CORRELATIONS BETWEEN BODY ANGLES AND SUBSTRATE CURVATURE IN THE PARASITOID WASP *TRICHOGRAMMA MINUTUM*: A POSSIBLE MECHANISM OF HOST RADIUS MEASUREMENT

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SUMMARY

The parasitoid wasps of the genus *Trichogramma* use the surface curvature of their insect egg hosts to set an upper limit to the number of progeny allocated to the host, as well as the duration of their host examination. In addition, host recognition and host acceptance are in part mediated by surface curvature. In this paper, the relationships between the positions of body parts of the wasp and surface curvature are examined in order to determine a possible mechanism for curvature detection by the wasp.

Wasps of different sizes were photographed in profile while examining glass bead models of different diameters. The positions of selected body parts were analysed using a digitizer and microcomputer. The height of the wasp above the model surface did not change with surface curvature. Furthermore, the angle of the head relative to the thorax was also constant over the range of models used. Only the scapal–head angle and flagellar–head angle changed significantly with surface curvature.

A curvature detecting mechanism is proposed in which the wasp uses the scapal–head angle to measure the curvature of the surface. The body of the wasp is maintained at a preferred height and angle to the substrate, serving as a fixed platform from which curvature measurements are made. Additional features of this mechanism, as well as its correlation with morphological and behavioural findings, are discussed.

INTRODUCTION

The minute parasitoid wasps of the genus *Trichogramma* use the eggs of a wide variety of insect species as hosts for their larval stages. An important component in host recognition and clutch size determination by these wasps is their ability to detect and quantify differences in substrate curvature. Salt (1935) and de Jong & Pak (1984) showed that only objects within a particular range of curvature are accepted for ovipositing, but the wasps will accept unsuitable objects such as mercury globules, glass beads or seeds, provided they are of suitable size and shape.

Key words: *Trichogramma*, parasitoid, oviposition, host examination, antennae, hairplates, posture.

J. M. Schmidt & J. J. B. Smith (in preparation) demonstrated that surface curvature alone is sufficient to elicit host examination and ovipositing behaviour.

The amount of time taken by the wasps to examine the host surface also depends upon the radius of the host (Klomp & Teerink, 1962; Schmidt & Smith, 1985a,b, and in preparation). This time dependence is unaffected by the extent to which the surface area of the host is exposed above the substrate, and is the constant for hosts and glass bead models of the same diameter (Schmidt & Smith, 1985a,b, and in preparation).

Trichogramma are gregarious parasitoids, and the female deposits a variable number of eggs into each host depending upon several factors, including host size, shape, distribution and chemical content (Klomp & Teerink, 1962, 1967; Marston & Ertle, 1969; Nettles *et al.* 1982, 1985; Schmidt & Smith, 1985a,b). The adjustment of clutch size to host volume results in improved reproductive success for the ovipositing female by reducing the deleterious effects of larval competition for limited host nutrient (Klomp & Teerink, 1967; Charnov & Skinner, 1985). Both curvature and the length of the wasp's initial transit over the surface of the host are used by the wasp to determine clutch size (Schmidt & Smith, 1985a, and in preparation). In the absence of other cues, host curvature sets an upper limit to the number of progeny allocated to the host.

In this paper, correlations between body angles and substrate curvature are examined to determine the possible mechanisms of host curvature measurement by *Trichogramma*.

MATERIALS AND METHODS
Culture of Trichogramma minutum

Trichogramma minutum Riley (Hymenoptera: Chalcidoidea: Trichogrammatidae) was cultured as described by Schmidt & Smith (1985a). Hosts used for rearing were frozen (killed) eggs of the tobacco hornworm, *Manduca sexta* (L.) (Lepidoptera: Sphingidae), obtained from Carolina Biological Supply Co. (Burlington, NC, USA 27215).

The wasps used in the experiments ranged in body length from 0·35 to 0·85 mm. These differences are expected phenotypic variations resulting from different numbers of larvae developing in a single host (Flanders, 1935; Salt, 1934; Klomp & Teerink, 1967). Smaller emergents are produced under conditions of larval crowding. Wasps with obvious physical deformities were not used.

Glass bead models

The glass bead models used in the experiment were spherical, with diameters ranging between 0·30 and 1·5 mm. The beads were cleaned by washing in acetone, ethanol and distilled water, and mounted individually on 2×2 cm white cardboard squares with a minimal amount of gum arabic. Clear plastic Petri dishes (5 cm diameter) with tightly fitting lids were used as experimental arenas.

All photographs were taken on Ektachrome colour slide film (Daylight, ASA 64), with a Nikon F camera attached with an adapter tube to a Bausch & Lomb binocular dissecting microscope. Illumination was provided with an electronic flash unit with a 30 W Xenon flash tube (Carl Zeiss Ukatron UN 60) mounted in a Zeiss microscope lamp housing. The lens of the flash tube was located 9 cm from the specimens at a 45° angle from the substrate. Additional lighting for locating the specimens and focusing was provided by a heat-filtered tungsten lamp. All photographs were taken from directly above the centre of the host.

Wasps of various body lengths were combined with glass bead models of different diameters in order to obtain the greatest possible range of relative substrate curvatures. Each of 320 wasps was photographed once in lateral profile during the examination of a glass bead model. 78 exposures were selected as the final data set, based on the following criteria: (1) the wasp was strictly in lateral profile, with only one antennal base and one lateral ocellus visible and the crest of the scutum clearly outlined; (2) the wasp was completely in focus, including the details of antennal structure and leg position; (3) the antenna on the side of the wasp facing the camera was in contact with the host, with the flagellar portion not bent by compression against the host. In addition, wasps standing on a level substrate were photographed, both from directly above and from the side.

Experimental design and data processing

Data from the photographs were entered into a microcomputer by means of a digitizer (Summagraphics Bit Pad One). The selected slides were projected onto the digitizer and the data points entered manually using a stylus. Eight points were entered for each wasp (Fig. 1). These were used to calculate head length, body length, height of the wasp above the surface, and the angles between the various body parts of the wasp and their relationship to the host surface. Three points on the circumference of the model were entered, from which the radius and the coordinates of the centre of the model were determined. All linear measurements, including the diameters of the models used, were calculated in terms of head length (DE) of the wasp used with that host. Accordingly, the relative radii of the models ranged from 0·75 to 5·0 head units. In addition, the distance between the pronotum of the wasp and the model centre (FO), the height of the crest of the pronotum above the substrate ($FO-R$), and the height of the pronotum above the mesothoracic tarsus (FT) were determined. Three angles were calculated for each wasp: the flagellar–scapal angle (ABC), the scapal–head angle (BCD) and the neck angle (CFG) (Fig. 1). All processing was done using a Corona Model PC-HD microcomputer using programs written in the STSC-APL PLUS language.

The proportional lengths of body parts of the wasps were analysed in order to determine if the size relationships between parts change over the range of wasp sizes used. The flagellar segments and scape of the antennae were measured, as well as head length and the distance between the pronotal crest and the abdominal tip
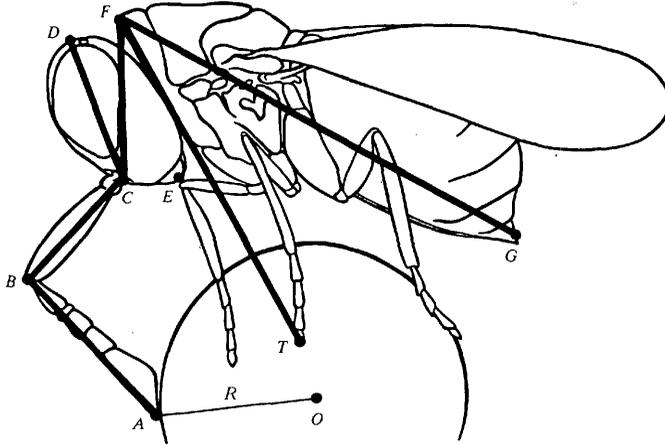
Fig. 1. Profile view of female *Trichogramma* on a glass bead showing points used to determine relative positions of body parts. The diameter of the glass bead shown is at the lower limit for acceptance by the wasp. R (model radius); A (flagellar tip) most distal and anterior point on the terminal flagellar segment (funicle); B (flagellar–scapal joint) articulation of the antennal pedicel and scape, most dorsal point; C (scapal–head joint) articulation of the proximal section of the scape (rondule) with the head, most ventral point; D (medial ocellus) most dorsal point of the head capsule; E (mouthparts) ventral-most tip of mandibles; F (pronotum) crest of the pronotum, most dorsal and anterior point of pronotal sclerite; G (abdominal tip) dorsal surface of ninth abdominal segment, indicated by long terminal hairs; T (tarsus) tarsal claws (darkly pigmented) of meso-thoracic leg; O (origin) calculated coordinates of the centre of the model; AB (flagellar length) length of the five distal antennal segments; BC (scapal length) length of the proximal antennal segment; DE (head length) distance between medial ocellus and mouthparts in profile; FG (abdominal length) distance between crest of the pronotum and abdominal tip; FT (height above tarsus) distance between tarsal tip and crest of pronotum; $FO-R$ (height above substrate) distance between pronotal crest and model substrate; ABC (flagellar–scapal angle) angle changes with extension/retraction of flagellar segments; BCD (scapal–head angle) angle changes with depression/elevation of scape; CFG (cervical angle) angle changes with depression/elevation of head.

Table 1. *Measured lengths of body parts*

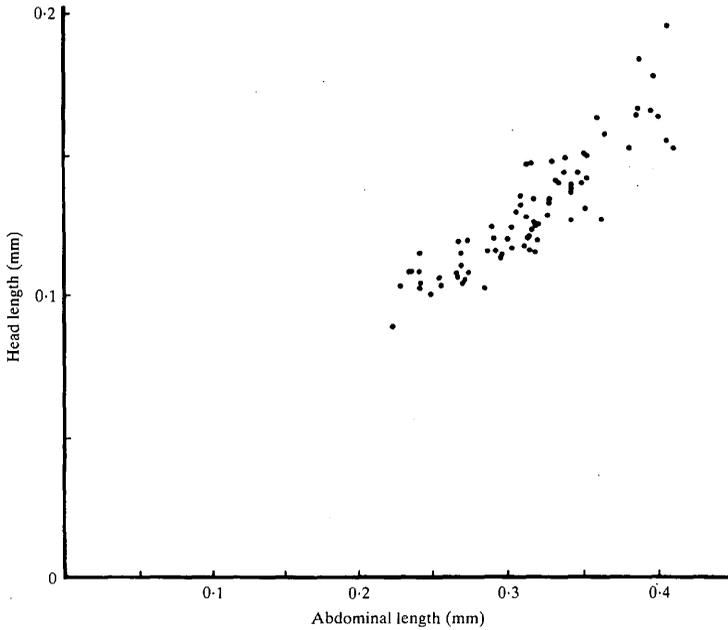| Part	Relative length in head units	Measured length for wasps with body length 0·6–0·7 mm (mm)
Flagellum	0·88 ± 0·08	0·20 ± 0·02
Scape	0·58 ± 0·07	0·13 ± 0·02
Abdomen	2·41 ± 0·36	0·54 ± 0·08
Head length	1·0	0·22
Pronotal height	1·36 ± 0·10	0·30 ± 0·02

Means ± 1 S.E.

Fig. 2. Head length plotted against body length. Linear correlation coefficient: $+0\cdot896$ $(N = 78)$. Equation of linear regression $DE = 0\cdot415FG$ (mm), where DE = head length and FG = abdominal length. Line of regression passes through the origin.

(Fig. 1). By comparing the correlation between two perpendicular measures (head and abdominal length) with the correlation found between nearly parallel measures (head and flagellar length), the possible distortion due to deviation from a completely lateral profile was evaluated. The leg span, height of the pronotum and antennal angles were also measured from the photographs of wasps standing on a level substrate. In addition, the lengths of the head and the antennal segments were measured directly from anaesthetized specimens using a binocular microscope and ocular micrometer (Table 1).

RESULTS AND DISCUSSION
Allometry of body parts

Over the range of wasp sizes used in this experiment, linear proportional relationships were found between scapal length and head length $(r = +0\cdot867, N = 78)$, between flagellar length and head length $(r = +0\cdot752)$, and between head length and abdominal length $(r = +0\cdot898)$ (Fig. 2). For all three correlations, the power (log–log) regressions showed linear relationships over the range of wasp sizes used

(exponent of regression between 0·96 and 1·01). Thus, the correlations measured between body angles and surface curvature are not significantly confounded by changes in the relative proportions of body parts, despite differences in body length between wasps. Since the relative proportions of the wasps do not differ significantly, the radii of the models can be compared to changes in body angle and height in terms of head length units. Since the correlations of scapal or flagellar length with head length did not differ significantly from the correlation found between head length and abdominal length, any deviations of the wasps' positions from exact lateral profiles were presumed to be not sufficient to introduce a significant bias in the angle measurements.

Body posture

No significant change was found in the height of the pronotum above the glass bead surface $(FO-R)$ $(1·4 \pm 0·1 \, mm)$ over the range of bead radii $(r = +0·036)$. The relationship between the distance of the pronotum from the centre of the bead (FO) and bead radius (R) was strictly linear $(r = +0·994)$ (Fig. 3). In addition, no significant correlation was found between the height of the pronotum above the mesothoracic pretarsus and the radius of the bead $(r = +0·11)$. These results indicate that the wasp keeps its body at a preferred height above the host surface.

From these data, it is not evident how the wasp controls its height above the substrate, or to what degree the wasp must actively adjust its position relative to the host. For example, the wasp could change the span between contralateral legs in order to raise or lower its body. To investigate the basis of the wasp's constant height above the substrate, the change in the height of the wasp above the centre of the glass bead with changing surface curvature was modelled (Fig. 4A). If the leg span remains constant, then the distance between the pronotum and the bead centre is given by:

$$FO = H + \sqrt{R^2 - \frac{w^2}{4}}, \tag{1}$$

where FO = distance between pronotum and bead centre, H = standing height of pronotum above the substrate, R = host radius and w = span between contralateral mesothoracic tarsi (Fig. 4A).

Using observed values for the height of the pronotum when the wasp is standing on a flat surface $(1·4 \pm 0·1$ head units) and the span of the mesothoracic legs perpendicular to the long axis of the wasp $(1·6 \pm 0·1$ head units) (Table 1), the pronotal–bead centre distance can be calculated and plotted against the observed data for wasps on models of differing relative radius (Fig. 3). From these, it is apparent that over most of the range of host radii the calculated values correspond closely with the observed data. This suggests that the wasps do not need actively to adjust either leg span or body height above the pretarsi in order to maintain the preferred height above the substrate. Only when host diameter is relatively small, close to the leg span distance itself, is there an apparent departure from the predicted line (Fig. 3), indicating some adjustment of wasp height to maintain the distance

between the wasp and the surface. This adjustment probably results from a re-
duction of leg span in order to maintain contact with the host surface. However, the
change in leg position must be very small, since no significant change in the height of
the pronotum above the mesothoracic pretarsi was observed. The maintenance of the
body at a preferred distance from the substrate has been shown for other insects
(Cruse, 1976; Kemmerling & Varjú, 1982), in which the placement and relative
position of the tarsi on the substrate depends upon contact of the tarsi with a
supporting surface (Cruse, 1979).

Clearly, for very small hosts the adjustment of leg position to maintain body height
could provide the wasps with some measure of host curvature. However, it would not
appear to provide significant measures over the range of host sizes accepted by the
wasp (radius > leg span).

An important factor in considering the possible role for the legs in the detection of
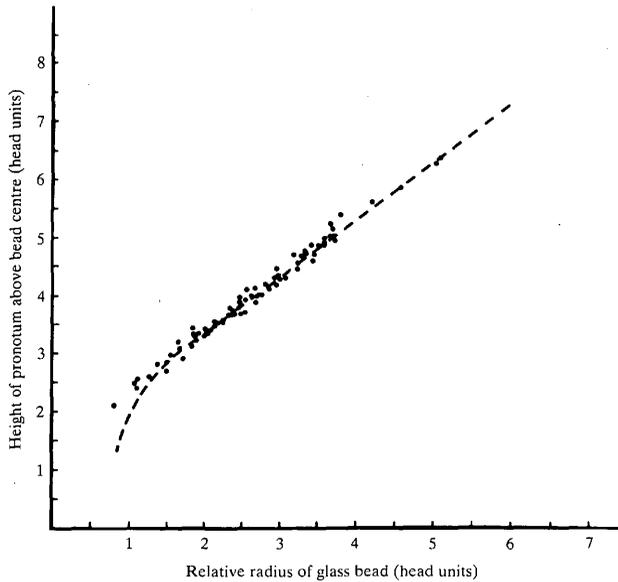curvature is the walking mechanism of the wasp. Like most other insects, including

Fig. 3. Height of pronotum above the centre of glass bead plotted against relative bead
radius. Linear correlation coefficient: $+0.996$ ($N = 78$). Equation of linear regression;
$FO = 1.00R + 1.35$ head lengths, where $FO = $ height of pronotum above centre and
$R = $ relative bead radius. Y-intercept $= 1.35$ head lengths. Broken line: plot of the
function (see text):
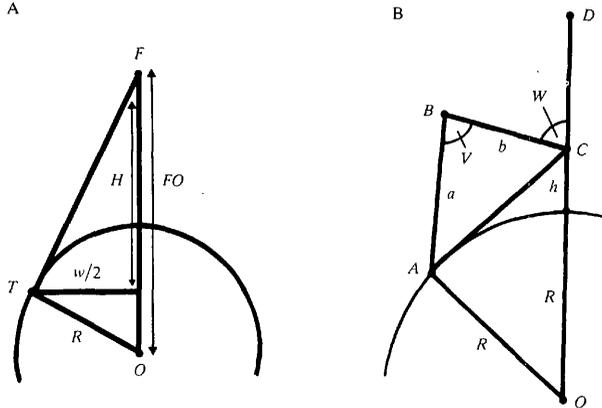
$$FO = H + \sqrt{R^2 - \frac{w^2}{4}}.$$

Fig. 4. Diagrammatic view showing relationships between body parts. Lettering as in Fig. 1. (A) Height of pronotum above glass bead centre (FO) as a function of radius (R), leg span (w) and standing height (H). (B) Scapal–head angle (W) as a function of scapal length (b), height of scapal base above substrate (h), flagellar–scapal angle (V), flagellar length (a) and radius (R).

Apis mellifera (Zolotov, Frantsevich & Falk, 1975; Delcomyn, 1985), *Trichogramma* appears to use the alternating triangle gait, at least when travelling in a straight path. In this case, during most of the walking cycle, only three legs are in contact with the substrate simultaneously (Delcomyn, 1981). A proportionately shorter time is spent with all six legs on the ground, a transitory period as the legs rapidly change position relative to each other and the body of the wasp. When only three legs contact the host, only two legs are ipsilateral. The three points at which the legs contact the surface thus describe a regular triangle on a plane which transects the surface of the host object, and can be circumscribed by a circle, which in the case of spherical hosts forms the perimeter of the transection. Clearly, the circle defined by the three contact points can be fitted to any arbitrary spherical surface of greater radius than that of the circle, independently of the radius of the sphere. Thus, contacting the substrate at only three points cannot provide the wasp with any information about the curvature of a spherical or near-spherical host, unless the points lie on the same line.

During the short period in which all legs contact the surface of the host, some relationships of relative position do arise between the legs and the body of the wasp which are dependent upon surface curvature. However, these relationships change rapidly during this period because of the forward movement of the wasp's body. Furthermore, it is unlikely that the wasp can use relative leg position to detect differences in curvature because of the small distances between the wasp's legs. For ipsilateral legs, the distance between the mesothoracic pretarsus and the pro- or metapretarsus is only 0·75–0·85 head units. For such small distances there is little

proportional change (<5 %) in the height of the mesothoracic pretarsus relative to the pro- and metathoracic pretarsi for most of the range of host radii tested. A larger change in leg position is required to maintain body height only when the host radius is near or below one head unit. Since such hosts are too small for larval development (Salt, 1935), this change of relative leg position could serve as a cue for host rejection, but would not provide a useful measure of size for larger hosts.

The alternate triangle gait is well suited to maintaining the body of the wasp at a fixed height and angle above the substrate. Furthermore, by keeping the span between contra- and ipsilateral legs relatively small, the wasps reduce the amount of change in height above the substrate without actively adjusting their posture. This suggests that the effect of the legs may be to maintain the body as a platform at fixed height and attitude with respect to the surface. Using the antennae, and possibly the angle between the body and the head, the wasp could measure the slope of the surface away from the centre of this platform to estimate curvature. To explore this possibility, changes in the neck and antennal angle with surface curvature were determined.

Correlation of model radius with body angles

Of the three body angles measured, only neck angle (Fig. 1) showed no significant correlation with model radius ($r = +0.09$). The neck angle is fixed at between 70° and 80°, maintaining the head at a constant angle and height relative to the legs and thorax. The same angle was observed on wasps walking or standing on a level substrate. During oviposition, the head is raised further from the substrate and retracted against the thorax so the neck angle is decreased to 60–65°.

In contrast, both the flagellar–scapal angle and the scapal–head angle (Figs 5, 6) change significantly as model radius is varied. The greatest linear correlation coefficient was found for the scapal–head angle ($r = -0.81$), the angle decreasing as radius is increased (Fig. 5). The relationship is non-linear and concave, the magnitude of the slope decreasing with increasing radius. The scapal–head angle ranges between 135° and 70° over a range of model radii from 0.75 to 5.0 head units.

The linear correlation coefficient between the flagellar–scapal angle and model radius was also significant and negative ($r = -0.57$) (Fig. 6). The flagellar–scapal angle ranges between 100° and 70°, decreasing with greater model radius. Flagellar–scapal angle and scapal–head angle with host radius also correlate significantly with each other ($r = +0.83$); the relationship is linear and has a positive slope (Fig. 7).

These observations suggest that *Trichogramma* could use the scapal–head angle to measure surface curvature. By maintaining its body at a fixed height and attitude with respect to the substrate, and the head at a fixed angle to the body, the wasp can determine the tangential slope of the substrate using its extended antennae. This method clearly has the advantage of utilizing the greatest linear span available to the wasp. The changes in scapal–head angle (Fig. 5) could also provide information about surface curvature over a wide range of host sizes. Since the relationship is concave, the sensitivity of the measure apparently decreases for comparatively large hosts. However, it is unlikely that the wasps require an as accurate measure of
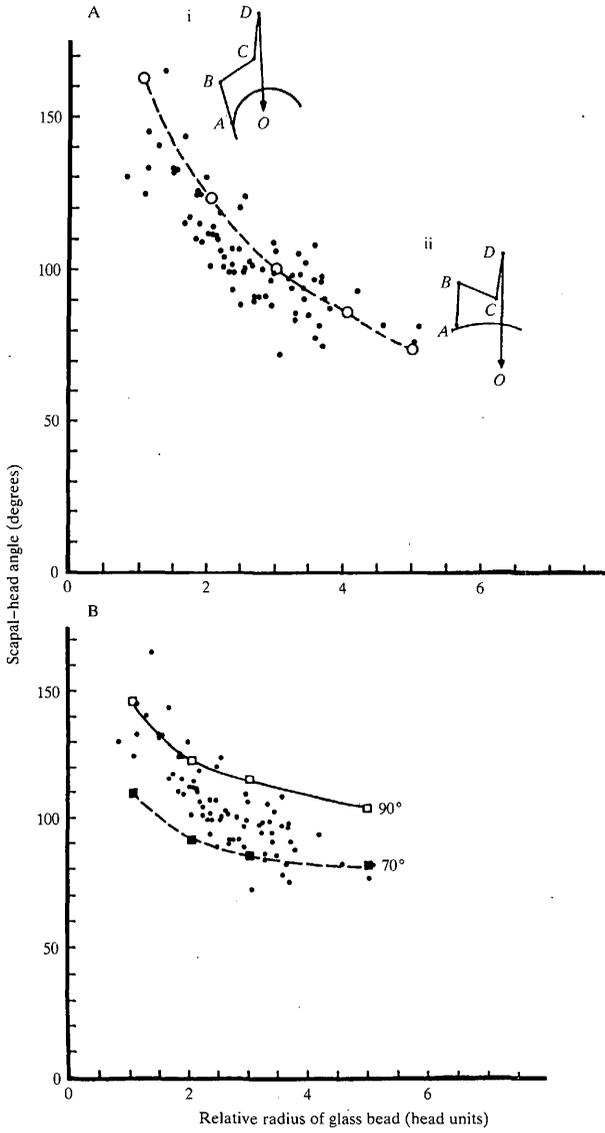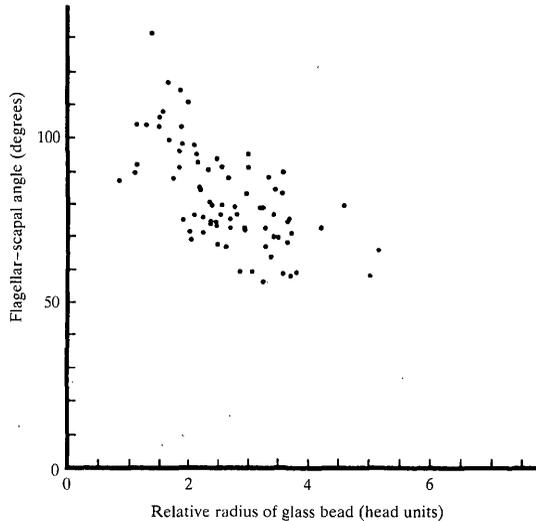
Fig. 5

Fig. 6. Flagellar–scapal angle plotted against relative bead radius. Linear correlation coefficient: -0.57 ($N = 78$). Equation of linear regression, $V = 108 - 9.6R$, where $V =$ flagellar–scapal angle and $R =$ relative bead radius.

curvature for large hosts (radius > 2.5 head units), since small variations in the number of progeny allocated to larger hosts will be less detrimental than for small hosts (Klomp & Teerink, 1967). Very large objects (radius > 6 head units) are rarely accepted as hosts (Salt, 1935; de Jong & Pak, 1984), probably because the wasp cannot distinguish the host object from the substrate on the basis of such small curvatures and scapal angles.

In order to contact the substrate it is only necessary for the scapal–head angle to change. However, a significant change in flagellar–head angle was also found for different surface curvatures. The linear correlation between scapal–head angle and flagellar–scapal angle (Fig. 7) suggests that the flagellar–scapal angle may be regulated by a reflex response to the scapal–head angle, or that both are adjusted by a common motor mechanism, resulting in a greater extension of the antennae the further they need to be lowered to the surface. This coupling of the flagellar–scapal

Fig. 5. Scapal–head angle plotted against relative bead radius. Linear correlation coefficient: -0.81 ($N = 78$). (A) Comparison of observed scapal–head angles with values obtained for model in which flagellar–scapal angle changes with scapal–head angle (open circles) (see text for details). Inset diagrams show angles formed between antennal segments and head for (i) small radius models and (ii) large radius models, both with respect to the fixed head–model centre axis *DO*. Abbreviations as in Fig. 1. (B) Comparison of observed scapal–head angles with values obtained for models in which flagellar–scapal angle is fixed at 70° (solid squares) and 90° (open squares) (see text for details).
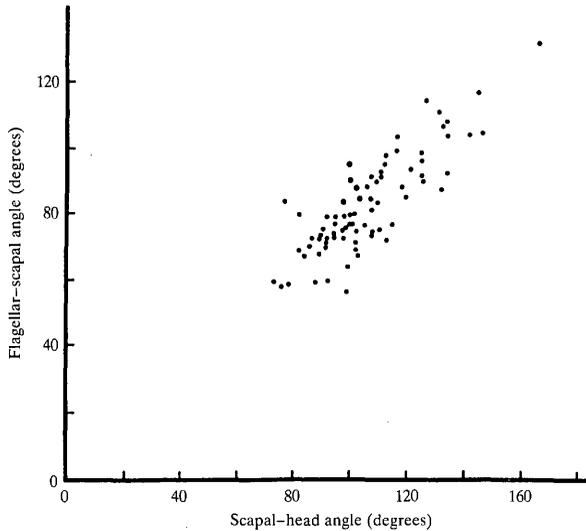
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Fig. 7. Flagellar–scapal angle plotted against scapal–head angle. Linear correlation coefficient: +0·83 ($N = 78$).

angle to changes in the scapal–head angle is of particular significance for the function of the antennae as surface curvature detectors. By increasing the antennal extension as they are lowered, the rate of change in the scapal–head angle with respect to radius is also increased for more highly curved surfaces. As a result, the wasp is able to make a more sensitive measure of surface curvature. This effect can be shown by modelling the changes in both angles for surfaces of different curvatures (Fig. 4B). With the height of the wasp constant, and the relative lengths of the flagellum and scapal sections of the antennae fixed, the change in the scapal–head angle can be estimated by:

$$W = 180 - \cos^{-1}\left[\frac{L^2 + 2Rh + h^2}{2L(R+h)}\right] - \sin^{-1}\left[\frac{a}{L}\sin V\right], \tag{2}$$

where:

$$L = \sqrt{(a^2 + b^2 - 2ab \cos V)} \tag{3}$$

and W = scapal–head angle, L = antennal extension, a = flagellar length (AB), b = scapal length (BC), R = host or model radius, h = height of antennal base above substrate and V = flagellar–scapal angle. If the measured values for flagellar length, scapal length and antennal base height above the substrate (Table 1) are substituted in equations 2 and 3, the effects of changing the flagellar–scapal angle can be analysed. When the flagellar–scapal angle is fixed, the change in the scapal–head angle with host radius is reduced (Fig. 5B). The slope of the relationship is less steep

than that observed, and the angle does not change appreciably over most of the host range. Setting the flagellar–scapal angle at different constant angles changes the slope slightly, but does not significantly improve the sensitivity of the response. None of the curves obtained agrees well with the observed changes in scapal angle.

However, the observed flagellar–scapal angle is not constant for hosts of different radii. Instead, the flagellar–scapal angle is given by:

$$V = 108 - 9{\cdot}6R, \tag{4}$$

the empirical relationship measured previously for different host radii (Fig. 6). If equation 4 is substituted in equations 2 and 3, then the calculated relationship obtained between scapal–head angle and model radius is a closer approximation to that observed (Fig. 5A). Evidently, the change in flagellar–scapal angle acts to amplify the differences in scapal–head angle, not only increasing sensitivity most for hosts with smaller radii, but also maintaining a greater slope over a greater range of larger hosts (Fig. 5A).

In deriving this model, it was assumed for simplicity that the points D, C and O lie on a straight line (Fig. 4B). As measured in the experiment, the angle DCO was found to be relatively small ($5{\cdot}7 \pm 2{\cdot}3°$), indicating that the estimates obtained from equations 2, 3 and 4 for the scapal–head angle may be slightly lower than the actual values. However, the resulting small increase in the predicted values of the scapal–head angle does not appreciably change the fit of the model to the observed values (Fig. 5A), nor does it invalidate the model as a first approximation.

The proposal that the wasp determines surface curvature by measuring changes in the maximum scapal angle is also supported by morphological studies of the antennae (J. M. Schmidt & J. J. B. Smith, in preparation). In most insects, groups of hairs in the joint regions of the legs, neck and antennae act as proprioceptors providing information about the relative displacement of body parts (McIver, 1985). In *Trichogramma*, hairplates found at the antennal joints (J. M. Schmidt & J. J. B. Smith, in preparation) could provide the wasps with information about the angles described previously. The position of the flagellum is monitored by a dorsal and a lateral hairplate. The arrangement of these hairplates is such that they can provide the wasp with information about antennal position only when the flagellum is near the limits of its movement, either retracted against the scape or fully extended. It is unlikely that these hairplates can contribute much to the wasp's curvature measures. The scapal–head joint is monitored by four distinct hairplates arranged around the ventral surface of the scapal radicular base. As the scape moves, the individual hair sensilla make contact with the socket of the antenna and are displaced to differing degrees from their resting orientations. Clearly, these sensilla could provide the wasp with detailed information about the scapal–head angle and hence surface curvature.

Although the correlations observed in these experiments do not demonstrate conclusively the mechanism by which *Trichogramma* measures surface curvature, they do indicate a set of body postures and relative angles which could be used to mediate the wasp's response. Since the wasps can respond to host curvature in the absence of other external cues, including visual information (Schmidt & Smith,

1985*a*, and in preparation), some mechanism involving proprioceptive cues appears most likely. In the absence of other significant changes in the relative position of body parts with surface radius, measuring the antennal angles is an obvious method of curvature detection.

Similar use of the antennae has been implicated for the egg parasitoid *Telenomus heliothidis* Ashmead (Hymenoptera: Scelionidae) (Strand & Vinson, 1983*a*). These wasps require both chemical and physical cues to mediate host acceptance (Strand & Vinson, 1982) and investigate the host surface by drumming with their elbowed antennae in a manner similar to that used by *Trichogramma* (Strand & Vinson, 1983*b*). By observing the response of *Telenomus* to models of various shapes, Strand & Vinson (1983*a*) have suggested that host shape is sensed with the antennae. Antennal measurement of host size and shape has also been proposed for *Encarsia formosa* Gahan (Hymenoptera: Chalcidoidea: Aphelinidae) (van Lenteren, Nell & Svenster-van der Lelie, 1980).

That insects use their antennae to determine the topography of their local surroundings suggests itself intuitively, as indicated by the common use of the term 'feelers' (Fühlern) for these structures. Despite this obvious function, relatively little work has been done to show how the mechanosensory structures associated with the antennae could be involved·in the detection of form or texture. *Trichogramma*, with its specialized dependence upon information about the geometry of hosts, is a good candidate for the detailed investigation of these sensory and integrative systems.

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