasp the perch exactly along its long axis, the line determined by the tips of the ipsilateral tarsi was used as the 'horizontal' for making angular measurements (dashed lines). Angles of the prothorax (λ) and pterothorax (κ) were measured between their dorsal edges (for the pterothorax, the edge of the wing which covers it) and the horizontal passing through the joint between them. The difference between these two angles and 180° is the angle between the pterothorax and prothorax (ρ). Position and orientation of the pterothorax is adjusted by the mesothoracic and

A



B



C

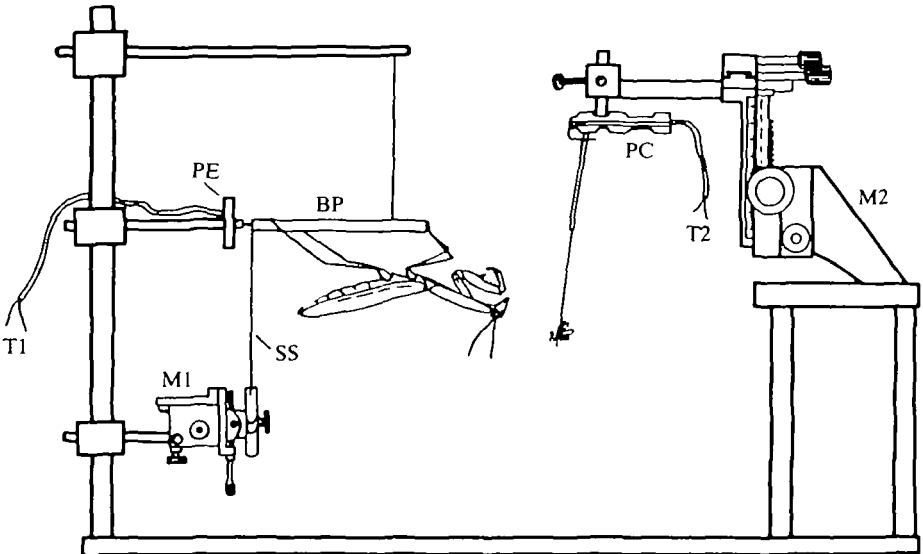


Fig. 1

Fig. 1. (A) Position of the foreleg and the prey relative to the prothorax. 'Relative' prey location is the distance d of the prey centre (radius= r) from the base of the forelegs (coxifer) and its angle μ with the dorsal prothorax. Foreleg position is indicated by relative angles of coxa (α), trochanter-femur (β), and tibia (γ). (B) Position of the mantis and the prey with respect to the perch used to analyse double-flash photographs. 'Absolute' prey location is the distance d' of the prey centre from the tip of the mesothoracic tarsus and its angle μ' with the 'horizontal' (dashed lines, determined by tips of the pterothoracic tarsi). Pterothoracic leg position is measured by sides of a triangle (t , h_1 , h_2) with vertices lying over tips of the tarsi and the joint between pterothorax and prothorax, and the angles formed by h_1 and h_2 with the horizontal (ω_1 , ω_2). Orientation of the pterothorax and prothorax are indicated by their angles with the horizontal (κ , λ) and the angle between them (ρ). During the lunge the coxifer is displaced over a distance (m) at an angle (ψ) to the horizontal. (C) Film stage used for double-flash photographs (example in Fig. 2A). Recoil from the lunge and foreleg contact with prey were registered by a piezo-electric device (PE) and a phonograph cartridge (PC), respectively, and their outputs (T1, T2) triggered two electronic flashes, producing a double exposure. A timer measured the interval between exposures. M1 and M2, micromanipulators for adjustment of PE trigger and prey location; BP, balsa perch; SS, spring steel support.

metathoracic legs. The position of these legs was approximated by a triangle with vertices lying over their ipsilateral tarsi and the joint between pterothorax and prothorax. Their lengths form two sides of this triangle (h_1 , h_2 , Fig. 1B), and the third side is the distance between their tarsi (t). Angular orientation of the pterothoracic legs is indicated by angles ω_1 and ω_2 formed by h_1 and h_2 with the horizontal. For the above measurements of body orientation, counterclockwise angles are positive.

The position of the head at the beginning of the lunge (not shown) was measured as a counterclockwise angle between the line of the median carina of the prothorax and a line defined by a conspicuous dark band of pigmentation on the lateral surface of the compound eye (Lea and Mueller, 1977).

Body position was also measured at the beginning of the lunge and at the time of contact with the prey. In the results, all the above variables refer to position at the beginning of the lunge and, as explained above, give the position of the mantis resulting from orienting movements. For analysis of the lunge, the difference between these two measures of body position was computed and is indicated by a Δ before the variable name. Measured from the coxifer, the lunge results in a displacement of the forelegs over a distance m at an angle ψ to the horizontal (Fig. 1B).

Orienting movements occur without changing the position of the mesothoracic tarsi on the perch. The 'absolute' location of the prey relative to the body of the mantis was therefore measured relative to the tip of the ipsilateral mesothoracic tarsus. Absolute prey location is the distance (d' in % fl , Fig. 1B) of the prey centre from this tip, and the positive angle (μ') formed between a line connecting it with the prey centre and the horizontal.

*Photography of prey capture**High-speed films*

Mantids were allowed to adopt an upside-down posture on a perch, as most commonly observed for resting animals in the culture. Prey was twirled on a thread to elicit capture behaviour, which was photographed on 16 mm colour film at 100 frames s^{-1} with a camera (Kodak Special Reflex) positioned perpendicular to either the horizontal or the vertical plane of the perch. These films provided information on the capture sequence used in making and analysing double-flash photographs and stroboscopic film strips, as described below.

Double-flash photographs of unrestrained mantids

Vibrations generated by recoil of the perch at the beginning of the lunge, and by contact of the foreleg femora with the prey, were used to trigger flash exposures of the mantis during prey capture. The mantis was placed on a balsa wood perch (BP, Fig. 1C), supported by a thread from above at one end, and by a thin strip of spring steel (SS) from below at the other, permitting only a slight horizontal displacement as a result of movements of the mantis. A metal pin fitted into one end contacted a piezo-electric device (PE, Vernitron 60690). Prey was impaled on the tip of a needle attached to a phonograph cartridge (PC) connected to a micromanipulator (M2). Triggering of the PE circuit from recoil of the perch at the beginning of the lunge produced a single flash of a strobe light (General Radio type 1538A), reset and started a digital timer, and gated the PC trigger circuit for a period of 200 ms (to minimize faulty PC triggers from prey movements). A PC trigger from contact with the prey during this gate period flashed a second strobe (type 1532D) and stopped the timer.

Photographs were made with a 35 mm oscillograph camera (Grass model C-4) located perpendicular to the vertical plane of the perch. Prey location was varied within an area of the vertical plane of the mantid perch in which prey capture occurred without eliciting locomotion. Under dim illumination, a blowfly was positioned within this area by movements of the micromanipulator (M2). For each position, the camera shutter was opened and the fly was made visible to the mantis by added illumination from a pair of fibre optic light guides directed from above. When struggling movements of the fly had not released prey capture after several minutes, the fly was repositioned in either horizontal or vertical steps of 0.5 cm and another photograph attempted. Mantids were allowed to consume all captured prey and to return to the normal resting position between photographs.

The above arrangement produced double-flash photographs of the mantis during prey capture (Fig. 2A). The first exposure registered the position of the mantis at the onset of the lunge and the second exposure was made at the instant the forelegs made contact with prey. The time interval (in ms) between these two exposures was measured by the timer. Double-flash photographs and time interval measurements of 55 successful prey captures were obtained using six female mantids.

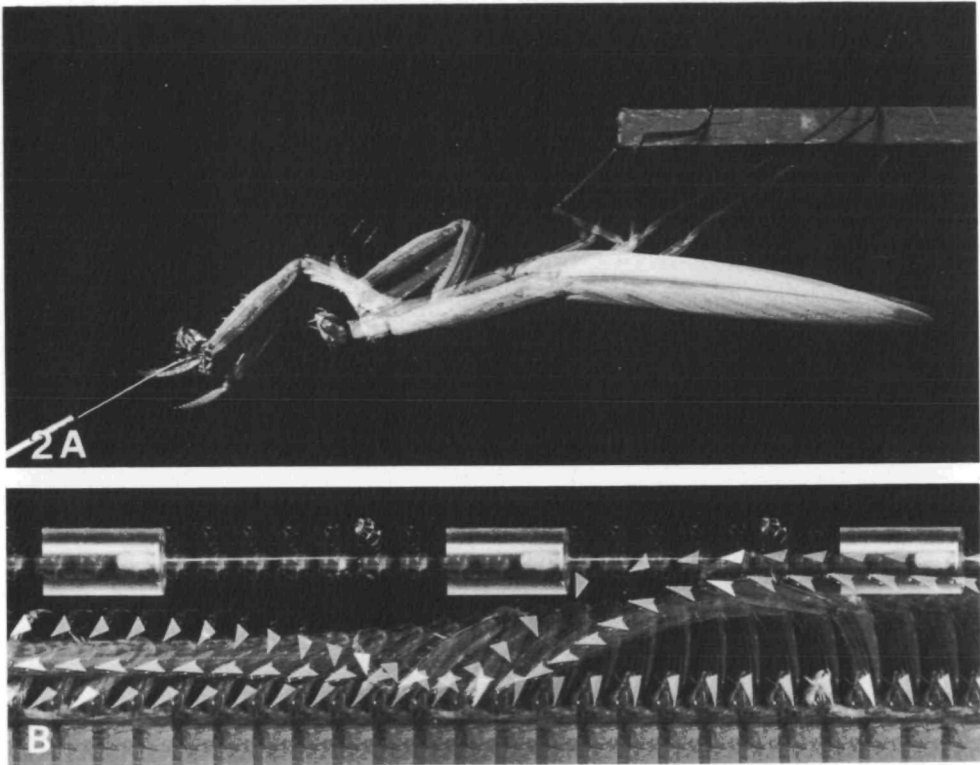


Fig. 2. (A) Double-flash photograph of a mantis obtained using the apparatus shown in Fig. 1C. The lunge is apparent in displacement of the body between exposures. Contact with prey (blowfly) has been made on the distal spined surface of the femur as rapid flexion of the tibia is beginning. Time interval between exposures is 65 ms. (B) Film strip of a strike photographed on moving film (500 mm s^{-1}) using stroboscopic illumination (200 Hz). Reflective triangles mark the position of tibia (upper wave of triangles, increasing time from left to right), femoro-tibial joint (middle wave) and coxifer (lower row). A second strobe highlighted the foreleg and triangles at repeated intervals (20 Hz) to simplify analysis. The prothorax was restrained to prevent movements out of the plane of focus. Prey (blowfly) and holder are clearly visible at the top of the photo when both strobes fire simultaneously.

Stroboscopic film strips of restrained mantids

A series of stroboscopic film strips was taken to examine detailed movements of one foreleg of prothoracically restrained mantids during predatory strikes. The 35 mm oscillograph camera was located perpendicular to the sagittal plane of the mantis with illumination provided by two strobe lights, firing synchronously.

In preparation for filming, a small acrylic plastic block with a V-shaped groove was fitted to the dorsal prothorax of the mantis. Matt black paint was brushed onto the lateral surfaces (but not the joints) of the prothorax and foreleg on the side of the mantis to be photographed. Three triangular reflective markers were glued to the foreleg to indicate the position of the coxifer, the femoro-tibial joint, and the

row of spines along the proximal tibia. To simplify the photographic image the coxo-trochanteral joint was not marked. The position of this joint was computed using the distance between markers on the coxa and femur and the lengths of the coxa and trochanter-femur previously measured from photographs.

The block was rigidly attached to a rod on a film stage so that the median carina of the prothorax was parallel to the horizontal movement of an insect needle in a micromanipulator used to present prey. The pterothoracic legs grasped a freely movable cardboard disk, counterbalanced for the weight of the mantis. Location of the coxifer was determined by positioning the prey needle-tip lateral to it, and noting the micromanipulator scale. Under dim illumination, the desired location of prey was selected by appropriate x - y displacements of the micromanipulator. Prey was made visible to the mantis by sudden illumination from above using a pair of fibre optic light guides.

Reflective markers on the foreleg were illuminated against a black background by one strobe light and photographed with the oscillograph camera at a film speed of 500 mm s^{-1} . This procedure imaged three waves of triangles on the film, indicating the position of the foreleg at 5 ms intervals during the strike (Fig. 2B). The second strobe light was triggered in phase with the first once every 50 ms, highlighting the three triangles at every tenth exposure to simplify their alignment during analysis. The oscillograph camera and strobe lights were started manually in response to orienting movements of the mantis to prey.

When prepared in this manner, mantids adopted a normal posture and their behaviour appeared normal, with the exception that movements of the prothorax during orientation and lunge were prevented and prey at longer distances were not captured. Prey location was restricted to relative distances ($d=40\text{--}80\%$ *fl*) and angles ($\mu=0\text{--}60^\circ$) from which predatory strikes could be readily elicited during filming. Fifty strikes were photographed using seven female mantids. Of these strikes 30 were selected for detailed analysis based on quality of the photographic image and an appropriate distribution of prey locations for comparison with results from unrestrained mantids (mean distance and angle of prey for both groups were not significantly different, t -test, $P>0.001$).

Variations in prey capture photography

To examine orientation of the mantis three-dimensionally, double-flash photographs were made with prey located to the left and right of the perch, with the camera located to give a ventral view of the mantis. The ability of restrained mantids to rotate the forelegs laterally during the strike was also examined by single flash photographs taken of the forelegs at the instant of contact with prey located lateral to the prothorax.

Coordination between lunge and strike was investigated by combining double-flash and stroboscopic film methods with unrestrained mantids. The mantis was marked with reflective triangles to simplify measurements of foreleg position and body displacement in the saggital plane. The trigger at the onset of the lunge turned on a strobe light to produce images at 20 ms intervals on a single frame of

35 mm film, until stopped by the trigger at prey contact which also released a single flash.

Data analysis

Measurement of photographs

Each double-flash photograph was enlarged on a projection table, and x - y coordinates determining positions of foreleg, pterothoracic legs, head and body of the mantis and prey centre were measured for the two exposures with a graphics tablet (Tektronix 4010). These coordinates were processed by computer (Digital Equipment PDP-8, PDP-11) to obtain values for absolute (d' , μ') and relative prey locations (d , μ and d_c , μ_c), mantid body (h_1 , ω_1 , h_2 , ω_2 , κ , ρ , λ), foreleg (α , β , γ) and head positions, and the distance and direction of the lunge (m , ψ), as described above.

Similar methods were used for stroboscopic film strips, but only position of the foreleg (α , β and γ) and relative prey location (restrained mantids continue to attempt both orientation and the lunge, so relative prey location is assumed to be that following orientation: d , μ) were measured.

Photographic resolution limited the accuracy of the above measurements, but deviations of repeated angular measurements were always less than $\pm 2^\circ$, and of distance measurements less than $\pm 1\%$ *fl* (approximately 0.5 mm).

Comparison of strikes by restrained mantids

Comparison of strikes proved difficult. Duration of the strike varies, and when the prothorax is fixed, prey is more frequently missed, particularly at longer distances (Maldonado *et al.* 1967). Even when capture occurs, contact with prey is not expected to be in normal phase with movements of the strike since displacement of the body is prevented. Comparison of movements of different strikes was therefore based on an estimated time of capture, termed 'tibial capture'. Tibial capture was defined as the time at which the tibia has flexed to an angle of $\gamma=90^\circ$ and was interpolated from angle-time functions. This value of γ differed slightly from the average position of the tibia at the instant of foreleg contact with prey from strikes by unrestrained mantids ($\gamma=100^\circ$), but produced a better alignment since the angle-time functions for the tibia were consistently linear about $\gamma=90^\circ$. Tibial capture was assigned a value of 0 ms (times preceding capture are negative) and used to align the time axes of different strikes for comparison.

To determine the onset of strike movements of individual joints, the angle-time functions for the coxa, trochanter-femur and tibia were examined with a computer program. Beginning at a time (150 ms before tibial capture) which is longer than the movements of any strike, the change of angle between individual data points (at 5 ms intervals) was examined until three successive intervals greater than $+1.5^\circ$ were found. Movement onset was then defined as the time of the first data point of this series. This method agreed in all cases with the onset of

movement determined by visual inspection of angle–time functions. The time from movement onset to tibial capture was used as a measure of strike duration for each segment.

Statistical analysis

To determine to what degree positions of the head, pterothoracic legs, prothorax and forelegs vary, distributions of positions of these structures measured at the same relative times during prey captures (double-flash photographs: beginning of the lunge, contact with prey; stroboscopic film strips: times relative to tibial capture) were examined. All measured parameters of the position of the mantis and the prey could be approximated by a normal distribution (χ^2 -test, $P \geq 0.05$) and are described by the mean and standard deviation. The range is also given to indicate the most extreme values observed from experiment.

The relationship between changes in position of each structure and prey location was estimated using multiple correlation (Croxtan, 1953) with absolute (d' , μ') or relative (d , μ) prey location or both, depending on the frame of reference being considered. No transformation of the data was made, since scatterplots indicated that linear relationships were adequate to describe the correlations which were present. In the results (Tables 1–3), partial correlation coefficients are given to permit the influence of distance and angle of the prey to be considered separately.

Results

The prey capture sequence

When undisturbed, *Tenodera* prefer an upside-down posture. Detected prey is fixated by saccadic movement of the head. When prey lies within the space directly in front of the resting mantis, an 'initial fixation' is followed by a re-orientation of the mantid body relative to its perch, combined with repeated fixation movements of the head (here referred to simply as 'orientation'). Orientation becomes slow or stops as the prothorax nears the prey. From this position (Fig. 3, 0 ms), movements of the prey can release the 'attack'. The attack (Fig. 3) consists of rapid movements of the forelegs ('strike') and of the pterothoracic legs ('lunge'). The strike begins with promotion of the coxa and extension of the tibia of both forelegs (Fig. 3, 0–10 ms). These movements accelerate, exposing the spined surfaces of the femur and tibia and moving them within reach of the prey (10–50 ms). The trochanter–femur is then rapidly extended in close synchrony with deceleration of tibial extension and of coxal promotion, followed by rapid flexion of the tibia (50–60 ms), grasping prey between the spines of the femur and tibia (70 ms). Extension of the pterothoracic legs occurs in conjunction with foreleg movements, producing a rapid lunge of the body in the direction of the prey (Fig. 3, 30–70 ms; the lunge is clearly seen in the altered position of the coxifer with respect to reference lines).

Foreleg movements of the strike occur predominantly parallel to the saggital plane of the mantis, but rotation outside this plane also occurs following initial

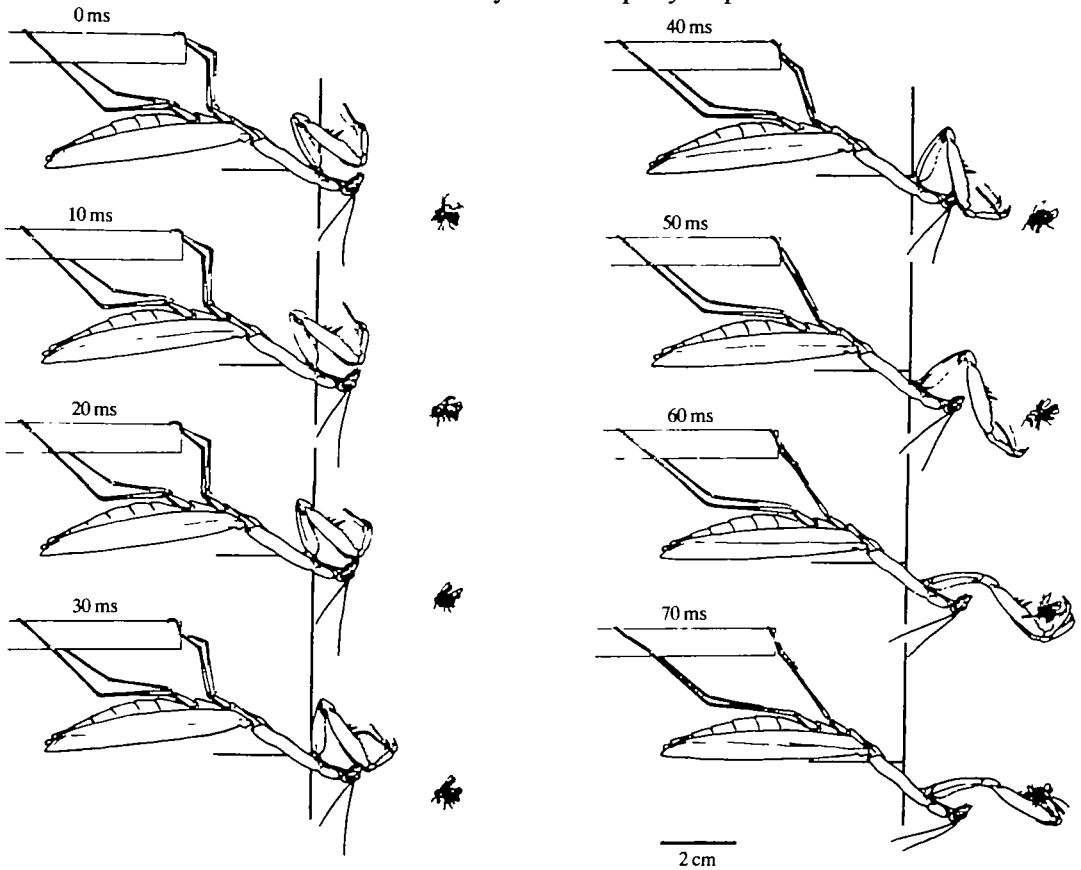


Fig. 3. The rapid attack consists of movements of the forelegs (strike, 0–70 ms) combined with delayed movements of the pterothoracic legs and prothorax (lunge, 20–70 ms). Reference lines indicate initial position of the base of the forelegs (coxifer, 0 ms) and make movements of the lunge more apparent. The prey (blowfly) was twirled on a thread (not shown). Tracings from a 16 mm film at $100 \text{ frames s}^{-1}$.

movements (Copeland, 1975). In the present study, ventral films indicate that foreleg rotation results from rotation of the coxae about their long axes, separating the distal femora. The femur of each foreleg also rotates medially about its incompletely fused joint with the trochanter, tilting the spined surfaces of femur and tibia relative to the saggital plane. These rotations result in a lateral to medial slash of foreleg femora during trochanteral extension, and have been suggested to increase the effectiveness of capture of prey not exactly centred in the saggital plane (Copeland, 1975). Although effectiveness may be increased, this rotation is also necessary to prevent collision of the femora with the head (Fig. 3, 30–40 ms).

Orientation and the 'capture zone'

Orientation involves changes in the posture of the mantis which move it into position in preparation for release of the attack. Mantids adopt a resting posture similar to that shown in Fig. 4A, but with the body slightly more retracted under

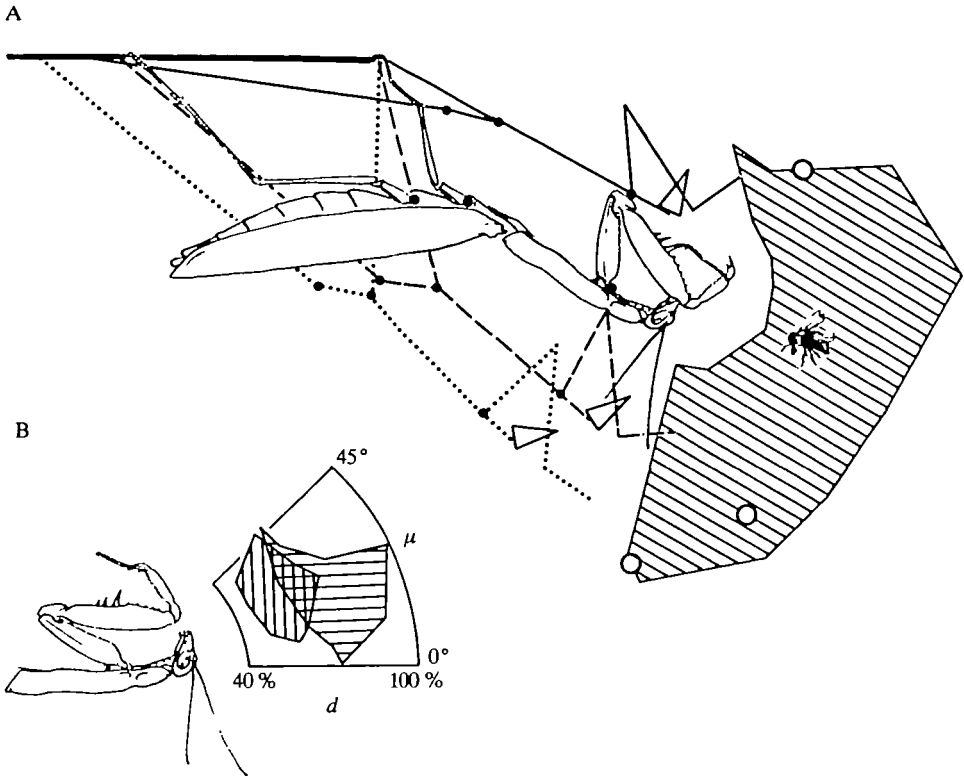


Fig. 4. Prey capture zones estimated within the vertical plane of the mantid perch. (A) Orientation permits a resting mantis to capture prey over an extensive capture zone (diagonal hatching). Four examples of position of a mantis at onset of lunge (end of orientation) are shown for prey in locations indicated (open circles and blowfly). In stick figures, joints of the legs with the body are indicated by points, head position by triangles. (B) The attack was released during orientation only when prey was located within a particular region in front of the prothorax (horizontal hatched area). The lunge produces a forward thrust of the prothorax and reduces the distance to the prey before it is struck by the forelegs within a smaller zone (vertical hatched area). Relative prey locations (d in % fl , μ in degrees) which enclose these two zones are shown. Data from double-flash photographs of unrestrained mantids.

the perch and the forelegs folded against the prothorax. Orientation alters this resting posture, as illustrated in Fig. 4A by four examples of the position of the body (drawing and stick figures) observed at the beginning of the lunge when the prey was positioned as shown (fly and open circles). The pterothoracic legs and prothorax are adjusted in a series of postural movements during orientation. Locomotion does not occur, the position of the mesothoracic tarsi on the perch remaining constant.

Orientation permits the mantis to release its attack over a large 'capture zone'. The area of this capture zone within the vertical plane of the perch was estimated from successful captures by unrestrained mantids and is shown by the hatched area in Fig. 4A. This zone lies between absolute prey locations of $d' = 126\text{--}218\%$ fl and

$\mu' = 12-64^\circ$. The capture zone is slightly larger than shown in Fig. 4A, but the boundary of this zone is characterized by a rapid decrease in the likelihood of release of the attack and an increased tendency of mantids to leave the perch, and was therefore avoided in these experiments. The capture zone also extends three-dimensionally on either side of the perch and is restricted primarily by anatomical limits on re-posturing of the mantid body.

Behavioural zones surrounding the capture zone

The complete prey capture sequence (initial fixation, orientation, attack) is only observed with prey located within the capture zone. When prey is detected peripheral to this zone, initial fixation and orientation occur, but the posture of the mantis reaches an extreme during orientation and release of an attack does not occur. In this case, mantids attempt to 'stalk' the prey, that is to bring it into the capture zone by changing their position on the perch. Orientation is then followed by behaviour associated with stalking, such as horizontal peering movements of the prothorax, waving of the forelegs in search of a foothold, and locomotion along the perch. Since orientation also precedes stalking, the capture zone and the peripheral 'stalking zone' together form an 'orientation zone'. The outer boundaries of the stalking zone have not been measured but, with extreme prey distances, no further response follows initial fixation, suggesting that a 'fixation zone' also exists peripheral to it.

The organization of these behavioural zones implies that mantids are not able to estimate distance accurately over the entire visual range. At most locations within the stalking zone, prey is out of range for capture, but orientation is still attempted before stalking occurs. This suggests that release of stalking is produced by proprioceptive cues from extreme posturing of the mantis and not by fine estimation of distance. Fine estimation of distance seems to be confined to the region directly in front of the prothorax in which prey is attacked.

The 'attack zone'

The attack is most readily released by rapid, jerky movements of an appropriately sized prey (Rilling *et al.* 1959), but such movements are only effective when prey lies within an 'attack zone' directly in front of the prothorax. This attack zone can be defined as all locations relative to the prothorax at which movements of prey are able to release the attack. The extent of the attack zone within the median plane of the prothorax was estimated by twirling prey on a thread at defined locations in front of the prothorax of restrained mantids and noting where attacks could be released. The attack zone was found to lie within a region enclosed by the boundaries $d=40-100\% fl$ and $\mu=0-60^\circ$. Release of an attack occurred most readily at intermediate angles and shorter distances within this range. Occasional attacks also occurred at more extreme angles or at slightly longer distances, but most often the restrained mantis struggled to free itself and a long-lasting inhibition of prey-capture behaviour followed.

When mantids were free to move, release of the attack occurred only within a

central region of the attack zone found for restrained mantids. Attacks by unrestrained mantids were released when prey was located in an irregularly shaped zone within the range $d=59-98\% fl$ and $\mu=0-47^\circ$, shown by the horizontally hatched area in Fig. 4B. As a result of the weak releasing stimulus (leg movements of stationary flies) used in these experiments, orientation was prolonged or stopped completely before the threshold for release of the attack was reached. These results therefore represent the region of the attack zone preferred by the mantis when conditions for orientation are ideal. As can be seen in Fig. 4B, the maximum range of distance occurs at a prey angle of $\mu=26^\circ$. With more extreme values of μ , the range of distance decreases and shorter distances around $70\% fl$ are preferred. The slight asymmetry of this zone relative to prey angle presumably results from the fact that a larger area of the capture zone (Fig. 4A) lies beneath the rest position of the mantis and increases the probability of attacks being released at smaller prey angles.

To investigate the structure of the observed attack zone, an estimate was made of the maximum region of the median plane within which contact of the femoral spines with prey should be possible. The structure of the foreleg (Corrette, 1980) and its movements during the strike are assumed to determine a 'contact zone', defined as all locations relative to the prothorax which can be reached with the femoral spines during the final movements of the strike. Position of the femoral spines is determined by positions of the coxa and trochanter-femur (see Fig. 1A). If all combinations of positions of these segments are considered which satisfy restrictions on their angles observed at the time when contact with the prey normally occurs during the strike (values from restrained mantids at the time of 'tibial capture' were used: $\alpha=87-158^\circ$, $\beta=66-151^\circ$, $-34^\circ \leq \alpha - \beta \leq 46^\circ$), a prey the size of a blowfly could be contacted by some point along the femoral spine rows within a region bordered by $d=40-77\% fl$ and $\mu=-13$ to 80° . This estimated contact zone has an irregular crescent shape, the range of distances being maximal at intermediate values of μ around 30° and tapering at angles to either side of this central axis (B. J. Corrette, unpublished results). This estimated contact zone is only slightly larger than that actually observed for restrained ($d=40-80\% fl$, $\mu=0-60^\circ$) and unrestrained mantids (vertical hatched area in Fig. 4B: $d_c=47-72\% fl$, $\mu_c=9-46^\circ$). During attacks by unrestrained mantids, the lunge reduced d ($\Delta d=-36$ to $-2\% fl$) and slightly increased or decreased μ ($\Delta \mu=-2$ to 15°) before the prey was struck by the femoral spines. If the normally small change of angle produced by the lunge is ignored, the combined strike and lunge should be able to contact prey within a similar crescent-shaped zone having the same limits of angle, but with a maximum distance of somewhat more than $100\% fl$. If the attack zone is also similarly shaped, the occasional release of the attack at extreme angles and long distances could be explained.

The attack zone also extends three-dimensionally, but the direction of the strike and movements of the prothorax during the lunge were not found to be influenced by lateral position of prey. In ventral photographs of unrestrained mantids, laterally located prey was centred on the long axis of the prothorax before release

of the attack. This alignment was produced primarily by lateral rotation of the body from the pterothoracic legs, but some lateral rotation of the prothorax was often visible. The lunge in this case was always directed along the long axis of the prothorax. In restrained mantids, attacks could be readily released and the prey captured when it was located within $\mu = \pm 15^\circ$ horizontal to the long axis of the prothorax. At $\mu = \pm 20^\circ$, attacks could only be released with extreme difficulty. The prey was hit with the lateral edge of a foreleg, triggering a photograph, but was never caught. In all these photographs, the outstretched forelegs were parallel to the long axis of the prothorax at the time of contact with prey. Thus the attack and contact zones can be considered to be two-dimensional.

Combining the above results, it can be assumed that release of the attack can occur at locations throughout an attack zone which lies mainly within the median plane of the prothorax. The threshold for release of the attack is reduced within a central region of this zone and increases as prey location deviates from this centre, both within the median plane and at slight lateral angles to it. This low-threshold region is characterized by a central axis ($\mu = 26^\circ$) at which the maximum range of distance can be captured. This axis corresponds closely with the central axis of the zone within which the femoral spines of the forelegs were estimated to be able to contact prey ($\mu = 30^\circ$) and suggests that anatomy of the forelegs and movements of the attack are optimized for capture within this region.

Orientation posture and the lunge

When posture of the mantis is examined, it becomes apparent that orientation not only re-positions the prothorax so that prey lies within the attack zone but also adjusts the angular relationship between pterothoracic legs and prothorax to preset the direction of the lunge. Which aspects of posture are changed by orientation is indicated by distribution measures of body position (see Fig. 1B) listed in Table 1. The degree to which these changes are consistently related to position of the prey within the capture zone was estimated by computing partial correlation coefficients for each parameter with absolute prey location, also shown in Table 1. Similar values are shown in Table 2 for the displacement of the body which occurs during the lunge. In the case of the lunge, mantids could be steering their movements based on position of either the body or the prothorax, and thus correlations with both absolute and relative prey location are given. Reference should also be made to the examples in Fig. 4A, for better visualization of postures and movements described below.

Examination of high-speed films and of the distribution of changes in orientation posture (Table 1) indicate that orientation results from three types of movements: (1) stepping movements of the metathoracic legs along the perch which adjust the distance between the pterothoracic tarsi (t), (2) alterations in joint angles of the pterothoracic legs (suggested by h_1 , h_2 , ω_1 , ω_2) which translate and rotate (angle κ) the pterothorax relative to the perch, and (3) rotation of the prothorax on the pterothorax (ρ).

These combined movements produce an orientation of the prothorax which

Table 1. *Postures of pterothoracic legs and body following orientation by unres-trained mantids and their correlation with absolute prey location*

	Range	Mean \pm s.d.	Correlation with absolute prey location			
			d'		μ'	
Pterothoracic legs						
Intertarsal distance (t , % fl)	30–134	89 \pm 25	-0.60	--	0.40	+
Mesothoracic length (h_1 , % fl)	37–105	76 \pm 16	0.82	++	0.53	++
Mesothoracic angle (ω_1)	18–88°	61 \pm 16°	-0.71	--	0.88	++
Metathoracic length (h_2 , % fl)	102–172	141 \pm 17	-0.01	NS	0.10	NS
Metathoracic angle (ω_2)	9–50°	28 \pm 9°	0.28	+	0.75	++
Body						
Pterothoracic-perch angle (κ)	-27–21°	3 \pm 10°	0.11	NS	0.81	++
Ptero-prothoracic angle (ρ)	138–163°	149 \pm 5°	-0.53	--	-0.01	NS
Prothoracic-perch angle (λ)	7–54°	34 \pm 12°	0.50	++	0.80	++

Correlation is multiple correlation of each variable ($N=55$) with absolute prey distance (d') and angle (μ').

Shown are partial correlation coefficients and their significance based on the t -test. Correlation: +, positive; -, negative. Significance: ++(--), $P < 0.001$; +(-), $P < 0.05$; NS, not significant.

changes consistently with the position of the prey within the capture zone (λ and its partial correlations, Table 1). The angle of the metathoracic legs (ω_2) shows a similar distribution and correlation with prey location, and is adjusted so that the prothorax and the vector determined by the metathoracic legs are nearly parallel. This vector is lengthened by extension of the metathoracic legs (Δh_2 , Table 2) during the lunge, but its direction remains nearly constant ($\Delta \omega_2$). Since orientation of the prothorax also changes only slightly ($\Delta \lambda$, Table 2), the lunge produces a nearly linear translation of the prothorax along its long axis, which is predetermined relative to the plane of the perch by adjustment of the angle of the metathoracic legs.

During orientation, the prothorax is raised, lowered and translated by movements of the mesothoracic legs (h_1 , ω_1 , Table 1). The vector determined by these legs is best correlated with absolute prey location, and determines the particular region of the capture zone faced by prothorax and forelegs (see Fig. 4A). With large changes in position of the mesothoracic legs required to reach prey in extreme locations, extension of the metathoracic legs beyond the range required for the lunge can occur. This is corrected by stepping movements of these legs along the perch which change tarsal separation (t , Table 1) and increase their flexion. Values of t are significantly correlated with d' and μ' , and the magnitude of these correlations suggests that significant changes in t are limited to extreme prey locations. Stepping changes the alignment between prothorax and metathoracic legs, which is readjusted by slight rotation of the prothorax on the pterothorax. As

Table 2. Lunge parameters from successful captures by unrestrained mantids and their correlation with prey location

	Range	Mean \pm s.d.	Correlation with prey location			
			Absolute		Relative	
			d'	μ'	d	μ
Magnitude (m , % fl)	3–37	13 \pm 7	0.19 NS	-0.05 NS	0.73 ++	-0.21 NS
Direction						
Tarsal (ψ)	4–59°	33 \pm 17°	0.46 ++	0.44 ++	0.03 NS	-0.12 NS
Prothoracic ($\lambda - \psi$)	-24–26°	-1 \pm 11°	0.25 NS	-0.17 NS	-0.07 NS	-0.16 NS
Displacement						
Pterothoracic legs						
Δh_1 (% fl)	2–24	11 \pm 6	0.48 ++	-0.25 NS	0.60 ++	-0.29 +
$\Delta \omega_1$	-26–3°	-5 \pm 5°	0.45 ++	-0.16 NS	-0.37 +	-0.06 NS
Δh_2 (% fl)	2–36	13 \pm 6	0.15 NS	-0.05 NS	0.72 ++	-0.20 NS
$\Delta \omega_2$	-4–4°	0 \pm 2°	0.35 +	-0.01 NS	0.02 NS	0.09 NS
Body						
$\Delta \rho$	-12–9°	-1 \pm 4°	0.16 NS	0.01 NS	0.13 NS	0.33 +
$\Delta \kappa$	-5–12°	2 \pm 3°	0.28 NS	-0.00 NS	0.26 NS	0.05 NS
$\Delta \lambda$	-6–9°	3 \pm 3°	0.07 NS	-0.01 NS	0.13 NS	-0.45 --
Duration (ms)	30–88	54 \pm 16	-0.02 NS	-0.26 NS	0.39 +	-0.30 -
Velocity (% fl ms^{-1})	0.08–0.49	0.23–0.09	0.41 +	0.05 NS	0.60 ++	-0.18 NS

Correlation is multiple correlation of each variable ($N=55$) with absolute or relative prey distance (d' , d) and angle (μ' , μ).

Shown are partial correlation coefficients and their significance based on the t -test. Correlation: +, positive; -, negative. Significance: ++(--), $P < 0.001$; +(-), $P < 0.05$; NS, not significant.

seen in Table 1, ρ shows a similar correlation with prey distance to that of t . The length of the metathoracic legs varies over a wide range (h_2 , Table 1) but, since stepping resets this length, it is independent of prey location.

Although the orientation posture is carefully adjusted, the relative prey location when the attack is released varies considerably. Since the lunge could reduce this variability in prey location by steering the forelegs in the direction of the prey, the direction of displacement of the base of the forelegs was also examined. Movement of the coxifer is adjusted relative to the pterothoracic tarsi (ψ , Table 2) with changes in absolute prey location, but changes in direction relative to the prothorax ($\lambda - \psi$) are entirely independent of prey location. In general, the lunge was directed very nearly along the long axis of the prothorax. With respect to the plane of the perch, then, it can be assumed that the lunge is not steered after its release, but has a fixed direction which is determined under visual control during orientation.

Although relative direction of the lunge is largely pre-adjusted by positioning of the metathoracic legs, its distance and some aspects of its movements do vary, depending on the relative location of prey when it is released. Displacement of the

mesothoracic legs (Δh_1 , Table 2) and rotation of the prothorax with respect to the perch ($\Delta\lambda$) are significantly altered with relative prey angle. This rotation occurs through changes in the angle of the prothorax ($\Delta\rho$) and not of the pterothorax ($\Delta\kappa$), and the direction of rotation changes relative to a central prey axis. Based on the regression line, the prothorax rotates in the direction of the prey when μ is greater than 26° , and away from the prey at values less than this angle.

The magnitude of displacement of the coxifer during the lunge (m , Table 2) was nearly identical with displacement of the metathoracic legs (Δh_2), and both parameters increase significantly with relative prey distance, but are independent of absolute prey location. Duration of the lunge prior to contact with the prey varied from 30 to 88 ms. Lunge duration increases significantly with relative distance and decreases with relative angle of prey. Average velocity of the displacement of the coxifer was also not constant, increasing significantly with both absolute and relative prey distance, suggesting a gradual build-up of velocity when the duration of the lunge is prolonged. Since the actual end of the lunge was not measured, it is not possible to determine if the duration of the lunge is actually programmed for prey distance, or if sensory events associated with prey contact stop its movements. How the time of release of the lunge is determined is discussed below after the movements of the strike have been considered.

Final position of the head following repeated fixations during orientation was also not constant (range: $51\text{--}94^\circ$, mean: 74° , see examples in Fig. 4A). Head angle was found to be well correlated with relative prey angle (partial correlation with μ : 0.49, $P < 0.001$, t -test, $N = 55$) within the saggital plane. Although head angle could not be measured with extreme accuracy, this suggests that neck proprioceptors provide information on relative prey angle at the time the attack is released.

Analysis of strike movements

Strike movements of the forelegs were examined by measuring the position of a single foreleg (joint angles α , β and γ , Fig. 1A) at 5 ms intervals from stroboscopic film records (see Fig. 2B) of strikes by prothoracically restrained mantids, as shown in the example of Fig. 5. Comparison of strikes proved to be difficult owing to extreme variation in both duration and starting movements. Flexion of the tibia at the end of the strike was found to be both rapid and stereotyped and, since this movement functionally produces the capture of prey, it was used to determine a fixed timepoint for comparison of strikes (tibial capture, γ flexed to 90° , see Materials and methods), and assigned a time of 0 ms (Fig. 5).

Movement phases of strike: approach and sweep

All strikes can be divided into two functionally distinct movement sequences (Fig. 5). Position of a single foreleg is shown at successive times (1–5) during a strike. Initial strike movements (Fig. 5, left inset) expose the spines of the grasping mechanism of the femur and tibia, and move the foreleg into position in preparation for capture. As these early movements serve to establish an appropriate position of the foreleg relative to prey, this sequence is termed the

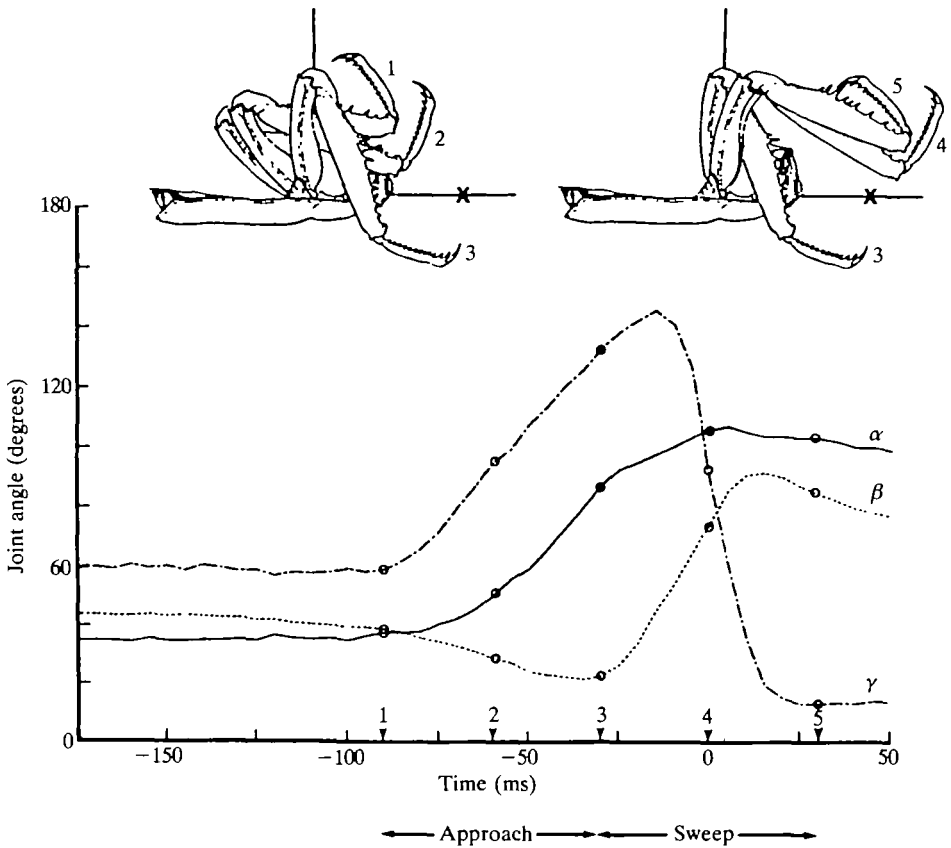


Fig. 5. Computer analysis of a stroboscopic film strip (example in Fig. 2B) of a strike by a restrained mantis. Joint angles of prothorax-coxa (α), coxa-trochanter-femur (β) and femur-tibia (γ) of a single foreleg are shown as functions of time. Time axis is labelled relative to flexion of the tibia to $\gamma=90^\circ$ (0 ms, tibial capture), the estimated time of contact with prey. Upper drawings correspond to positions of the foreleg (open circles, graph) at various times (numbered arrows) during the strike and illustrate the two phases of movement: approach (left, 1-3) and sweep (right, 3-5). Prey location ($d=40\% fl$, $\mu=0^\circ$) is indicated by x. Foreleg position was measured at 5 ms intervals but, for clarity, individual data points are not shown in plots of joint angle.

'approach'. Final movements of the strike rapidly rotate and close the grasping mechanism to capture the prey, and will be referred to as the 'sweep'.

Influence of prey location on the strike

Approach

The approach consists of a fairly stereotyped promotion of the coxa which is coupled to extension of the tibia of each foreleg. During these movements, either slow flexion or extension of the trochanter-femur can occur (Fig. 5, 1-3). Fig. 6 shows the angular position of the tibia (angle γ) as a function of the coxa (angle α)

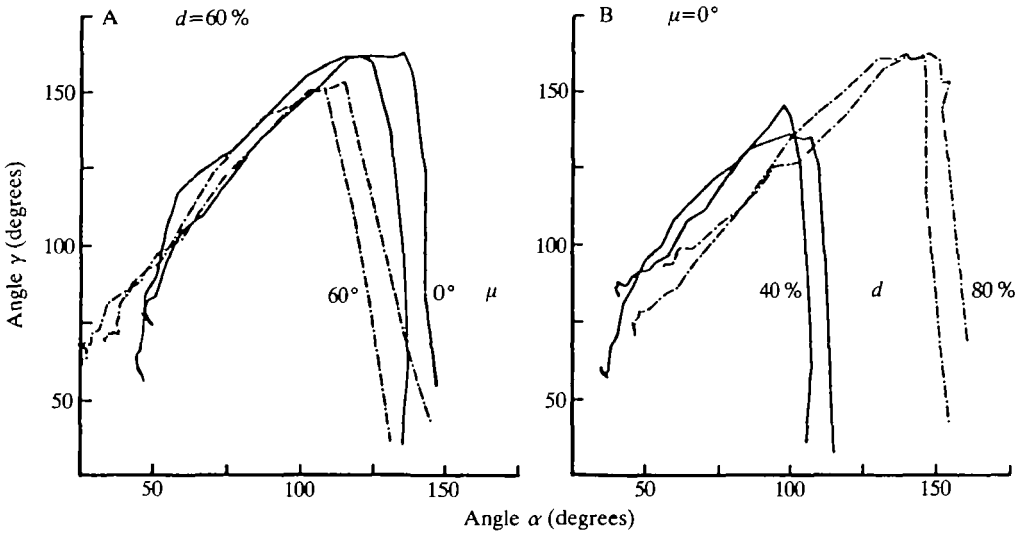


Fig. 6. Tibia position (angle γ) as a function of coxa position (angle α) during strikes with four prey locations (d in % fl , μ in degrees) differing in angle (A) or distance (B). During the first phase (the approach) of all strikes, extension of the tibia and promotion of the coxa are coupled, as seen in the constant linear relationship of their angles. The sweep (apparent here as a rapid decrease in the angle of the tibia) is released at different positions of the coxa depending on prey location. Two strikes are shown for each prey location.

during eight strikes by restrained mantids. In Fig. 6A, relative distance of prey is constant and two pairs of replicate strikes are shown which differ in prey angle. A similar comparison of strikes with constant prey angle but differing distances is shown in Fig. 6B. Starting postures of coxa and tibia vary somewhat, but in all eight strikes changes in the position of these two segments is uniformly linear during the approach (from onset of the strike until the beginning of flexion of the tibia). Prey location, particularly prey distance, influences the extent of these movements which occur prior to release of the sweep, but the basic coordination of coxa and tibia during the approach is independent of prey location.

Movements of the trochanter-femur during the approach are illustrated in Fig. 7. Changes in angle β from 150 ms before to the time of tibial capture (0 ms) are shown for six strikes differing in prey distance (A) and prey angle (B). In contrast to coxa and tibia, movements of trochanter-femur before release of the sweep (at -20 to -30 ms, see below) vary in duration, velocity and direction. Consistent changes occur with relative prey distance, but little variation is seen with prey angle (Fig. 7A,B).

Sweep

Both coordination and timing of final movements of trochanter-femur and tibia during all strikes are relatively constant, regardless of prey location. In Fig. 8 are shown angle-time functions of the movements of trochanter-femur (angle β) and

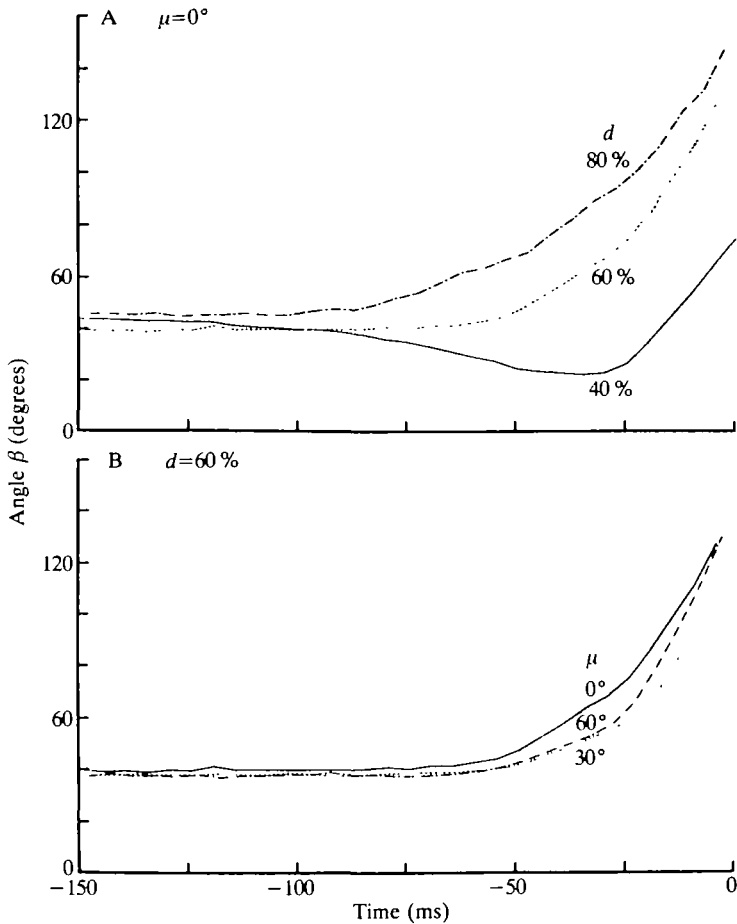


Fig. 7. Position of trochanter-femur (angle β) as a function of time prior to tibial capture (0ms) from six strikes with differing relative prey location (d , μ). (A) β is adjusted for variations in prey distance by flexion or extension during the first phase of the strike (approach) prior to release of the sweep (-20 to -30 ms). (B) Femur movements are similar when prey distance is held constant.

tibia (angle γ) at the end of four strikes with widely varying relative prey locations (d , μ) as indicated. For comparison, the examples have been aligned based on the time of tibial capture (0 ms). Although absolute positions of both trochanter-femur and tibia vary with prey location, the velocity and coordination of their movements are very similar for the final 20–30 ms prior to tibial capture. Stereotypy of these movements results from a marked angular deceleration of the tibia and acceleration of the trochanter-femur occurring concurrently at the beginning of this period (approximately -30 ms), as indicated by inflections in their movement functions. In many strikes, a distinct deceleration of promotion of the coxa occurs with rapid trochanteral extension during the sweep (see Fig. 5).

In terms of function, movements during the approach serve to bring coxa and

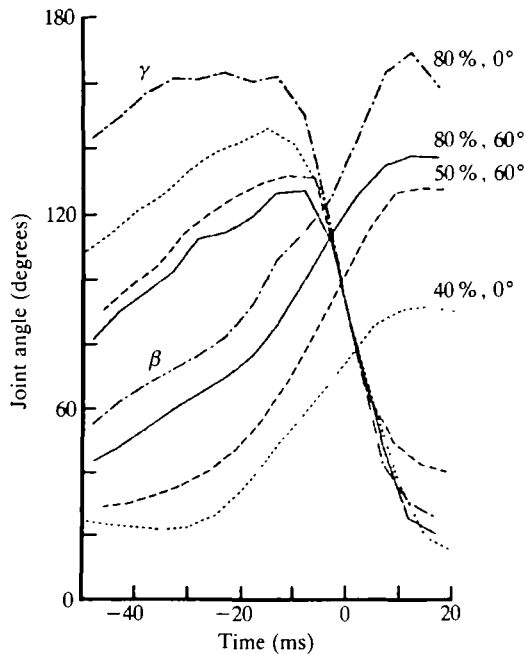


Fig. 8. Sweep movements of the trochanter–femur (joint angle β) and tibia (γ) of a single foreleg during four strikes with differing prey locations (d in % fl , μ in degrees). Position of trochanter–femur and tibia at the beginning of the sweep (-20 to -30 ms before tibial capture, 0 ms) varies with prey location, but slope-velocity, amplitude and duration of these movements are stereotyped.

trochanter–femur into an angular relationship, so that the opened prey-capture mechanism faces an appropriate prey location within the attack zone. When this position is reached, prey is captured by releasing stereotyped movements of the sweep. Two positions of a single right foreleg are shown in the drawings of Fig. 9 at the approximate beginning and end of the sweep. These two positions of the foreleg are shown for four strikes, differing in the distance (Fig. 9Bii) or angle of the prey (Fig. 9Aii). At the onset of the sweep, the position of the coxa varies with distance and angle of prey, and the position of the trochanter–femur changes with distance. Stereotyped displacements of trochanter–femur and tibia during the sweep move the grasping mechanism through very different ranges of prey location (as indicated by the background grid). These ranges of prey location are consistent with the actual location of the prey (filled circle), but are inaccurate with respect to distance, in the absence of the thrust of the prothorax normally produced by the lunge in unrestrained mantids. Position of trochanter–femur (angle β) as a function of coxa (angle α) is also plotted in Fig. 9Ai, Bi for pairs of strikes at each of the same prey locations as in the drawings. Starting postures and relative positioning of coxa and trochanter–femur during initial movements can vary somewhat but, for each prey location, a particular combined position of coxa

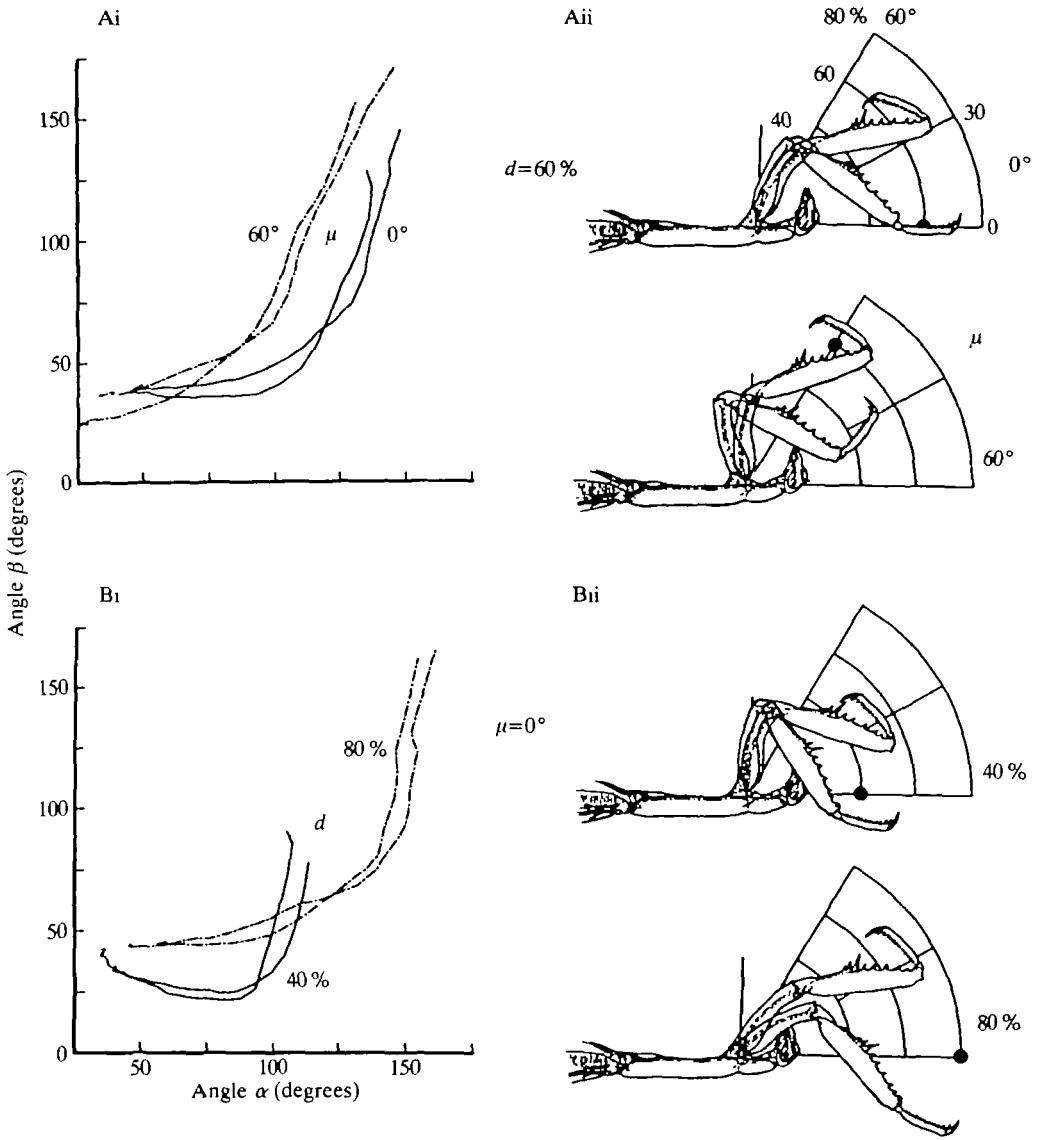


Fig. 9. In the graphs (left), trochanter-femur angle (β) is plotted as a function of coxa angle (α) from 150 ms before to 5 ms after tibial capture for strikes differing in prey angle (μ in degrees, Ai) and prey distance (d in % fl, Bi). Two strikes are plotted for each prey location. The drawings (Aii, Bii) show examples of the actual position of a single foreleg at the approximate beginning and end of the sweep (25 ms before and at the approximate time of tibial capture) for strikes with identical prey locations (filled circles) as in the graphs. During the approach, promotion of the coxa is coupled with variable extension or flexion of the trochanter-femur (plots prior to inflection point) to produce an appropriate position of the foreleg for a particular prey location. This position determines which region of the attack zone will be contacted by the spine row during the sweep (final linear portion of plots, drawings). Data from restrained mantids. Further explanation in text.

and trochanter–femur is consistently reached before release of the sweep occurs. Release of the sweep is apparent in these plots as the trochanter–femur starts to extend rapidly.

Combined strike data from restrained and unrestrained mantids

The examples presented above illustrate basic variations in the movement of strikes when prey is captured within the attack zone in front of the prothorax. To substantiate that the control mechanism suggested by these examples occurs in all strikes, and to investigate which aspects are being actively varied, parameters of all strikes obtained from both restrained and unrestrained mantids were combined (Fig. 10) and the significance of their correlation with relative prey location was examined (Table 3).

Fig. 10A summarizes the position of coxa (α), trochanter–femur (β) and tibia (γ) at particular behavioural timepoints during strikes by both restrained (open symbols) and unrestrained (filled symbols) mantids. Shown are the mean and range for each joint angle at the beginning of strike (IP, initial posture), at lunge onset (LO), at approach end (AE), at capture (C, contact with prey) and at tibial capture (TC). These behavioural timepoints are arranged from left to right in the normal sequence in which they occur during the strike. Extreme variability in position of joints of the foreleg from strike to strike is immediately apparent. The assumption that strikes of restrained mantids are not aberrant is also supported. For all three joints, mean values change consistently across these relative timepoints and imitate the basic form of angle–time functions of these joints from individual strikes (example in Fig. 5), in spite of differences in the methods used to obtain them.

Correlation of joint angle with relative location of prey at three critical timepoints during the strike is shown in Table 3 (foreleg position) for data from Fig. 10. Prior to release of the strike, slight changes in the foreleg posture can occur which are significantly correlated with prey location. When prey is distant, all three joints of the foreleg tend to open slightly. With high-angle prey, a more tightly folded posture of coxa and tibia tends to be adopted. As seen in Fig. 10, however, posture of the trochanter–femur is much less variable than that of coxa and tibia. Just before the sweep begins (approach end, Table 3), the same pattern of significant correlations is observed, but it becomes much stronger for coxa and trochanter–femur as a result of adjustment in their positions during the approach. Significant correlations are also observed for coxa and femur positions at the moment of contact with prey in unrestrained mantids, but here the degree of correlation is not as strong as in the previous results from restrained mantids. This reduction in correlation is probably the result of slight changes in foreleg position caused by contact with the prey holder and inherent variations in the phase at which contact actually occurs, both of which would diminish the accuracy of foreleg position.

Mean and ranges of duration (Fig. 10B) and average approach velocity (Fig. 10C) from strikes of restrained mantids are also shown for promotion of the

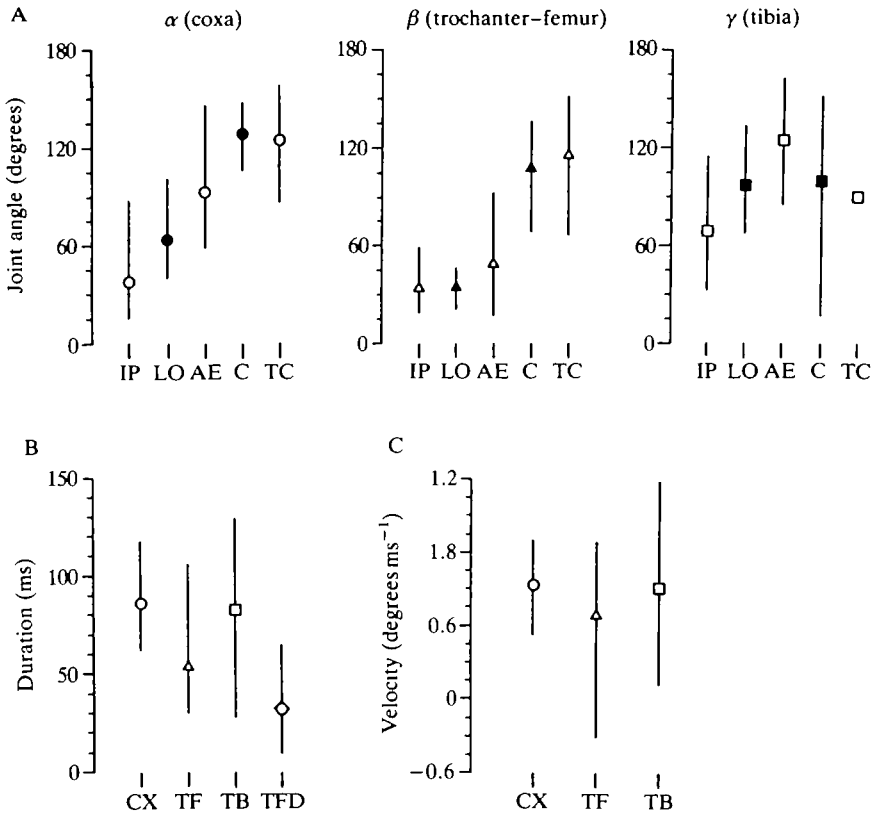


Fig. 10. (A) Variability of foreleg position (joint angles α , β and γ) measured at various relative timepoints during strikes by both restrained (open symbols, $N=30$) and unrestrained mantids (filled symbols, $N=55$). Shown are minimum and maximum (lines) and mean values (data points: coxa, circles; trochanter-femur, triangles; tibia, squares). Foreleg position was measured just prior to the approach (IP, initial posture), at lunge onset (LO), at approach end (AE), at capture (C) and at tibial capture (TC, by definition γ is exactly equal to 90°). Duration (B) and average velocity (C) values (mean, range and symbols as in A) computed over the time interval: onset of movement of coxa (CX, promotion), trochanter-femur (TF, extension) and tibia (TB, extension) to just before the release of sweep (35 ms before tibial capture). Also shown is the delay between the onset of coxal promotion and the onset of trochanteral extension (TFD, trochanter-femur delay). The extreme variability of strikes is apparent, but only foreleg position at approach end and capture, and TFD proved to be highly correlated with prey location (Table 3 and text).

coxa (CX), extension of the trochanter-femur (TF) and extension of the tibia (TB). The delay between onset of coxal promotion and trochanteral extension is also shown (TFD, Fig. 10B). As with joint angles, these parameters are extremely variable from strike to strike but, as seen in Table 3 (foreleg movement), most of this variability is intrinsic to the motor system controlling the strike and not specific to the mechanism which adjusts the strike for prey location. Significant

Table 3. *Correlation of strike parameters with relative prey location*

	Correlation with relative prey location ^a			
	<i>d</i>		μ	
Foreleg position				
Restrained mantids				
Initial posture ^b				
α (coxa)	0.48	+	-0.55	-
β (trochanter-femur)	0.38	+	-0.36	NS
γ (tibia)	0.44	+	-0.39	-
Approach end ^c				
α	0.72	++	-0.73	--
β	0.69	++	-0.11	NS
γ	0.46	+	0.57	-
Unrestrained mantids				
Capture position ^d				
α	0.39	+	-0.50	--
β	0.53	++	0.13	NS
γ	-0.32	+	-0.19	NS
Foreleg movement				
Restrained mantids				
Duration ^e				
Coxa	0.20	NS	-0.55	-
Trochanter-femur	0.48	+	-0.02	NS
Tibia	-0.25	NS	-0.19	NS
Trochanter-femur delay ^f	-0.46	-	-0.64	--
Approach velocity ^g				
Coxa	0.18	NS	0.04	NS
Trochanter-femur	0.54	+	0.33	NS
Tibia	-0.09	NS	0.03	NS

^a Correlation is multiple correlation of each variable (restrained, $N=30$; unrestrained, $N=55$) with relative prey location (d , μ). Shown are partial correlation coefficients and their significance based on the t -test. Correlation: +, positive; -, negative. Significance: ++(--), $P<0.001$; +(-), $P<0.05$; NS, not significant.

^b Joint angles 175–180 ms prior to tibial capture.

^c 35 ms before tibial capture, approach ends somewhat later, but this interval ensures all rapid changes of the sweep are excluded.

^d Contact of forelegs with prey.

^e Onset of movement (coxa, promotion; trochanter-femur and tibia, extension) to tibial capture.

^f Onset of coxal promotion to onset of trochanteral extension.

^g Average velocity over the time interval: coxa and tibia, onset of coxal promotion to 35 ms before tibial capture; trochanter-femur, onset of coxal promotion (when trochanteral flexion begins movement) or onset of trochanteral extension to 35 ms before tibial capture.

changes in duration of the movements of coxa and trochanter–femur occur. When prey distance is held constant, the sweep is released earlier at smaller angles of the coxa, and duration of promotion of the coxa shows a significant decrease. Similarly the trochanter–femur must be in a more extended position prior to release of the sweep when prey is more distant, and this is in part accomplished by a significant increase in the duration of this extension.

The timing between coxal promotion and trochanteral extension is also a significant factor in adjusting the strike for differing prey locations (Table 3, trochanter–femur delay), but a mechanism based on timing alone is inadequate to explain control of the strike, given the degree of intrinsic variability in velocities of these movements (Fig. 10C). Changes in the velocity of the trochanter–femur form a part of the prey adjustment mechanism. Velocity of the coxa is independent of prey location but, though well-controlled in comparison with that of the tibia, is not held constant. When these results are considered together, the adjustment in timing and velocity of movements of the trochanter–femur with changes in prey location must rely on a combined signal representing both prey location and the actual velocity of promotion of the coxa.

Coordination of strike and lunge

In the above results, movements of the strike and lunge have been examined separately. It is clear from previous results (Copeland and Carlson, 1979 and example in Fig. 3) that the lunge is delayed with respect to the strike but, given the variability in the strike demonstrated in the results of the present study, the exact coordination between lunge and strike was re-examined. To determine the exact point in the movements of the strike when the lunge is released, stroboscopic exposures were made of captures by unrestrained mantids which were triggered by recoil of the perch at the beginning of the lunge and stopped by contact with prey. Fig. 11 shows four examples of measurements from these photographs. The upper curves show change in the position of the base of the forelegs produced by the lunge. Position is shown as x, y coordinates measured from the starting position of the coxifer (0,0) and relative to the long axis of the prothorax ($y=0$). The lower curves are simultaneous angle–time functions for the trochanter–femur (angle β). As pointed out above, the lunge is primarily a linear translation of the prothorax along its long axis, which increases in velocity as the movement is prolonged. In all cases in Fig. 11, start and acceleration of this translation parallel those of extension of the trochanter–femur of a foreleg. If the lunge and extension of the trochanter–femur of the forelegs occur simultaneously in all prey captures, then the duration of the lunge measured from captures by unrestrained mantids (mean \pm s.d. 54 ± 16 ms) should be similar in duration to trochanteral extension from strikes by restrained mantids (54 ± 17 ms). The extremely close agreement in these two distributions and the significant correlation of each of these movements with relative prey location give added strength to the conclusion that lunge translation produced by the meso- and metathoracic legs is both triggered and controlled by the same mechanism as movements of the trochanter of the forelegs.

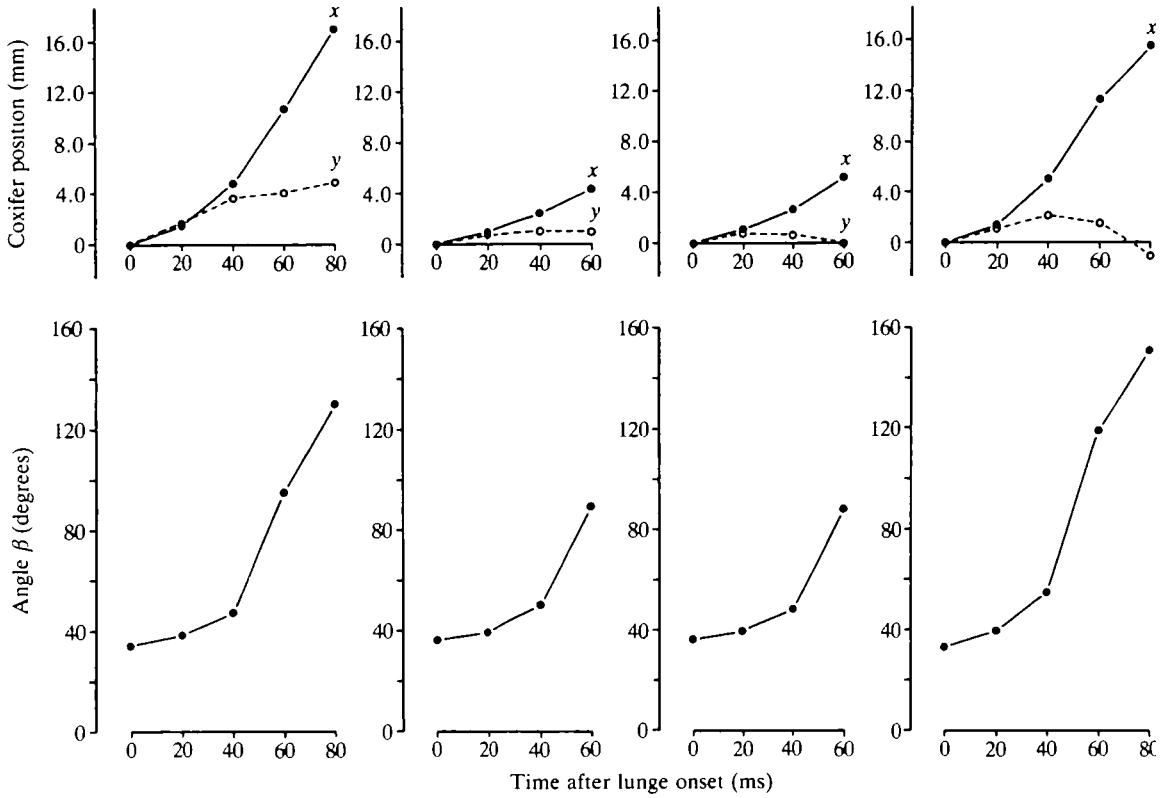


Fig. 11. Coordination of lunge and foreleg trochanter-femur extension during four strikes by unrestrained mantids. The lunge (upper graphs) is shown by the x (solid lines) and y (dashed lines) displacements of the base of the foreleg (coxifer) relative to the start position of the prothorax (0,0 in mm), trochanter-femur extension by changes in the joint angle β (lower graphs), at 20 ms intervals between lunge onset and contact of the femur with the prey. The lunge is seen to be primarily a linear translation of the prothorax in the direction of its long axis which is synchronous with trochanteral extension of the forelegs. Results from triggered stroboscopic photographs of prey capture.

That is, the strike and lunge form a single attack movement sequence which is adjusted for variable prey location by the same underlying mechanism.

Discussion

In the following discussion, the findings of this study of prey capture by the praying mantis are compared with those from previous investigations. In addition, capture performance is contrasted with results from studies of their visual behaviour, and a mechanism for encoding prey location to permit variable control of the attack is suggested.

Prey capture range

Maldonado and co-workers (Maldonado *et al.* 1967, 1974; Maldonado and Barrós-Pita, 1970) determined the capture distance for *Coptopteryx viridis* and *Stagmatoptera biocellata* and concluded that the maximum catching distance for these mantids is the sum of two constant components produced by strike and lunge. Their results show a similar range of prey locations to those found here for *Tenodera* but, since prey capture movements were not measured, the significance of this variability was not considered.

Lunge

Copeland and Carlson (1979) found that both distance and direction of the lunge of tethered *T. aridifolia sinensis* are adjusted for the three-dimensional location of prey. In agreement with their findings, control of distance and direction of the lunge is verified here for unrestrained mantids, but the direction of translation was not found to change with relative prey location, as observed by Copeland and Carlson under 'open-loop' conditions. Movements of the lunge, though, were correlated with relative prey location, and more extensive control of the lunge may occur when conditions for orientation are not optimal.

Copeland and Carlson (1979) also found that the lunge occurs with a fixed delay (22 ± 4 ms) relative to the strike, but only a small range of prey locations was examined. In the present study, the lunge was found to be coincident with, and to follow the same phasing as, movements of the trochanter-femur of the forelegs. The delay between onset of the strike and these movements was found to vary from 10 to 65 ms and to be functionally important for steering the attack.

Strike

Gray and Mill (1983) calculated torques and muscle output for the strike of *Heirodule membranacea* and concluded that the strike is the result of direct muscle action. The torques for earlier slow extensions were indistinguishable from postural torques and a clearly defined onset of torque first occurred during later stages of the strike. Although no significant variation in the movements of strikes was observed (Gray, 1981), these torque phases correspond well with movement phases (approach and sweep) found for *Tenodera*. The finding that these movement phases are varied to produce fine adjustments in steering of the strike gives added behavioural support for the importance of direct muscle action.

Gray and Mill also noted that one of the muscles responsible for rapid extension of the trochanter spans two joints, having both an extensor moment arm for movements of the trochanter and a remotor moment arm for movements of the coxa. They suggest that a transfer of kinetic energy from promotion of the coxa into extension of the trochanter occurs as a result of deceleration of the coxa produced by this muscle, and this permits the development of large extensor forces at low strain rates. Results of the present study suggest that deceleration of promotion of the coxa produced by this muscle is also functionally important for

accurate steering of the capture movements. In angle–time functions of strikes, an added deceleration of promotion of the coxa, as would be produced by this two-joint muscle, is apparent during extension of the trochanter (see example in Fig. 5). The sweep can thus be accurately released during all phases of promotion as required by prey location, since this added deceleration will automatically help stabilize the coxa near its release position.

Capture mechanism of the foreleg and attack accuracy

The movements of mantid prey capture have a single goal: to bring the spined region of the femora into contact with the prey so that it can be firmly grasped by the tibiae. The exact mechanism for grasping prey sets limits on the final position of the femora that will permit capture. Loxton and Nicholls (1979) showed that the largest spines on the femur are necessary for accurate capture of prey, and the grasping mechanism which they postulate implies that an exact angular orientation of the spined surface of the femora is important for optimal function. In the present study it has been shown that mantids regulate the pitch of the prothorax during the lunge. It is likely that the grasping mechanism and the movements of the strike are optimized for capture along the central axis of the attack zone, and these pitch adjustments therefore occur relative to this axis.

Evolution of the prey-capture sequence

As discussed by Roeder (1959), prey-capture behaviour of the mantis can be assumed to be the result of a natural selection in which speed and accuracy have been optimized within limits imposed by parsimony of units within its nervous system. The findings of the present study suggest some compromises which permit speed and accuracy to be matched to behaviour of prey and to the capture habitat while maintaining simple neural mechanisms.

Mantids capture prey from a perch within vegetation in which free movement is often hindered. Orientation overcomes this habitat limitation by permitting the resting mantis to position itself optimally relative to its prey over a large three-dimensional range. Orientation, though, is time consuming and the mantis risks detection by the prey during its final stages. A mechanism for steering the attack allows a rapid response to detection by the prey, since escape movements can release the attack during the final moments of orientation. Steering is also likely to be important when obstacles prevent completion of orientation. Although success of the attack is reduced when prey location is not optimal, such a steering mechanism could increase the percentage of prey encounters which lead to capture.

The attack is only steered within the median plane of the prothorax, and orientation must centre prey on this plane prior to its release. Since centring can occur at a distance from the prey and need not be exact, the efficiency of capture is not greatly affected by this restriction. Lateral steering has presumably not evolved, since it would require a complex neuromuscular control beyond the capabilities of the mantid nervous system. The path which the foreleg must follow

is complicated by the extreme width of the head, which is important for accurate distance estimation. Elaborate processing of sensory information would also be required since the prey must be localized in three dimensions. If the attack is only steered in two dimensions, its movements and their neural control can be simple.

The form of the lunge suggests that it may also have evolved as a simple solution to a problem created by the large separation between the head and the base of the forelegs of the mantis. Increased separation was probably selected because it permits the extreme head rotation used to fixate prey. At the same time, this would have complicated prey capture, since the movement axis and the optical axis would be widely separated. When conditions for orientation are optimal, the distance of the lunge averages 13 % *fl* (Table 2), placing the base of the forelegs in the position that the compound eyes had at the beginning of the lunge (see example in Fig. 2A). This 'ideal' lunge effectively aligns the movement and visual coordinate systems, eliminating the need for complicated neural conversion mechanisms, and may have represented one evolutionary stage in the development of this behaviour.

Studies of fixation and tracking of prey

A number of studies have examined fixation and tracking of prey by the praying mantis. In these studies, prey and head angles were measured relative to the head articulation. For comparison with prey angles measured relative to the coxifer, a value of μ was estimated using the average attack distance ($d=70\%$ *fl*) and the separation between coxifer and head articulation (14% *fl*, Corrette, 1980) and assuming that the head is centred on the prey. These values of μ are shown in parentheses after the reported values in the following discussion.

Mittelstaedt (1954) observed that mantids are able to hit prey which deviate by approximately $\pm 45^\circ$ ($\mu=\pm 37^\circ$) from the median plane of the prothorax. He therefore assumed that movements of the forelegs are directed laterally during the strike and he performed a number of experiments to examine how the direction of these movements is determined by the mantis (Mittelstaedt, 1957). The results indicated that the head is not exactly centred on the prey but shows a slight fixation deficit. Also, either unilateral deafferentation of neck-hair proprioceptors or fastening the head with a lateral deviation of 10–30° ($\mu=8-24^\circ$) significantly increased the frequency of misses, and the strike tended to be directed to the opposite side of the prey. These effects were found to be superimposed, a rotation of the head by 20° ($\mu=16^\circ$) to one side being able just to compensate for the bias produced by deafferentation on the other side.

Mittelstaedt's results clearly indicate an interplay between neck proprioceptors and compound eyes in localization of prey by the mantis, but his interpretation of these results is based on two false assumptions concerning normal prey-capture behaviour. First, when orientation movements are possible (Lässig and Kirmse, 1972), or in tethered animals when prey is located in a well-defined area relative to the prothorax (Rossel, 1980), fixation deficits do not occur. Also, in the present study, the mantids always centred the prey on the longitudinal prothorax before

releasing the attack. Second, restrained mantids only released the strike when prey was located within a much smaller lateral range ($\mu = \pm 20^\circ$) than that reported by Mittelstaedt. The direction of the strike remained parallel to the prothorax and was biased to one side of the prey, as occurred in Mittelstaedt's experiments when the head was fixed with a similar range of deviations. Prey could only be captured up to a maximum lateral deviation of $\mu = \pm 15^\circ$. This represents a similar head deviation to that found by Mittelstaedt to just compensate for unilateral deafferentation ($\mu = 16^\circ$) and suggests that loss of the signal from one set of proprioceptors occurs when the prey is out of range.

Mittelstaedt proposed the existence of two feedback systems which control fixation: an optic loop tending to centre prey on the compound eyes and a proprioceptive loop tending to centre the head on the prothorax. The above considerations suggest that these feedback systems are essentially correct, but that the interplay between them is not designed to determine the direction of the strike but to control the movements during orientation. Since fixation deficits do not occur, these orienting movements permit a position of the head to be reached in which both optic and proprioceptive feedback systems are in equilibrium. This equilibrium is reached when the head of the mantis is centred on the longitudinal prothorax and prey is centred on the compound eyes, as observed in the present study before release of the attack and as predicted by Mittelstaedt's model. At other positions of the head following fixation, both optic and proprioceptive signals are used to direct orienting movements. The attack can occur before equilibrium is reached, when both signals indicate that the prey is within the attack zone. To understand how the attack zone is recognized by the mantis, studies on specializations of the compound eyes need to be considered.

Regional differences in the structure of the compound eyes have been found in several species of mantis (Barrós-Pita and Maldonado, 1970; Horridge and Duelli, 1979; Rossel, 1979). In *Tenodera australasiae*, Rossel has shown that the compound eye is divided into two zones, a high-resolution frontal eye region (termed a fovea by analogy with the vertebrate eye) and a surrounding region. The fovea lies within the binocular region of the eye and is tilted slightly towards the saggital plane. Rossel (1980) has shown that the fovea is the fixation centre of the compound eye. Within the median plane, targets could be fixated on the fovea from $+60$ to -130° (negative angles ventral; $\mu = -50$ to 121°) and it can be assumed that all targets within the orientation zone in front of the mantis can be fixated. Most accurate centring of targets on the fovea occurred at positions from 0° to -90° ($\mu = 0-78^\circ$), overlapping with the attack and contact zones found in the present study. The fixation centre was found to lie 42° ($\mu = 34^\circ$) ventral to the prothorax and corresponds closely with the central axis found for prey capture. In *Mantis religiosa*, Berger (1985) also found that a large number of visual interneurons react to movements of targets within a restricted visual field which is centred at an angle of 34° ($\mu = 28^\circ$) ventral to the prothorax. Thus, it can be assumed that the axes for fixation and movement detection coincide with the axis for optimal capture of prey.

The fovea of the mantis is tilted to look at a point within the saggital plane of the mantid head. In *Tenodera australasiae*, the normal capture distance is 25 mm from the head (Rossel, 1980) and the visual axes of the foveas cross about 40 mm in front of the head (Rossel, 1979), so the intersection point must lie at the distant edge of the attack zone. In the normal rest position of the head, then, the foveas are directed at a fixed point along the central axis of the attack zone, which can tentatively be assumed to represent the maximum distance for capture. The image of prey located at this fixed reference distance will be exactly centred on both foveas. At other points along the central axis, the image will deviate from the foveal centres. By painting regions of a compound eye of mantids and comparing their capture performance with monocular mantids, Maldonado and Barrós-Pita (1970) have already shown that the region surrounding the fovea, and not the fovea itself, is crucial for estimation of distance. Deviation of the prey image can be encoded as coordinates relative to the foveal centre, and a measure of relative distance of prey can be obtained by binocular comparison of these coordinates, as has been suggested by Rossel (1986). When the head is not in the rest position, distance estimation occurs in the same manner, but the angle of the head, and hence the signal from neck proprioceptors, additionally indicates the angle of the prey relative to the central axis. This measuring system provides the mantis with two signals from compound eyes and neck proprioceptors which deviate about a fixed reference. These two signals would be sufficient to account for changes in behavioural sequence based on the three-dimensional zone in which prey is detected and on the aiming of the attack in two dimensions observed in the present study.

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