THE ROLE OF THE TRIOMMATIDIUM IN THE VISUAL BEHAVIOUR OF APTEROUS APHIS FABAE SCOP.

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Abstract

The triommatidium is a group of three ocular facets, mounted on a tubercle and appended to the postero-lateral part of the compound eye in most aphids. It is derived from compound eye facets, differentiates precociously in the embryo and appears to act as a functinally independent receptor in the adult.

Reorientation and probing in apterous, female A. fabae was examined on the flat and on wax ridges. To reach a black pillar on the flat, nymphs and adults less than 90 mins. old followed sinuous paths, adults over 12 hrs. old followed simple curved paths and adults between 3 and 8 hrs. old followed paths which partially orbited the pillar, without ever reaching it.

Extirpation of the triommatidium prevented the paths previously typical of nymphs and adults under 12 hrs. old and it was assumed that stimulation of the triommatidium was involved in the expression of these behaviour patterns.

Probing was apparently attributable to a critical angle subtended at the compound eye by an image dead ahead and the same response was seen in aphids walking along ridges.

Aphids on ridges made abrupt turns and climbed down from the ridge when the angular acceleration of an image across the compound eye reached a critical value. The movement of an image into or out of the triommatidial field of view apparently elicited probing.

It was inferred that the compound eyes and the triommatidia comprise functionally separate visual systems which mediate different responses in walking aphids when simplified visual situations are presented under controlled conditions. A "compromise" response apparently occurs in adults between 3 and 8 hrs. old which leads to the avoidance of visually salient features in the aphid's vicinity and may contribute towards dispersal behaviour in young adult apterae.

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INTRODUCTION

The Occurrence of the Triommatidium

Nomenclature

The word "triommatidium" denotes the distinct group of three large, ocular facets which usually protrudes from the postero-lateral surface of the compound eye in aphids (Fig. I). The cuticular process which bears these facets is termed the ocular tubercle and the term has been used by some authors to denote the process and facets together (Grasse 1951; Torre Bueno 1962; Imms 1964).

The presence of a triommatidium in aphids has been known at least since 1843, when it was described by Kaltenbach. This author did not give it a name, other than "Höckerchen" or "little lump", and Witlaczil (1882) merely refers to it as a "group of three facets". It has since been described as a "supplementary eye" (Lydekker 1896), "eyelet" (Theobald 1926-29), "larval eye" (Weber 1930), "triommatidium" (Hille Ris Lambers 1935) and "primary compound eye" or "proto-oculus" - translations of the Japanese "gensei-fukugan" (Watase 1961a & 1961b).

Distribution

Visual organs supplementary to the compound eyes and ocelli have been found in the Aphidoidea (including the Adelgidae and

Phylloxeridae) and also in the Coccidae and one genus of the Psyllidae, but are best considered separately in each taxonomic group.

Families and sub-families are classified according to Kloet and Hincks (1964), although the generic and specific names quoted from some texts are not always those used by these authors. Where possible, accepted synonyms are given.

Aphidoidea

According to Imms (1964), a triommatidium is present in "many aphids". Other authors are similarly vague about the actual occurrence of this structure within the super-family, although isolated references occur. Theobald (1929) refers to the absence of ocular tubercles (by which he means the triommatidial facets as well as the tubercle itself) as a characteristic of the genera Saltusaphis Theobald (syn. Subsaltusaphis Quednau 1953) and Thripsaphis Gillette (syn. Trichocallis Borner 1930), both in the family Callaphidae, subfamily Saltusaphidinae. The description of Subsaltusaphis ornate Theobald by Hille Ris Lambers (1935) contains the following:

" ... eyes without triommatidion, but with one facet isolated, on the upper side of the posterior half."

Stroyan (1952) included the following entry in his key: "Compound eyes without any apparent posterior process or triommatidion (representing the larval eye) ..... Coloradoa Wilson 1910." Coloradoa is placed by Kloet and Hincks in the Aphididae, Myzinae. Watase (1961b) lists Capitophorus hippaphaes Walker (Aphididae,

Myzinae), Eulachnus thunbergii Wilson and Cinara pineti Koch (both Lachnidae, Cinarinae) as lacking a triommatidium as newly-hatched larvae.

In species which possess it, the triommatidium is always present from the embryo stage, while the compound eye may not develop fully until the later instars. For this reason, the triommatidia are sometimes referred to as "persistent larval eyes" (Weber 1930; Pflugfelder 1936) or as "primary compound eyes" (Watase 1961a).

In the Adelgidae and Phylloxeridae, the larval forms all have triommatidia only (Borner 1908) and the three facets are arranged in a triangle, either on the side of the vertex (Fig. 2), or on the gena (Fig. 3). In the adult apterae, the triommatidia remain the only visual organs. In the nymphal alatae, small round or oval facets develop anteriorly to the triommatidia (Grasse 1951), although they are divided by varying areas of cuticle and not regularly arranged at first (Fig. 4). These initial, as yet unpigmented ommatidia are the predecessors of the normally-pigmented, numerous and regularly-arranged ommatidia of the compound eyes (Fig. 5). Whereas the facets of the larval and nymphal triommatidia protrude only slightly from the surface of the head, in the adult the ocular tubercle forms a noticeable excrescence.

Several members of the Thelaxidae and Pemphigidae (Pemphigus, Tetraneura, Caratovacuna etc.) also lack compound eyes, except as adult alatae (Witlaczil 1882; Watase 1961a). Compound eyes first become discernible in the third nymphal instar of the alatae, as speckles

of pigment between the triommatidia and the antennae.

In other aphids within these families (e.g. Anoecia corni Fab.), compound eyes are absent from the first two instars of all forms. The compound eyes develop in the third instar nymphs of both apterae and alatae, except in apterae hatching from overwintering eggs, where they never develop (Watase 1961a).

In most of the Aphididae, the compound eyes are present in addition to the triommatidia from the larval stage. They can be seen as rudimentary structures in the unborn embryos of Macrosiphum (Fig. 6 and are visible as groups of distinct facets in the larvae of several other species (Figs. 7 & 8 and Table I).

Coccoidea

Larval and female coccids have no other visual organs than the triommatidia (Weber 1930). The males of many species have several large, isolated facets, which superficially resemble ocelli, and with direct connection to the optic lobes of the brain that shows them to represent a secondarily divided compound eye (Pflugfelder 1936; Grasse 1951; Figs. 9 & 10). In Pseudococcus Westwood, Berlese (1893-1909) established that the small, lateral facet represents a triommatidium and Pflugfelder (1936) describes how the imaginal eyes (compound eye) develop alongside the triommatidium in male Parthenolecanium corni (Bouche). In other species, such as Drosichoides haemoptera, a more normal type of undivided compound eye occurs (Fig. II).

Psyllidae

The supplementary eyes present in the genus Livia Latreille (Imms 1964) are referred to as "pre-ocular tubercles" by Crawford (1914) and by Grasse (1951). They are situated anteriorly to the compound eyes, as opposed to the posteriorly placed triommatidia of aphids (Fig. 12). The main anatomical literature on the Psyllidae (Scott 1876; Witlaczil 1885; Edwards 1896; Weber 1929 & 1930 etc.) takes the genus Psylla Geoffroy as representative of the family and gives no information on the visual organs of Livia. To suggest that the pre-ocular tubercle may be the homologue of the triommatidium would be premature without a close neurological investigation of the former, a task outside the scope of this work.

Aleyrodidae

Although no recognisable triommatidium is present in the Aleyrodidae, the visual organs are unusual. The compound eyes are divided into dorsal and ventral parts, the dorsal eye having smaller facets than the ventral eye (Fig. 13). How far this division may be compared with that occurring in the compound eye of some male coccids, or with the adult compound eye and triommatidium of aphids, remains at present a matter for speculation.

The Morphology of the Visual Organs in Insects

Insect visual organs are usually classified into compound eyes, ocelli and stemmata and the type of receptor from which the

triommatidium may be derived is not immediately apparent.

The Compound Eye

Compound eyes are present in most adult insects, usually bulging out to either side of the head so as to provide a wide field of view. Like other insect visual organs, the compound eyes are in a constant state of neurological activity from the light impinging upon them during the lifetime of the insect (Dethier 1963). The compound eye is composed of a number of transparent facets in the cuticle. Each facet overlies an elongated light-sensitive system, which is capable of receiving incoming radiation and translating it into electrical energy. The complete unit is called an ommatidium.

An ommatidium consists of a distal "dioptric apparatus", which includes the cornea and underlying crystalline cone, together with the proximal retinula, which is composed of eight retinal cells grouped around the central rhabdom. The whole ommatidium is curtained by pigment cells containing a black visual pigment. The retinal fibres pass through a fenestrated basement membrane directly into the optic lobe of the brain where some synapse at the periphery and others synapse further in (Hanstrom 1927).

Aphid compound eyes have relatively few ommatidia and those of the apterous form of a particular species usually have less than the alate form. First instar nymphs of apterous Aphis fabae Scopoli have about sixteen ommatidia in each compound eye. These are small, round or oval facets with a reddish-brown pigmented region beneath

each one, separated from one another by undifferentiated cuticle (Fig. 7) In subsequent instars, the number of ommatidia increases progressively to about seventy-eight in the adult.

The Ocellus

In addition to the compound eyes, adult insects and the larvae of exopterygote insects typically have three simple eyes called ocelli. In aphids, these are present only in the alate forms (Theobald 1926, Kalmus 1945). The ocellus typically has a single, thickened, cuticular lens, beneath which lie a number of retinal cells, usually arranged in groups around central rhabdoms. Pigment may be present between the groups of cells or at the periphery of the whole ocellus. The retinal fibres pass out of the ocellus and extend at least halfway down the ocellar nerve, making repeated synaptic contacts with the axons of second order cells lying in the pars intercerebralis of the brain (Ruck et al. 1964; Goodman 1970). Where the ocelli are best developed, the lens and retina are well differentiated, but in some insects the ocellus is no more than an unpigmented spot in the cuticle, beneath which lie a few irregularly arranged visual cells (Dethier 1963).

The Stemma

Stemmata are the only visual organs present in larval endopterygote insects and are rather variable in structure. They are

typically somewhat similar to individual ommatidia, with a thick, domed lens beneath which lies a broad crystalline cone and a group of seven retinal cells. The retinal fibres pass directly to the optic lobe of the brain (Dethier 1942; Fox & Fox 1964). In some larvae which possess only one stemma on each side of the head, a single lens overlies several retinulae.

The Triommatidium

Structure

In larval aphids, the triommatidium consists of three facets arranged in a t riangle and directed laterally (Figs. 2, 3 & 14). During the nymphal instars, the ocular tubercle grows by bulging out in the centre of this triangle so that the facets gradually lose their lateral orientation and come to lie in such a position that one is directed forwards, one backwards and upwards and one backwards and downwards (Fig. I). Watase (1961a & 1963) distinguished between them by calling them the ventral, dorsal and posterior facets respectively and the same terminology is used in the present work.

The ocular tubercle increases in basal diameter very little during the nymphal instars and is usually about 20-30μ in diameter in larvae hatching from overwintering eggs (Table I). The facets are about 10μ in diameter on hatching, with the posterior facet often a little larger than the other two. The dimensions of the facets in Anoecia corni Fab., at the various stages of its life cycle, are shown in Table 2.

The fine structure and innervation of the triommatidium has been studied in Pemphigus Hartig and other genera. The ommatidia are broader and shallower than those of the compound eye (Witlaczil 1882). The cornea is dome-shaped and projects considerably from the surface of the ocular tubercle, while the crystalline cone is greatly developed in width to give the appearance of a biconvex lens (Fig. 15). The retinal cells are usually only six in number (although this is variable) and pigment cells envelop each retinula (Pflugfelder 1936). The retinal fibres pass directly to the optic lobe and may share a common route with those of the compound eye for a part of the way (Figs. 16-19). The triommatidium of many coccids differs from that of the aphids in the presence of a single convex lens, beneath which the three ommatidia are fused (Pflugfelder 1936) (Fig. 20).

Apterous adult Aphis fabae were embedded in "Paraplast" and sagittal sections were made through the head. Sections were stained using Mallory's Triple Stain (which coloured the nerve fibres mauve) or Buxton's Silver Nitrate Method (which coloured the nerve fibres yellow). The preparations obtained supported the morphological descriptions of earlier authors, showing that the triommatidium is innervated directly from the optic lobe (Fig. 16).

Morphogenesis

The prima facie similarity between triommatidial facets and stemmata, which emerges from the above descriptions, is unlikely to be of any ontological significance, since stemmata are not generally

considered to occur in exopterygote insects. An intriguing coincidence occurs, however, with some lepidopterous larvae, where the cuticular lens of each stemma is secreted by three epidermal cells and may consist of three small, separate facets. The crystalline cone is likewise secreted by three cells and may have a tripartite structure (Chapman 1969). The superficial appearance of a tripartite stemma of this type would be similar to that of the triommatidium of a first instar aphid.

Since the innervation of the triommatidium obviates its interpretation as an ocellar structure, it has been suggested that it constitutes a precociously differentiating part of the compound eye (Grasse 1951; Watase 1961a & 1961b). To dismiss it as such, however, does not explain its relationship with the adult compound eye and would seem an over-simplification. If the triommatidium evolved from part of a normal compound eye, it has since become morphologically specialised to a degree which suggests its functional independence.

The appearance of a well-developed triommatidium in nymphs, when the compound eye is in a rudimentary condition, would support this theory of functional independence. Moreover, the persistence of the triommatidium throughout the adult stage as a morphologically distinct organ suggests its continued necessity as a supplementary receptor, although it may not receive information in the same way as does the compound eye. If the triommatidium were no more than three compound eye ommatidia, which develop precociously to constitute the larval visual organs, these may be expected to become less obvious as the compound eye develops and to integrate with it as normal facets. For the triommatidium to remain a morphologically discrete visual

unit throughout the life of the aphid suggests a specialisation of some phylogenetic (and hence behavioural) significance.

THE FUNCTION OF THE TRIOMMATIDIUM

It is not clear, from the literature cited so far, whether the triommatidium is adapted to perceive visual information of a particular type. Nor is it clear how the information which it receives is correlated with that received by the compound eye. In order to understand the functioning of the triommatidium, it is necessary to consider first the various ways in which visual receptors may interpret the environment of an insect and the behavioural responses which visual stimulation may elicit.

Wavelength Discrimination

Wavelength discrimination is apparently attributable to both compound eyes and stemmata. The retina is usually more sensitive to some wavelengths than to others, with peaks of sensitivity in the near ultra-violet, green and occasionally red regions of the spectrum (Cameron 1938; Weiss 1943; Weiss et al 1943; Autrum et al 1953; Pospisil 1971). Most insects can perceive wavelengths well into the ultra-violet which are invisible to man.

Ocelli may also be capable of wavelength discrimination, in some insects at least. Those of Periplaneta are sensitive to the same overall spectrum as are its compound eyes, with a single sensitivity peak at 500μ, in the green part of the spectrum (Goldsmith et al. 1958). In Apis, the ocelli show two sensitivity maxima, at 490μ and at 335-340μ respectively (Goldsmith loc cit).

Intensity Discrimination

The discrimination of changes in the overall light intensity is a basic ability of all three main types of visual organ. The threshold value for intensity discrimination may be expressed as the smallest percentage change in illumination detectable by the eye. Early behaviouristic work estimated such threshold values from the smallest intensity change in the compound eye necessary to produce certain reflex responses in the insect. Thus Wolf (1933 a & b) obtained a threshold value of 24% for the compound eye of the honey bee. The true threshold of sensation may, however, be considerably lower than the observed response threshold and more recent electrophysiological studies have indicated threshold values in the region of 7.5% for compound eyes (Burtt et al 1966).

The ocelli are also well adapted to the immediate perception of small changes in light intensity (Ruck 1958 b). The corneal images produced by ocelli are too far behind the retina to be of any functional significance and it is unlikely that ocelli are capable of evoking behavioural responses on their own (Cornwell 1955). They are generally regarded as "stimulatory organs" which increase the sensitivity of the compound eyes to changes in light intensity. The rhinaria present on the antennae of many aphids may also be photoreceptors, not olfactory organs as was originally thought. Booth (1963) suggests that they may act as "stimulatory organs" which increase photokinesis, in the same way as do the ocelli.

Perception of Flicker

In behavioural terms, changes in the overall light intensity must be considered in conjunction with intensity changes between different parts of the compound eye. Any pattern of varying light intensities which moves in relation to the compound eye will cause changes in the amount of light impinging on individual ommatidia. The translocation of, say, a vertical black stripe (against a white background) laterally across the ommatidia would have an effect on each ommatidium similar to the brief interruption of a light source. The perception of this "flicker" effect between ommatidia is instrumental in the visual orientation of insects with well-developed compound eyes.

The dark interval between two light impressions is called the "flicker frequency" and an important limiting factor in visual perception is the maximum value of flicker frequency which can be discerned by an insect, above which the images fuse into a single, continuous stimulus. This value alters with the intensity of the light falling on the eye, being greatest at moderately high illumination and lower when the light intensity is either low or very high.

Under normal illumination, the neurones of the optic nerve of Dytiscus discharge at different rates and it is these differences in the rate of discharge that make the perception of a visual pattern possible (Adrian 1937). When the eye is stimulated by a very bright light, the optic nerve shows rhythmic oscillations in its electrical potential at the rate of 20 to 40 per second. These oscillations show that the neurones are discharging simultaneously and imply the

absence of a visual pattern in the retina.

The compound eye can detect flicker occuring at 200 to 300 flashes per second in fast-flying diurnal insects and 10 to 40 flashes per second in nocturnal insects (Mazokhin-Porshnyakov 1969a & b). Glossina reacts to flicker at least up to 100 flashes per second and also to rates as low as one flash per 25 seconds. The weevil Chlorophanus responds to a movement of its visual field of 1.3° per minute, which is less than a quarter of the speed of the large hand of a clock (Hassenstein 1951). In addition to luminosity differences, it has already been mentioned that some insects will respond to the flicker produced by differences in the plane of polarisation of light (Korte 1965).

Studies of electrical activity within insect eyes have also shown that many insects fail to discriminate between the higher rates of flicker. Compound eyes give an electrical response to light, which can be measured to produce an electroretinogram (abbreviated to ERG). The electrical response may be measured by implanting one electrode through the surface of the cornea to the appropriate depth and placing the other at any convenient point on the body. Although this is a relatively crude measurement to make, and one which is subject to a host of experimental variables, concealed in the ERG is the code to some of the primary events that occur in photoreceptors when they are stimulated by light (Dethier 1963).

The form of even the most basic type of ERG has suggested to many authors that the summation of a number of components is

involved (Hartline 1928; Jahn et al. 1942; Autrum 1950; Burtt et al. 1964a). With a few exceptions, a negative component commonly originates in the retina and a positive component in the optic ganglion. The relative prominence of the two components varies with the anatomy of the eye and certain external factors. An ERG in which both component waves are strongly expressed usually indicates a very high threshold of flicker frequency (Autrum et al. 1951).

Superimposed upon these basic components, "on" effects and "off" effects, of either positive or negative potential frequently occur as characteristic deflexions associated with the initiation and termination of stimulation respectively. These effects may be produced at different regions within the eye (Burtt et al. 1965). The "on" effect for flicker stimuli of between one second and I/200 sec. depends only on the light intensity and not on the duration of the flash (Autrum 1949). The "off" effect depends on the product of the intensity and the duration.

The results obtained from the ERG studies of numerous authors would indicate that a close relationship usually exists between the maximum flicker frequencies at which receptors can still separate stimuli and the maximum frequencies involved in motion perception as evidenced by behavioural experiments. It is probable that any discrepancies between the results obtained by the two methods of experimentation will become resolved as behavioural recording methods become more sophisticated.

Visual Orientation : Intensity

Directed behaviour in relation to a light source (phototaxis) is shown by most insects, whether they possess compound eyes or stemmata only. Such behaviour may be dependent on comparison by the insect of the intensity of stimulation on the two sides of its body, either successively (klinotaxis) or simultaneously (tropotaxis). These responses are seen most readily in larvae, which only possess stemmata, and in insects with poorly developed compound eyes, such as the louse Pediculus (Patten 1916; Loeb 1918). Where the compound eye is well developed (e.g. in dragonflies), the comparison of light intensity on different parts of the same eye may be an important factor in orientation (Mittelstaedt 1950).

Ocelli alone are insufficient for light-directed behaviour (Homann 1924; Muller 1931; Cornwell 1955), although elimination of the ocelli may cause a temporary reversal in the direction of phototaxis (Muller 1931).

Visual Orientation : Form

Ocelli are not generally considered to be capable of form perception, whereas an appreciation of form is shown by some lepidopterous larvae, which possess stemmata only. Lymantria larvae will walk towards vertical silhouettes, such as dark paper cylinders set against a pale background. The larvae can differentiate between cylinders 9 cm. and 10 cm. high at a distance of 30 cm., always walking towards

the taller (de Lepiney 1928).

The dioptric apparatus in the stemmata of such larvae admits a relatively large amount of light and forms a clear, inverted image. Together the stemmata form twelve points of light, each representing the mean light intensity of a different area, which make up a very coarse mosaic. By movement of its head from side to side during walking, the larva is able to pick up small differences in light intensity and thus achieve a considerable degree of form perception (Dethier 1943).

The retinal image formed by the compound eye also consists of a mosaic of points of light, varying in intensity and colour. The sharpness of the image will depend upon the number of facets per unit area. If an insect responds to changes in this visual pattern, it may be regarded as having some degree of form vision.

Locusta responds to a pattern of black stripes on a white ground, being attracted to the contrast boundary at the edge of a stripe. Vertical stripes are preferred to oblique or wavy-edged lines and taller figures are preferred to short ones. If no vertical stripes are present, the more complex figure is preferred (Wallace 1958).

Bees can be trained to respond to any shape on a contrasting background. Solid figures of different shapes are not differentiated from one another, nor are broken figures. Bees readily differentiate between solid and broken patterns, however, showing a preference for broken patterns which is not easily overcome by training (Hertz 1929-1935). The number of visits paid by bees to a particular pattern

is proportional to the length of its contour. This suggests that the choice depends on the frequency of change of retinal stimulation as the bee moves, that is, on the flicker effect which the pattern produces in the eye. The settling of bees on flowers is increased if the flowers are moving slightly (Wolf 1933, 1935).

Many hunting wasps (Hymenoptera : Sphecoidea) can apparently recognise particular types of insects. Mellinus arvensis preys only on Diptera and is able to distinguish syrphid flies which mimic Hymenoptera (Hobby 1932). Such selectiveness in prey capture is strongly suggestive of a high level of form vision. Mellinus appears to stalk its prey and to sway from side to side prior to jumping on it from a distance of a few centimetres. This swaying may play an important part in form recognition.

These experiments indicate that movement is of greater importance in form perception than the ability to resolve stationary patterns. Zerrahn (1933) and Wolf et al. (1937) suggest that the perception of form may be no more than the perception of different degrees of flicker and discrimination between shapes may not depend on any qualities of configuration per se. Form perception and movement perception may thus be two aspects of the same phenomenon and both have been described as eliciting "optomotor" behaviour.

Optomotor Behaviour

An optomotor reaction is made to a change in the whole visual

pattern perceived by an insect, whether this change is due to actual movement of the objects in the visual field or to movement of the insect relative to those objects.

Visual changes which involve actual movements of objects in the visual field are termed "ex-afference" (von Holst 1954). Optomotor reactions to this type of movement have been investigated by a large number of authors (Hecht et al. 1929, 1934; Hassenstein 1950, 1951; Suzuki 1960; Thorson 1965; Turner et al. 1973; etc.). The insect is usually confined or held down while a pattern of contrasting stripes is moved past the eyes. In each case, a threshold is found for a certain separation of stripes (either spatial or temporal), which corresponds to the maximum detectable flicker frequency discussed earlier. Burtt & Catton (1966) point out that the subthreshold condition is rarely examined statistically. A threshold value for stripe width is given which produces consistent results, but it would be of interest to know the percentage response at a stripe width slightly below this.

Changes in the visual input which result solely from the movement of the insect itself are described as "re-afference" (von Holst loc cit). Responses of insects which are walking or flying past a stationary pattern have been investigated in locusts (Wallace 1958, 1959; Goodman 1965), aphids (Ibbotson 1966) and other insects (Buddenbrock 1931).

The insect eye itself is incapable of distinguishing between these two types of image movement, but the central nervous system is sometimes able to do this (von Holst et al. 1950; von Holst 1954). When a striped cylinder is rotated around a stationary insect (e.g.

the fly Eristalis), the insect turns itself in the same direction. Spontaneous movements of the insect are not, however, hindered by the stripes of the stationary cylinder (Mittelstaedt 1962).

The optomotor responses of insects which are forced to remain stationary usually involve reflex movements of the antennae, the head or the whole body, in the direction of motion of the visual field. Insects which are free to move tend to follow the movement of the visual field. Acquatic insects will swim round a glass container if vertical stripes are rotated round it, keeping themselves in line with one particular stripe. This optomotor "station keeping" behaviour is essential in insects which live in running water to prevent their being carried away by the current. By swimming to keep the image of the stream bed or bank constant, they are in effect keeping pace with the apparent movement of the visual field (Schultz 1931; Zeisner 1934). Gregarious behaviour in locust hoppers and adults also depends on this type of reaction; when one insect advances, its neighbour advances with it and the swarm moves en masse (Kennedy 1951; Ellis 1961).

The relationship between the stimulus of a moving pattern of edges or stripes and the optomotor behaviour which it elicits is not, however, as simple nor as constant as the foregoing examples may suggest. In the house fly Musca domestica, stronger responses are elicited by a pattern of stripes moving backwards over the compound eye than by the same pattern moving forwards. A contrast boundary where movement is from light to dark elicits a stronger response than when movement is from dark to light and a broad stripe will evoke a stronger

response than either a narrow stripe or a single edge (Geiger 1974).

Where image movement is due entirely to the movement of the insect, there is often a change in orientation which tends to minimise the motion of the image across the eye. If the visual pattern is a simple one, the angle of incidence of a conspicuous object or contrast boundary is kept constant as locomotion continues. The insect turns progressively more acutely towards the object, so that it is approached along a logarithmic curve (von Buddenbrock 1931; Wallace 1958). A response of this type may be involved in food finding and in aggregation by aphids (Ibbotson 1966).

The maintenance of a constant pattern of stimulation on the retina may also account for the "light compass" reorientation seen in many insects. By keeping the angle of incidence of a distant light source (the sun or the moon) constant, the insect is able to follow a virtually straight path (Brun 1914; Buddenbrock 1917, Buddenbrock et al. 1933; Lindauer 1963; Carthy 1965). Day time light compass reorientation may also involve orientation to the heat of the sun or to the polarisation pattern of the sky.

Behaviour in which an insect reorientates by relating to a single object or light source has also been described by Tonner (1935, 1938) as a "fixation response". He suggests that it is distinct from a true optomotor response and inhibits the release of optomotor behaviour. This distinction seems arbitrary and relative, depending as it does on the apparent complexity of contrasts in the visual field. With a single source of flicker and no points of relation, the sensory input has the

same effect as the movement en bloc of a whole complex visual field. The response is optomotor in both cases.

The basic optomotor reaction is a neurophysiological response to a very specific type of sensory input, which leads to a muscular contraction, such as the head movement of locusts (Horridge 1966). Such responses, evoked in isolation under laboratory conditions, may not fully reflect the optomotor behaviour of an insect in a complex and constantly changing environment. Behaviour is always the end point of a selective process which monitors the entire sensory input and produces the appropriate afference. The initial response movement may trigger another stimulus/response sequence, as in the maintenance of stability by flying locusts. A dorsal light reaction and an optomotor reaction to the position of the horizon both contribute to the maintenance of stability in the rolling plane (Goodman 1965).

Flying locusts always turn so that the horizon is horizontal and the brighter half of the visual field is uppermost. The optomotor reaction itself is a head movement, the body then being aligned by differential wing movements, monitored by proprioceptive hair plates on the first cervical sclerites. When a locust is flying as part of a swarm, the optomotor input provided by the rest of the swarm, moving at the same rate, evokes "station keeping" behaviour. Individuals at the front of the swarm do not receive this strong optomotor input and react instead to the sight of the ground, apparently moving away beneath them, by alighting on it. The locusts which have alighted then find themselves stationary, with the swarm moving above them,

and soon take off again in response. Due to these three optomotor reactions, the swarm moves as an entity, while individuals are constantly both dropping out from it and rejoining it (Kennedy 1951).

Discussion

Behavioural studies have shown a marked correlation between the interommatidial angle and the smallest angle subtended by stripes which will still elicit an optomotor response, and it is often assumed that the ommatidia behave as functionally independent units (Hassenstein 1951). McCann et al. (1965) found, however, that the detection of motion involves interactions between adjacent ommatidia in the direction of movement. Suzuki (1960) inferred the existence within the visual centres of the brain of areas associated with the co-ordinated functioning of discrete groups of ommatidia in the eye of the mosquito.

Flicker is usually thought of in terms of uneven excitation of different ommatidia at the same time, but it could equally well be interpreted by the brain as uneven excitation of the same ommatidium at different times (Mazokhin-Porshnyakov 1965). This mechanism would work when an image transverses the eye, only if the eye or central nervous system possesses some kind of "memory" and is able to compare a previous retinal excitation with a subsequent one. It is thus possible that the triommatidium, whilst lacking the refinement of the compound eye, receives visual information in much the same way as the more complex receptor by comparing present and previous light

intensities.

Evidence for the existence of an optokinetic memory comes largely from the work of Horridge (1966). If a locust is held relative to a stationary visual field of contrasting stripes and the light then switched off and the field moved, the locust moves its head in an optomotor response when the light comes on again. A locust can "remember" the former position of a visual pattern to within 0.1° after a dark period of 10 seconds. Some insects, when confined to a ridge or maze and forced to turn from a straight path, will make a compensatory turn in the opposite direction as soon as a choice situation is presented (Dingle 1965; Wilson et al. 1968). This so-called "reactive inhibition" is thought to involve memory of the change in the visual field.

The triommatidium could be considered as an organ which, although incapable of perceiving flicker as the translocation of a stimulus between adjacent ommatidia, may be able to appreciate object motion as a temporal series of varying intensities, in each ommatidium separately. Hassenstein (1951) assumes that movement is perceived as a vector without spatial connotations when two stimulated ommatidia in the compound eye are separated by an unstimulated one. Similarly, the facets of the triommatidium may perceive object motion without allowing any appreciation of form or direction of movement. From consideration of the capabilities of other visual organs, it seems likely that the triommatidium perceives both wavelength and intensity and it is probable that, as in the compound eyes of other insects, these two inputs are interdependent (Fingerman et al. 1952, 1953).

Unless the triommatidium serves simply as a "stimulatory organ" in the same way as ocelli, it is reasonable to assume that the insect responds to the action potentials set up within it in a characteristic way. The reorientation behaviour of aphids towards visual c ues may involve both the compound eye and the triommatidium and, in Aphis fabae, stimuli received by the triommatidia may elicit one type of turning response in walking apterae, whereas a different orientation response is mediated by the compound eye (Ibbotson 1966).

The role of the triommatidium in the behaviour of walking aphids could be investigated at any of several levels from electrophysiological studies to ethology and, before any behaviour pattern can be properly understood, compatible results must be available from a wide range of experimental approaches. Since no definitive study of the behavioural significance of the triommatidium appears to have been made previously, the present work is set, as it were, at a midpoint between electrophysiology and ethology. It is hoped that subsequent research will "branch out" to approach the problem from other directions.

Consideration is given here to whole animal reactions to simplified visual stimuli under controlled laboratory conditions. It is outside the scope of this work to investigate either integrated behaviour under more natural conditions or the detailed functioning of stimulus reception and response initiation at the physiological level.

THE VISUAL BEHAVIOUR OF APTEROUS APHIS FABAE

Three alternatives were distinguished in the overt behaviour of aphids, _viz_. locomotion, probing and orientation. During locomotion, the aphid simply continued to walk forwards in a fairly straight line unless diverted. When probing, the aphid remained stationary, with the rostrum vertical and the stylets apparently inserted into the substrate. Orientation involved unequal leg movements on the two sides of the aphid and occured during both locomotion and probing behaviour.

Probing involved the arrest of forward locomotion, the protraction of the rostrum and, with the antennae pointing forwards and vibrating, the delivery of a number of decisive jabs at the substrate with the forepart of the body. At the same time, the aphid sometimes re-positioned its legs and occasionally moved sideways for a few millimetres in a crablike fashion. The proboscis was eventually brought to rest on the substrate, where slight penetration by the stylets may have occured. Finally, the antennae were swept back over the body and the aphid became quite motionless.

On experimental wax substrates, it is unlikely that deep penetration of the stylets occurs, since the rostrum was never seen to "elbow" in the way which it does when aphids feed on plants, with their stylets inserted deeply into the phloem. Ibbotson _et al_. (1959) found that probes lasted longer on a wax substrate than they did on glass, so some exploratory insertion of the stylets may have occured.

Probing behaviour is characteristic of most aphid species and it is likely that it provides the aphid with information on both the physical and chemical properties of the material into which the probe is made (van Emden et al. 1969).

Probing and walking in apterous aphids and settling and flying in alate aphids both constitute antagonistic relationships and show sustained alternation under constant conditions (Kennedy et al. 1963a & b, 1964; Kennedy 1958, 1965, 1966, 1975), so that probes may occur with apparent spontaneity. Under such circumstances, any stimulus that arrests or hinders locomotion will also be responsible indirectly for the probe which invariably ensues. Probes may thus be elicited not only by visual and olfactory stimuli but also by mechanical interference with locomotion, such as cotton fibres lying across the path of an aphid (Ibbotson et al. 1959). At any time, individual aphids are to be found either walking or with the stylets inserted into the leaf and aphids which are simply stationary are only rarely observed.

GENERAL METHODS

Stock Cultures

Apterous, virginoparous Aphis fabae Scopoli were collected on broad bean plants (Vicia faba) at Close House Field Station, Heddon-on-the-Wall, Northumberland, in August 1972. Starting with a single aphid, a stock culture of apterous virginoparae was established on broad bean seedlings in the laboratory, as described by Kennedy et al. (1950).

Bean seeds (variety "Express Longpod") were planted every day in "John Innes No. I" potting compost, at the rate of seven beans to a five inch diameter pot. The pots were kept initially in a heated greenhouse and were transferred to a constant temperature room when the seedlings showed above the soil.

Each pot was enclosed in a cylindrical cage (14" tall x 7" diameter), which had a circular aluminium container for the base, transparent celluloid walls and a ventilated aluminium lid. The temperature in the cages containing growing plants fluctuated slightly around a theoretically constant 20°C, with 85-90% relative humidity. Sixteen such cages were kept under a bank of eight "Atlas Artificial Daylight" fluorescent tubes. Illumination within the cages was 2000 to 3000 Lux, with a photoperiod of sixteen hours in every twenty-four.

In the cages containing the oldest plants, newly-moulted adult aphids left the plants and walked around the rims of the pots and on the walls and lids of the cages. These aphids were transferred to 3" x I" glass

tubes, by means of a capillary suction tube applied to their backs. Each tube was inverted over a fresh bean shoot when thirty aphids had been collected in it. The oldest plants in the culture were removed and replaced by the inoculated shoots as appropriate.

Experimental Aphids

Cultures

In sub-cultures, ten adult aphids were caged over a newly-emerged bean shoot and allowed to remain for about sixteen hours before they were removed. The larvae which had been dropped on the shoot were thus of similar ages and developed at comparable rates. All the nymphs underwent the final moult about seven days after birth and at this time the sub-cultures were examined at thirty minute intervals over a period of eight or nine hours. Aphids which were in the process of moulting were picked out and isolated in small glass tubes and the time when ecdysis was complete was noted for each. The age of the adult aphid was measured from this point.

Extirpation of the Triommatidia

Of the several methods of extirpation tried, cauterisation with a hot tungsten needle was the most practical and gave a consistently high level of success. The very fine point required was obtained by dipping

the end of a piece of fine gauge tungsten wire into hot, fused silver nitrite and the resulting needle was mounted in a glass rod. A minute, insulated coil of nichrome high resistance wire surrounded the needle between 5mm and 10mm from the tip, with an asbestos shield to protect the aphids from the radiant heat of the coil. Power from the mains supply was run through a 6V stepdown transformer and the flow of current to the coil monitored exactly through a spring-loaded contact switch (Fig. 21).

The glass rod holding the tungsten needle was fused to a microscope slide and held on the mechanical stage of a "Vickers Patholette" microscope. When used in conjunction with the focussing adjustment, this gave controlled, three dimensional manipulation of the needle. The tip of the tungsten needle was viewed at a magnification of x100 by means of a "Vickers Steros" binocular microscope, with a variable intensity lamp, focussed to a narrow beam, to provide illumination. The light intensity was kept as low as was practicable in order to avoid damage to the aphids from the heat of the lamp.

Aphids were anaesthetised with CO_2 gas, then mounted on their backs, in a thin smear of glycerol jelly, on a small cork disc. The aphid was centered in the field of view of the binocular microscope and the cork disc was fixed to the stage with a small piece of "Plasticine". The triommatidia were extirpated by pressing the point of the needle firmly against each ocular process and turning on the current for two seconds.

At first, more than 50% of the treated aphids were unusable due to non-recovery from the anaesthetic or to locomotory difficulties from damage to the central nervous system or direct damage to the forelegs by burning. This percentage dropped as more experience was gained in the use of the apparatus.

Anaesthesia

In order to provide a control to the experiments in which the triommatidia were cauterised under anaesthetic, all the experimental aphids were anaesthetised by exposure to CO_2 gas for about two minutes. For nymphs, this was done two hours before they were used in the experiments and for adults, immediately after the final moult. Those aphids which recovered (about 90%), did so completely within thirty minutes of being placed in a normal atmosphere.

Johnson (1958) found that light anaesthesia affected the subsequent behaviour of alate aphids. Flying aphids were knocked down with CO_2 gas and placed on leaves. On recovery, they wandered over the leaves and probed before taking off. Brief doses of ether did not produce this effect and on recovery aphids took off almost immediately, without wandering or probing.

In the present work, aphids were allowed at least two hours (in most cases) in which to recover from any such side effects. As a further control, ten aphids which had not been anaesthetised were used in each trial. There were no noticeable differences in behaviour between the two groups.

Experimental Conditions

The large leaves of their main host plants, broad beans and sugar beet, provide apterous Aphis fabae with two basic behavioural situations. In one they are free to reorientate themselves in any direction on the flat surface of the leaf lamina. In the other, they tend to follow, with considerable tenacity, the more prominent leaf veins, where they feed and frequently encounter other aphids (Ibbotson et al, 1951). In an attempt to parallel these two situations, the experiments were divided into two main phases.

In the first phase, the visual responses of walking aphids were examined in situations where maximum scope for lateral reorientation was provided. Aphids were induced to walk across a flat, circular wax plate, 15 cm. in diameter. A strong tendency to walk straight across the empty plate was engendered by making the aphids debouch onto the plate from a 2 mm. wide cardboard causeway, along which they had been walking for at least 5 cm. (c.f. Dingle 1965; Ibbotson 1966).

The second experimental phase involved the restriction of lateral reorientation by walking aphids so that they approached conspicuous objects in a regular and repeatable manner. This was achieved by making the aphids walk along wax ridges. Aphids will walk continuously along a wax ridge, the width of which just fits the span of their tarsi at normal extension, and respond most readily to visual stimuli (by either probing or turning) when on ridges which are semi-circular in cross section (Ibbotson et al 1959). The tarsi of the aphid make

contact at varying levels down the sides of such a ridge, so that the amount of leg extension is irregular from step to step and from leg to leg. The stimuli received by the tarsi are insufficiently symmetrical to keep the aphids astride the ridge without the addition of further symmetrical stimulation from strong, overhead illumination, which elicited a dorsal light reaction.

Ridges 2 mm. wide were constructed by repeatedly dipping the edge of an aluminium strip, or the rim of an inverted 9 cm. Petri dish into molten wax, until a sufficiently thick layer had accumulated. A semi-circular cross section was obtained by scraping the hardened wax with a metal template.

The experimental arrangements were enclosed in a cylinder of white paper, 30 cm. in diameter and 55 cm. high, with a small observation window, screened with white muslin, near the top. A 100 watt "Atlas Spotlight" electric light bulb, at a height of 60 cm. above the experimental surface, provided illumination of 2800 Lux and was the only light source in the room. The light intensity was checked before each experiment and the bulb was changed when it started to fade; with the light on, the temperature immediately above the experimental arrangements reached a maximum of 23°C. The relative humidity was maintained between 80% and 90% by a sheet of wet blotting paper beneath the apparatus. The aphids used in the experiments were all lifted carefully with a capillary suction tube, to minimise disturbance during handling.

The events which occured during the experiments could be

considered from three points of view:

1. The changes which occured in the visual characteristics of the "targets" as a consequence of the aphids' movement. The speed of walking of individual aphids was not measured accurately throughout each experiment and a mean walking speed was calculated from timed runs of a sample of similar aphids. In this sample, walking speed varied very little between aphids and between experimental arrangements, with a mean value of 3 mm./sec.

2. The possible visual events to which the aphids responded - i.e. common features of changes in the visual characteristics of the targets which were apparently associated with particular behavioural changes in the aphids.

3. The type of change in the aphids' behaviour which was apparently occasioned by these visual events.

METHODS ON THE FLAT

In the present work, black pillars against a uniform white background were used to provide a simple, well-defined visual stimulus. Variable factors included the height and width of the pillar, its distance from the point where the aphids debouched onto the wax plate and its angular position with respect to the antero-posterior axis of an aphid at that point. Visual behaviour was most easily assessed by inspection of aphids' tracks in different stimulus situations.

Thirty aphids of approximately the same age were made to walk in turn along the causeway and onto the wax plate in each trial. The track made by each aphid was traced on a working diagram by reference to faint squares ruled on the surface of the wax plate itself. The pillar was moved from one side to the other of the median line (the prolongation of the causeway across the plate), with consecutive aphids. The fifteen tracks made with the pillar to the left of the median line in each trial were re-traced as mirror images to show the pillar to the right. They could thus be directly compared with the tracks made when the pillar was to the right. From the thirty tracks obtained for each experiment, only ten were shown in the figures for greater clarity. These are the tracks made by every third aphid used and are a representative sample of the total. In some experiments where tracks show a definite trend, a mean track was calculated from all thirty to summarise this trend.

Nymphs in the first three instars were unsuitable for use in the

experiments since they walked very slowly and probed continually and at random, both on the causeway and on the empty plate. On reaching the wax plate, they frequently turned about and walked back up the causeway. The fourth (last nymphal) instar made fewer random probes, behaved in a fairly uniform manner on the wax plate and was used throughout the experiments where "nymphs" are referred to. A slightly narrower causeway was used for nymphs, which just fitted the span of their tarsi.

The visual targets consisted of tight rolls of black paper, with exception of the 0.5 mm. wide pillar, which was a piece of stiff, black wire. The dimensions of the pillars, their angular deviation from the median line and their distance from the point at which the aphids left the causeway were as follows:

1. "Standard" pillar (2 mm. x 30 mm.) at "normal" distance (30 mm.)
   (a) at 30° (standard angle) to the median line,
   (b) at 50° (wide angle) to the median line,
   (c) at 90° (right angle) to the median line.
2. "Standard" pillar at "standard" angle (30°) to the median line,
   (a) at 15 mm. distance (near),
   (b) at 60 mm. distance (far).
3. A pillar at "normal" distance (30 mm.) and "standard" angle,
   (a) 2 mm. x 5 mm. (short pillar),
   (b) 0.5 mm. x 30 mm. (narrow pillar),
   (c) 12mm. x 30mm. (wide pillar).

4. Two "standard" pillars (2 mm. x 30 mm.), at "normal" distance (30 mm.) and "standard" angle (30°), one on each side of the median line at the same time.

Aphids of different ages were exposed to situation 1(a) (standard pillar at normal distance and standard angle) as follows:

Nymphs;

"Very young" adults (30 mins. old);

"Young" adults (90 mins., 3 hrs., 5 hrs. and 8 hrs. old);

"Old" adults (12 hrs., 16hrs., 24 hrs. and 48 hrs. old).

With all the other situations, nymphs, "young" adults (3-8 hrs. old) and "old" adults (over 12 hrs. old) only were used.

To simplify the description, the term "dead ahead" and "dead astern" are used to denote positions directly ahead of and directly behind the aphid and "dead abeam" for positions at right angles to the antero posterior axis on each side.

RESULTS ON THE FLAT

Controls

Thirty aphids of mixed ages with the triommatidia entire and thirty with the triommatidia extirpated were made to walk in turn across the plate in the absence of visual targets.

The tracks made by both groups of aphids were fairly straight; those of the treated aphids were spread fanwise on either side of the median line to a slightly greater degree than those of the entire aphids. Ten of the entire aphids and twelve of the treated aphids probed (Figs. 22 & 23).

Triommatidia Entire

Age of Aphids

The tracks made by entire aphids of different ages walking towards a standard pillar (30 mm. x 2 mm.) at normal distance (30 mm.) and standard angle (30°) to the median line, are shown in Fig. 24a-j.

To reach the pillar, nymphs and very young adults followed sinuous paths, old adults followed a simple curved path, whilst young adults followed an orbital path with the pillar as the centre of the orbit and never reached the pillar at all.

Since the visual target was the same for each experiment,

differences between these paths can be translated in terms of the apparent movement of an hypothetical image of the pillar due to the aphid's forward locomotion, assuming a constant walking speed. These values are expressed graphically for calculated mean tracks in Fig. 25 a-c.

In sinuous path orientation, the image swept back and forth across the eyes as the aphid walked forwards (Figs. 24 & 25). With the pillar to the right of the median line, the image initially moved quickly from the right of the head to the dead ahead position, then to the left, moving less quickly and stopping briefly at an angular deviation of about 40° to the longitudinal axis of the aphid. It then moved forwards again, rapidly crossing the dead ahead position to stop at an angular deviation of about 12° to the right, before moving back to the dead ahead position as the aphid reached the pillar.

In constant angle orientation (simple curved path), the aphid apparently made continuous re-adjustments to the marginal movements of the image resulting from its (the aphid's) own locomotion. In consequence, the aphid moved along an approximation to the logarithmic spiral characteristic of some forms of optomotor behaviour (c.f. von Buddenbrock 1931) and very little change occured in the apparent position of the image until the aphid was almost at the pillar. As with sinuous path orientation, during the last few millimetres the aphid usually turned so as to bring the image into the dead ahead position and a number of aphids (about 60%) probed at this point (Figs. 24(i) 25(b)).

In orbital orientation, the initial part of the path was somewhat similar to the constant angle orientation of old aphids, but course control appeared to be less exact and with some aphids the image would have moved forwards to the dead ahead position. Several millimetres before the pillar, the aphid made a sudden turn, which brought the image to the dead abeam position, and continued along an orbital path with the image almost dead abeam throughout (Figs. 24(e) & 25(c)). At some point along this perimeter, a second turn in the same direction as the first then brought the image to the dead astern position and the aphid continued to walk forwards across the plate, away from the pillar, in a more or less straight line. The sudden turns at the beginning and end of the orbital part of the path resulted in a magnitude of image movement greatly in excess of any movement due to simple locomotion and in a complete, uncompensated change in the visual situation.

Visual Targets

Further trials were carried out to determine the effect on orientation of changing the attributes of the visual targets (Figs. 26 - 33), as follows:

Pillar height

At normal distance and standard angle, a short (5 mm.) pillar apparently elicited the same response as a normal (30 mm.) one (Fig. 26). For this size range at least, the response was

independent of pillar height, but the effect of pillars which were shorter than they were wide was not investigated.

Pillar width

A narrow pillar elicited very little response at all (Fig. 27).

Nymphs approaching a wide pillar (12 mm.), behaved in the same way as when they approached a standard pillar, except that they were segregated into those making deep sinuosities, which were delivered at the near vertical margin, and those making shallow sinuosities, which were delivered at the far one (Fig. 28).

The radius of the orbital path pursued by young adults was approximately the same for a wide pillar as for a normal one. This suggests that the aphids either saw even the wide pillar as a whole, or responded to two edge effects, which tended to reinforce one another. The angle subtended by the wide pillar at the eye of an aphid during the orbiting path was more than 100° for some tracks. An hypothetical aphid, having turned so that its longitudinal axis was perpendicular to the radius of a circular pillar, could maintain a perfect orbit with the pillar subtending 100° at the eye by keeping the image of the forward edge of the pillar at a deviation of 40° and the hind edge of the pillar at 140°

It may be inferred from these results that:

1. The narrow (0.5 mm.) pillar was probably too narrow to be discriminated from the background by more than a few aphids.

2. Although the normal (2 mm.) pillar was visible, its edges were too

close together for discrimination between them to be apparent in the tracks.

3. The edges of the wide (12 mm.) pillar were sufficiently far apart to constitute separate visual stimuli.

Angle of pillar

Aphids responded to a pillar at 50° angular deviation as they did to one at 30°, although with deeper sinuosities in the tracks (Fig. 29). Most aphids failed to respond in a recognisable manner to a pillar at 90° angular deviation, the stimulus being apparently insufficient to evoke an effective sequence of reorientation behaviour (Fig. 30).

Pillar distance

For each age group of aphids in turn, near and distant normal pillars elicited common patterns of behaviour, except that these patterns became miniaturised or extended according to whether the pillar was near or far. Thus when approaching a near pillar, nymphs made only one sinuosity, young adults orbited at relatively small radius and old adults approached along a spiral as before. When approaching a far pillar, nymphs made three sinuosities on average, young adults orbited at a considerable distance from the pillar and old adults swept out on a long, curved path which usually brought them further round the pillar than before (Figs. 31 & 32).

Two pillars

Aphids approaching two pillars situated one to either side of the

median line continued to walk straight ahead for a short distance after leaving the causeway and then turned decisively towards one pillar or the other. Their subsequent tracks were the same as for a single pillar (Fig. 33). This behaviour is reminiscent of that of some lepidopterous caterpillars approaching two symmetrically positioned light sources Lammert 1925; Brandt 1934). Caterpillars maintain the symmetry of stimuli until the images are separated by approximately 130° of arc, then apparently inhibit the response to one stimulus and turn towards the other. In the present experiments with aphids, the "deciding point" was slightly earlier than this, when the images were separated by approximately 100° of arc.

Triommatidia Extirpated

In order to determine the extent to which the triommatidium was involved in the foregoing responses, the experiments were repeated using aphids with both triommatidia extirpated. The tracks made by aphids of different ages, walking towards the various visual targets, are shown in Figs. 34-41.

Neither sinuous path orientation nor orbital orientation was evident and nymphs and most very young adults made tracks resembling those made by entire aphids walking across the empty plate. Some very young aphids encountered a pillar, apparently by chance, particularly when it was close to the end of the causeway or was very wide. The frequency of probing was about the same as for entire aphids of

the same ages, probes occuring in about 25% of the tracks.

It may be inferred that visual reorientation in nymphs and very young adults apparently involved the triommatidium in some fundamental way and, as regards any directional component in their visual behaviour, aphids of these ages with the triommatidia extirpated were effectively blind.

With successive age groups from 3 hrs. to 24 hrs. old, an increasing proportion of individuals performed constant angle orientation comparable to that seen in entire adult aphids. The responses of old adults to the various visual targets resembled those made by entire old adults almost exactly.

Probes were distributed similarly to those made by entire adults, most being made during directed reorientation, shortly before reaching the pillar.

Discussion

Apart from the final few millimetres of the approach walk, when the pillar was sometimes dead ahead to the advancing aphid, the tracks are consistent with the hypothesis that orientation behaviour was elicited by the apparent lateral movement of a vertical boundary of contrast between the black pillar and its white background. Constant angle orientation as shown by old aphids apparently affords an example of step by step correction of such movement, normally associated with

optomotor behaviour (c.f. Ludwig 1933). When confronted with two pillars, or the two edges of a wide pillar, such aphids appeared to inhibit the response to one of them and respond to the other without cross effects.

Aphids did not respond to the narrow (0.5 mm.) pillar, which would have subtended an angle of about 1° at the eye as an aphid left the causeway. This same value has been given as the minimum stripe width capable of causing an optomotor response for both the honeybee (Hecht et al 1929) and the ant Formica rufa (Jander et al 1963). Both of these insects have highly developed compound eyes with very numerous facets and a relatively high degree of visual acuity. Apterous A. fabae, on the other hand, have a relatively poorly developed compound eye and, presumably, a correspondingly poor degree of visual acuity. Old aphids still failed to respond to the narrow pillar when their tracks passed as closely as 10 mm. from it, where it would have subtended at an angle of 3°, but aphids passing closer than this orientated towards the pillar (Fig. 27). The standard (2 mm.) pillar subtended an angle of 4° at the eye as the aphid left the causeway and most old adults orientated towards it from this point. It would appear that the smallest subtended angle for an image which produces optomotor behaviour in A. fabae is between 3° and 4° under the conditions of the present experiments. This value must be similar for both the compound eye and the triommatidium (if one accepts the premise that the triommatidium mediates visual behaviour in nymphs), since nymphs orientated with respect to the 2 mm. wide pillar immediately on leaving the causeway.

With entire aphids, sinuous path orientation was most pronounced with the nymphs, diminished in amplitude with the 30 min. and 90 min. old adults and was replaced by orbital path orientation in adults up to about 8 hrs. old. Orbital path behaviour then diminished in turn and was replaced by constant angle orientation for adults older still, until with the oldest aphids of all an almost common constant angle track occured.

When the triommatidium was extirpated on the other hand, neither sinuous path nor orbital path orientation appeared at all and constant angle orientation first appeared with a few of the 90 min. and 3 hrs. old aphids.

It may be inferred that the triommatidium is involved in both sinuous path and orbital path orientation, whereas the compound eye alone mediates constant angle orientation. The shape of the initial part of the orbital path (before the first abrupt turn) is superficially somewhat similar to the constant angle path and the almost perfect orbits of the pillar made by some aphids suggest constant angle course control. Unless these similarities are purely coincidental, it is tempting to assume that this control is effected, to some extent at least, by the compound eye. The newly formed compound eye of the young adult may be incapable, at this stage, of mediating step by step control of orientation without some sort of complementary information provided by the triommatidium, at least in the initial approach towards the pillar.

The constant angle paths made by old aphids and the orbiting phase of orbital path orientation in young adults appear to constitute examples of "closed" orientation systems in the sense of Land (1972). In such a system, the execution of a turning response results from visual feedback from the consequences of an animal's own motion. Such maintenance of course by feedback control of the angle between an insect's long axis and a spatially orientated visual stimulus has also been described as "allothetic" course control (Mittelstaedt-Burger 1972).

Sinuous path orientation appears to have been the consequence of successive compensatory turns involving stimulation of the right and left triommatidium alternately. The shape of the tracks suggests that turns were immanent as the aphid walked down the causeway, but were inhibited by its "railroading" effect. With the pillar to the right, a fairly sharp turn to the right was made in the first few millimetres of locomotion on the wax plate, taking the image across the dead ahead position and (presumably) out of view of the right triommatidium and into view of the left one. Compensation for this image movement may have been responsible for the subsequent turn to the left which brought the image back through the dead ahead position and into view of the right triommatidium in turn.

According to von Holst (1954), reafferent feedback serves not only to stimulate turning, but to limit it. The efference which results in a turning response is nullified by the re-afference which it subsequently produces and is then re-initiated by the re-afference resulting from its absence. If the triommatidial facets act as discrete receptors,

the image movement necessary to elicit a response may not have reached a critical value until the pillar was in diametrically opposite view of the triommatidial facet, i.e. at about the same angular deviation as when the aphid first left the causeway. With such widely separated receptors as the triommatidia on each side of the head, in which each turn was progressively nullified by the re-afference resulting from the next, a given response would not have been completely extinguished until an equivalent degree of angular displacement had been reached in the opposite eye as the aphid locomoted "on the other tack".

Sinuous path orientation may thus be attributed also to a form of "closed system" orientation, but as between widely divergent receptors instead of those which are closely apposed, as in the triommatidia of a single compound eye.

By contrast, the turns which brought the young aphids into and out of the orbit of the pillar were of sufficient magnitude and rapidity, vis a vis the contemporary changes in the visual field, as to appear to constitute the expression of an "open" system of orientation (Land 1972) in which turns, once initiated, proceed to completion independently of feedback control.

Young adults which were about to orbit the pillar followed an initial path which was broadly similar to the constant angle orientation of old adults, but which diverged from it in many of the tracks by the gradual progression of the image of the pillar towards the dead ahead position. If both the compound eye and the triommatidium were

involved at this stage, compensation for image movement by both the receptors may have initially involved turning towards the pillar and the paths the aphids actually followed suggests a compromise resolution of the two. Slightly greater compensation than would be appropriate to a constant angle path and considerably less than would be appropriate to sinuous path orientation occured. In a case where the image crossed the dead ahead position and was perceived by the eye on the other side of the head, the sinuous path syndrome may not yet have been extinguished, whereas compensation for constant angle orientation was now initially appropriate in the other direction. Such a situation and the consequent response are typical of the "reactive inhibition" described by Dingle (1965), where insects constrained to follow a given path make a compensatory turn in the opposite direction as soon as a choice is presented.

These turns carried the image into the dead abeam position, where it may not have been visible to the facets of the triommatidium, which are directed more or less anteriorly and posteriorly, but not laterally. If this was so, the orbit of the pillar would then have been controlled by the compound eye alone and the close proximity of the pillar at this stage of the path may have facilitated this. The final turn, which carried the aphid out of orbit, is clearly comparable with the first, in that it occured with equal rapidity and in the same direction. It is not associated with any specific concatenation of visual events and the turns occured at varying distances round the perimeter. The most likely possibility is that the pillar entered the visual field of the

rear facets of the triommatidium due to the approximate constant angle orientation mediated by the compound eye being insufficiently accurate to maintain a perfectly orbital path, so that a further "reactive" response occured.

It is clear that a number of questions remained unanswered at this stage, regarding orbital path behaviour:

1. Is the compound eye actually involved in orbital path behaviour at all? This would not appear to be so from the fact that the whole behaviour pattern was absent in aphids with triommatidia extirpated; on the other hand, the approach to the pillar and the orbital part of the path apparently contain a constant angle component, which suggests mediation by the compound eye.

2. If the compound eye <u>is</u> involved in orbital path behaviour, why does it apparently fail to mediate any sort of optomotor reaction in most young adults with triommatidia extirpated? One possible explanation would be that the compound eye of the newly-moulted adult is not functionally perfect for some hours after moulting (hence the difference in behaviour during the first 12 hours) and visual behaviour at first requires a "reinforcing" component provided by the triommatidium. This may take the form of a simple photokinesis or some more complex system.

3. If orbital path behaviour operates as described for a situation in which the image of the pillar crosses the dead ahead position during the initial part of the track, how does it operate in those tracks where

the image clearly never reaches the dead ahead position and yet the first abrupt turn still occurs at a comparable point in the track? This question will be considered in detail later.

RESULTS ON RIDGES

Aphids moving on the leaves of their host plants tend to locomote along the more prominent veins. They are consequently frequently delivered into the immediate vicinity of other aphids feeding in the phloem and it has been observed (Ibbotson et al. 1951) that such encounters frequently result in a probe being made.

In an initial analysis of such behaviour, the aphids were found to be "railroaded" by ridges which just fitted the span of their tarsi and to probe when they encountered the visual stimuli provided by the simulated presence of another aphid. In particular, it was found that whilst the aphids hardly probed at all on ridges which were square in cross section, they readily responded to probe-evoking stimulation if the ridge was semi-circular in cross section when they were prevented from leaving it by their dorsal light response to an overhead light (Ibbotson et al. 1959).

Probes were elicited by a variety of stimuli, with the common factor that they were initially of such a character as to interrupt locomotion, either immediately or after a period of summation for stimuli not individually strong enough to evoke an immediate response.

These observations were extended in the present work, with a view to investigating the degree to which the triommatidium mediated the probing response. The aphids were made to walk along ridges which followed different paths, towards or past a variety of visual targets likely to elicit probes. On a given ridge, with a given target, each aphid followed the same path and received the same optomotor

input as any other aphid walking at the same speed.

Lateral reorientation was restricted to sudden turns in which an aphid stopped, turned through approximately 90° and climbed down from the ridge. The point at which a turn occured could thus be recorded exactly. Turns were also elicited by visual stimuli, but independently of probes. Aphids which made turns were gently replaced on the ridge, using a capillary suction tube and continued walking in the same direction as before from the point at which they had turned.

Aphids on ridges in the absence of any visual targets made infrequent probes, apparently at random, and no turns (Figs. 46 & 47a). Probes were distributed similarly for both entire aphids and those with extirpated triommatidia.

Visual Changes I : Re-afference

Lateral Movement

The re-afferent optomotor input provided by the visual targets could be inferred as of three types. Firstly, on straight ridges with a single pillar to one side, or on circular ridges with a single pillar inside a circle, lateral movement of the image occured in one eye only. Secondly, with a single pillar outside the rim of a circular ridge, or to one side of a specially designed curved ridge, lateral movement of the image was first across one eye and then across the other. Lastly, when pillars were situated symmetrically on both

sides of a straight ridge at the same time, both eyes received a similar input simultaneously.

In one eye only

Visual targets

Although image movement in one eye is considered here as a single visual circumstance, three separate stimulus situations were in fact presented to the aphid:

1. On the straight ridge, image movement was only posteriorly across the eye.

2. On the circular ridge, with a pillar to the inside, movement was successively anteriorly and posteriorly.

3. With the pillar on the circular ridge itself, movement was consistently anteriorly across the eye.

The visual targets consisted (as before) of tightly rolled cylinders of black paper. These were situated vis a vis wax ridges as follows:

1. Straight ridge, 10 cm. long, with one vertical pillar
   (a) "standard" pillar (2 mm. x 30 mm.), 15 mm. dead abeam of the mid-point of the ridge, to the left or right (standard distance);
   (b) "wide" pillar (6 mm. x 30 mm.), situated as (a);
   (c) "standard" pillar, 15 cm. from the start of the ridge, at an angular deflection of 30°, to left or right (far distance).

2. Circular ridge, 9 cm. diameter, with one standard pillar dead abeam of the aphid and successively

(a) at the centre of the circle

(b) 3 cm. inside the rim

(c) 2 cm. inside the rim

(d) 1 cm. inside the rim

(e) on the rim.

As before, the terms dead ahead, dead astern and dead abeam are used to denote positions directly in front of, directly behind and directly to one side of the aphid.

Thirty aphids of known age were made to walk in turn along each wax ridge, past each target. The position of probes and turns were recorded by reference to a millimetre scale mounted along the side of the ridge itself. In experiments where a single pillar was situated to one side of a straight ridge, the side was alternated for consecutive aphids.

With a standard pillar at standard distance from the straight ridge, aphids were used at 3 hrs., 6 hrs. and 24 hrs. old. Nymphs and very young adults were inconsistent in their behaviour and tended to probe continually and at random. In the other experiments, all the aphids were approximately 12 hrs. old. The term "treated aphids" is used here to refer to aphids with both triommatidia extirpated, unless otherwise indicated.

Young adults

With a standard pillar at standard distance from a straight ridge, aphids started walking with the pillar at an angle of about 18° deviation from dead ahead. As an aphid progressed, the image of the pillar would have moved back across the eye, its angular velocity increasing until it was in the dead abeam position. It would then have decelerated as it continued moving posteriorly, to a final angular deviation of about 162° as the aphid reached the end of the ridge.

Entire aphids

Turns only occured on a short region of the ridge, immediately preceding the midpoint, where the angular deflection of the pillar was 46°-90° (Fig. 42a & b). Ten of the 3 hrs. old aphids turned and 26 at 6 hrs. old. Within the region of the ridge where turns occured, the apparent angular velocity of the pillar would have been increasing rapidly for an aphid walking at constant speed. Most probes, on the other hand, were distributed in two groups, one before the midpoint of the ridge was reached (angular deviation of the pillar 29°-57°) and the other after it had been passed (angular deviation of the pillar 125°-153°). There were no probes in the region of the mid-point of the ridge, where most turns occured. The way in which these patterns of probes and turns were composed by the behaviour of individual aphids is summarised in Table 3.

Treated aphids

Probes were made by nine 3 hrs. old aphids and by eleven 6 hrs. old aphids and were distributed at random along the ridge

(Figs 43a & b). No aphid probed more than once. Turns were grouped in the 20 mm. before the midpoint of the ridge (angular deviation of the pillar 38°-90°), as were those made by young aphids with the triommatidia entire.

Old adults

Entire aphids

With standard pillar and distance, probes and turns were both distributed similarly to those made by young adults (Figs 42 c & d).

The apparent movement of a "wide" (6 mm.) pillar would have been similar to that of a standard pillar, with both at standard distance and the aphid walking at the same speed. A pillar at "far" distance would have appeared to move much more slowly than one at standard distance, only traversing an arc of 30° to 70° angular deviation across one eye. The acceleration of the image across the eye would also have been less.

A similar pattern of distribution for probes and turns appeared for the wide pillar as for the standard pillar, whilst with the pillar at the "far" distance, no turns occured but the probes became progressively more frequent until a point some 20 mm. short of the distal end of the ridge, when they ceased entirely. No probes were made after the point on the ridge where the angular deviation of the pillar exceeded 57° from dead ahead.

A pillar at the centre of a circular ridge would have had no apparent movement and would have provided no re-afference as an

aphid walked round it. With a pillar inside the rim but away from the centre, the aphid started walking with the pillar in the dead abeam position. As the aphid continued round the ridge, the image of the pillar would have moved gradually forwards across the eye, slowly decelerating until it stopped. The direction of movement of the image would then have been reversed and it would have accelerated rapidly in a posterior direction to the dead abeam position of the same eye and then continued past it. After rapid deceleration, it would have stopped briefly again, at an obtuse angle of deviation, and then moved slowly anteriorly once more to arrive at the dead abeam position once more as the aphid completed one full circuit of the ridge.

The angular deviation of the pillar at the points during the circuit when image movement was nil, depended on the distance of the pillar from the nearest point on the ridge. With the pillar 3 cm. inside the ridge, the image would have moved forwards across the eye to an angular deviation of 71° from dead ahead and backwards to 109°. With the pillar 2 cm. inside the ridge, these limits were 57° and 123° respectively. When the pillar was 1 cm. inside the ridge, image movement would have been nil with the pillar at angular deviations of 39° and 141°

For an aphid walking at constant speed round a circular ridge with a pillar on the ridge itself, the image of the pillar would have moved forwards across the eye at a uniform speed, from dead abeam to dead ahead. The pillar was removed by remote control as the aphid reached it and was replaced after it had passed. As the aphid

walked round the second half of the circular ridge, the image would have moved forwards at a uniform speed from dead astern to dead abeam, in the same eye as before.

With a pillar at the centre of, or at 3 cm. inside, the circular rim, no turns and very few probes occured (Figs 47b & c). With a pillar 2 cm. or 1 cm. inside the rim, turns were made when the pillar was at an angular deviation of 45° to 90°, as on the straight ridge. All the aphids which probed did so when the angular deviation of the pillar was less than 60° or more than 120° (Figs. 48a & b). With a pillar 1 cm. inside the rim, probes were more numerous than with a pillar 2 cm. inside the rim (49 and 20 probes respectively). With a pillar on the ridge itself, no turns were made and probes extended right up to the pillar (Fig. 48c). Probes which occured as the pillar was being removed or replaced were discounted, since they may have been due to the sudden actual movement of the pillar. A second, smaller group of probes occured a few centimetres past the point where the pillar was located.

Theoretically derived curves were drawn for the apparent angular velocity and angular deviation of a black pillar, as they would be perceived by an aphid making one complete circuit of the circular ridge at a uniform speed of 3 mm./sec. with the pillar in each of the positions used (Figs. 50 & 51; Tables 4 & 5). The positions of probes and turns were then plotted along the curves so that points at which such behaviour was frequent could be defined in terms of the angular velocity and angular position of the pillar.

The interpretation of these graphs is considered in the discussion at the end of this section on lateral movement of an image, in conjunction with results obtained from experiments where the pillar was situated outside the ridge.

Treated aphids

With pillars at standard distance from a straight ridge, probes were few and were apparently at random along the ridge, whereas turns were grouped as for entire aphids (Figs. 46 & 52). When the pillar was at "far" distance, no turns and a few random probes were made (Fig. 53).

With pillars to the inside of a circular ridge, probes were sparse and apparently at random with all positions of the pillar. Turns were distributed in the same way as for entire aphids (Figs. 54 a-c; 55a & b).

With a pillar on the circular ridge itself, probes were few, except in the final few millimetres before the pillar was reached, when they were frequent and formed a compact group (Fig. 55c).

From one eye to the other

Visual targets

The following experimental arrangements were used to provide image movement through 360°.

3. A circular ridge as before, with a standard pillar situated dead abeam of the aphid at its starting point,

(a) 1 cm. outside the rim,

(b) 2 cm. outside the rim,

(c) 3 cm. outside the rim.

A specially designed ridge, whereby a standard pillar would appear to move once completely round the aphid at a constant angular velocity, assuming the aphid walked at a constant speed.

With pillars outside the circular ridge, the image would have moved anteriorly across the left eye, accelerating slowly until it was in the dead ahead position. It would then have moved rapidly across the right eye, accelerating until it reached the dead abeam position, after which it would have continued moving posteriorly, but now decelerating, to dead astern. The image would then have crossed the posterior part of the left eye, moving slowly forwards to the dead abeam position, decelerating a little as it did so.

When the pillar was situated 1 cm. outside the ridge, it was in the dead ahead position to an aphid which had walked through about 150° of arc. With the pillar at 2 cm. and 3 cm. outside the ridge, it appeared in the dead ahead position to aphids which had walked 140° and 130° around the circumference respectively. Similarly, the pillar was in the dead astern position to aphids which had walked approximately 210°, 220° and 230° around the circumference of the ridge, with the pillar 1 cm., 2 cm. and 3 cm. outside the ridge respectively.

A ridge was also constructed of such a shape that a pillar, in the correct position relative to the ridge, would appear to move once completely round an aphid walking the length of the ridge. Given the aphid walked at a constant speed, the speed of relocation of the image across the eyes would also be constant, although the actual distance

between the aphid and the pillar (and hence the image size) would vary. The pillar would have started and finished in the dead ahead position and would have appeared to move backwards across the right eye and forwards across the left eye.

Entire aphids

On the circular ridge, with pillars outside the rim, the aphids turned when the angular deviation of the pillar was as little as 10° from dead ahead. Probes occured in more diffuse groups than before, but were always made where the deviation of the pillar was less than 60° or more than 120° (Fig. 56).

Curves for the apparent angular velocity and the angular deviation of the pillar were compiled as before and probes and turns were plotted for each experimental arrangement (Figs. 50 & 51; Tables 4 & 5).

On the specially constructed ridge, no turns at all were made (Fig. 57). The distribution of probes was translated in terms of the angular deviation of the pillar at the point where each probe was made and these data are presented in Fig. 58.

Treated aphids

The distribution of probes was similar to that recorded when no pillar was present (Fig. 59 a-c). Turns were distributed as for entire aphids and were slightly more numerous than the latter in some cases. With the specially designed ridge, no turns and a very few random probes occured (Fig. 60).

In both eyes simultaneously

Visual targets

In these experiments, the visual organs on both sides of the

head received the same stimuli at the same time. With one or more pillars diametrically opposite one another on each side of a straight ridge, the optomotor input was the same as that provided by a single pillar on one side only, but in both eyes at the same time, instead of in only one.

The experimental arrangements were as follows:

(a) two standard pillars to each side of a 10 cm. ridge, at the standard distance from the midpoint;

(b) 12 standard pillars to each side of a 16 cm. ridge, arranged in opposite pairs and all at the standard distance; the first pair opposite a point 4 cm. from the start, the next pair opposite a point 3 cm. further along the ridge and thereafter at progressively shorter intervals, until the last four pairs were opposite points 4 mm. apart;

(c) as (b), above, but with the aphids starting from the other end of the ridge;

(d) 6 standard pillars to each side of a 16 cm. ridge, arranged in pairs 1 cm. from the ridge on each side at 2 cm. intervals along it, screened with white card so that only one pair at a time was visible to an aphid walking along the ridge.

With 12 pillars to each side of the ridge, images of the successive pairs of pillars would have crossed the eyes with increasing rapidity, whilst with the reverse arrangements the angular velocity of the images would have decreased with each successive pair of pillars. Aphids traversing the ridge with screened pillars would have started walking in

uniformly white surroundings. After a few centimetres, a pillar would have appeared to each side of the head, at an angle of about 40° and would have moved backwards across the visual field of each eye to a position about 110° from dead ahead. The pillars would have then disappeared and the aphids would have continued walking in a uniformly white environment. This sequence of visual stimulation would have occured five times more as the aphid continued walking along the ridge.

Entire aphids

With two pillars, the distribution of probes and turns was similar in all respects to that recorded with a single pillar (Figs. 42c & 61a).

With 12 pairs of pillars, three turns only occured, all at about the point where the first two pillars were dead abeam (Fig. 61). Probes were distributed in two main groups, one preceding the dead abeam position of the first pair of pillars and the other midway between the dead abeam positions of the first and second pairs of pillars. A small group of three probes occured between the dead abeam positions of the second and third pairs of pillars.

The way in which the above distribution was made up by the probes of individual aphids is shown in Table 6. It can be seen that some of the aphids did not probe at all, while others made one, two or three probes, but no aphid made more than one probe in any of the three groups defined above.

With 12 pairs of pillars and the direction of walking reversed, two small groups of turns were made, at about the dead abeam positions of the eleventh and twelfth pairs of pillars respectively (Fig 61).

Probes were made in three groups, the first of which extended from a point 15 mm. before the dead abeam position of the first pair of pillars to about the dead abeam position of the third pair of pillars. The two other groups of probes were situated before and after the dead abeam position of the twelfth pair of pillars. Records for individual aphids (Table 7) showed that some aphids probed two or three times in the region of the first group of probes, then again in the second or third group.

With screened pillars, turns occured when each pair of pillars was about dead abeam of the aphid and probes were made at the points where each pair of pillars became visible to the aphid.

Treated aphids

With each of the four visual situations presented, probes were scattered sparsely along the ridge, in no apparent pattern (Fig. 62). When 12 pairs of pillars were presented, no turns occured, but with one pair of pillars or with screened pillars, turns were numerous and distributed similarly to those made by entire aphids.

Discussion

Consideration of the criteria of angular deviation and angular velocity of the image of a pillar as seen by a walking aphid, suggests that probes occured only rarely when the pillar was at a deviation of 57° to 122°, or more than 164°. from dead abeam. When the angular deviation of the pillar fell outside these limits, probes were numerous (Figs. 51 & 58). Turns were not strictly correlated with either angular deviation or angular velocity, but occured beyond a limiting minimum

value for angular acceleration of the image (Fig. 50).

The turns which normally occured when the image of the pillar was accelerated across the compound eye were practically non-existent when a number of successive pairs of pillars were presented, suggesting that in such situations the presence of other pillars ahead somehow inhibited the expected response. Where only one pair of pillars was visible at a time, turns occured with much greater frequency.

As with aphids on the flat, turning on ridges may occur as a response to asymmetrical stimulation (when one pillar is present). Alternatively, turning may be the result of a "choice" situation in which opposite directional stimuli delay implementation of the efference (when two pillars are used). These two responses are easy to distinguish on the flat, by the shapes of the aphids' tracks. On the ridge, however, the inhibitory effects of the ridge and the dorsal light reaction tend to obliterate the distinction and turning is always abrupt and at the point of maximum stimulation. Successive pairs of pillars may provide an additional symmetrical component to the afference, which eventually becomes strong enough to prevent turning entirely.

Probes occured prior to the dead abeam positions of only the first three of the twelve successive pairs of pillars and this may have been due to adaptation by the aphids to repetition of the same stimulus pattern. When closely spaced pillars were encountered first, the initial group of probes may have been due to a combined effect of the first four or five pairs together. From the angle at which the aphid perceived them, these would have appeared at first as a uniform black area, which

broke up gradually into distinct pairs of pillars as the aphid progressed. That some aphids probed two or three times in this region lends support to this theory and suggests that the lack of probes along the central region of the ridge may have been due to adaptation. The probes made to either side of the dead abeam position of the twelfth pair of pillars may then have been due to the decreasing effects of adaptation with increasing distance between successive pairs of pillars.

With screened targets, the gradual decrease in the numbers of probes and turns in each group would also seem to indicate adaptation, although this may not have been the only reason for the lack of turns and probes with the experimental arrangements in this section.

Subtended Angle

Visual targets

Ibbotson *et al.* (1951) found that walking aphids stopped and probed shortly before reaching tethered aphids or aphid substitutes on the leaf surface and concluded that probes were elicited by visual stimulation of this kind.

In addition to black pillars, black cut-out silhouettes were accordingly used as visual targets, since aphids on ridges could be made to approach them in a repeatable manner. Solid silhouettes of various shapes and sizes were presented, together with broken silhouettes designed to augment the degree of flicker. In addition to the optomotor effect of the silhouette margins, possibly represented in isolation by the

pillars, such silhouettes may also have produced a "loom" effect in the visual field of the aphid. Both the lateral translation of the contrast boundaries away from one another and an increase in the number of ommatidia occluded by the black area may thus have been involved.

Most insects are incapable of assessing the absolute size of objects and can only discriminate between differences in the angle subtended at the compound eyes. Thus a small, near silhouette may be indistinguishable from a large, distant one, when both subtend the same angle. The bumble bee Bombus sylvorum L. can select black spots of optimal size regardless of their proximity (Jacobs-Jessen 1959), but aphids do not show this "size consistency" and the subtended angle of a silhouette, rather than its absolute size, appears to release probing behaviour (Ibbotson et al. 1959).

With the following experimental arrangements, re-afference was limited to the apparent increase in size of the object as the aphid approached it. The aphids were made to walk along a straight ridge, 10 cm. long, with the following black silhouettes at one end, facing the walking aphids:

Size of silhouette

Circles of diameters 2 mm., 4 mm. and 8 mm. These silhouettes were designed to test for a correlation between the apparent size of a silhouette and the distance from it at which probing occured.

Shape of silhouette

(i) a circle 6 mm. in diameter,

(ii) a rectangle 4 mm. wide and 7 mm. high,

(iii) an isosceles triangle 8 mm. wide and 7 mm. high.

These silhouettes all had the same surface area.

Components of stimulus situation

Rectangles (width x height);

(i) 4 mm. x 4 mm.

(ii) 4 mm. x 8 mm.

(iii) 8 mm. x 4 mm.

(iv) 8 mm. x 2 mm.

(v) 8 mm. x 1 mm.

Tests with these silhouettes aimed at establishing whether surface area, height or width was the critical factor in eliciting a response.

(vi) A series of six rectangular silhouettes, 10 mm. x 16 mm. wide, the first being completely black and subsequent silhouettes having central white gaps of 1 mm., 2 mm., 4 mm., 8 mm. and 12 mm. respectively.

(vii) A rectangle 16 mm. high x 16 mm. wide, having four vertical black stripes, each 2 mm. wide, on a white background.

These "broken" silhouettes were designed to separate the two factors of apparent size (number of ommatidia occluded) and speed of relocation of contrast boundaries.

Entire aphids

No turns occured with any of the solid silhouettes. With circular silhouettes, probes were made in discrete groups, the distance of which from the silhouette was directly proportional to the diameter of the silhouette (Fig 63 a-c, Table 8). Probes occured about 4 mm. from

the 2 mm. silhouette, about 8 mm. from the 4 mm. silhouette and about 16 mm. from the 8 mm. silhouette. The angle subtended by the silhouette on the region of the ridge where probing was most frequent was between 20° and 35°. There was no difference in the position of the probes made in response to the 4 mm. diameter silhouette between young adult and old adult aphids (Fig. 64 a-c).

With silhouettes having the same surface area, but different shapes, the distance from a silhouette at which an aphid probed was proportional to the width of the silhouette (Fig. 65 a-c). With rectangular silhouettes of various sizes, aphids probed at distances proportional to the silhouette width, except where the rectangular silhouettes were wide and low and probing was sparse and diffuse (Fig. 65 a-e).

Probes and turns made with the series of silhouettes with central white gaps are shown in Fig 67 a-f. A group of probes occured about 30-35 mm. from the solid silhouette, where the angle subtended by the silhouette was about 27°. As the gap increased in width with successive silhouettes, probing in this region diminished and a new group of probes occured between 5 mm. and 10 mm. from the silhouette, where the outside edges subtended an angle of about 100-110°. These latter probes apparently corresponded to those made in response to a pair of black pillars (as used previously) in that they increased in frequency up to the point at which the edges of the silhouette were each at an angle of about 55° to the longitudinal axis of the aphid. This suggested a change from probes made in response to subtended angle to probes made in response to lateral movement.

No turns occured with silhouettes having central gaps of 4 mm. or less, but became more numerous with subsequent silhouettes, where the apparent angular velocity of the edges was accelerating (Fig. 67 d-f).

With the silhouette composed of four vertical black stripes, two adjacent groups of probes occured, corresponding to the positions where the outer and inner pairs of vertical black stripes respectively subtended about 110° (Fig. 68). No probes occured where the outer edge of the silhouette subtended 25° to 30° and it was assumed that no response was made to the silhouette as a whole with this arrangement. Turns occured close to the silhouette, where the apparent lateral movement of both pairs of black stripes was increasing rapidly.

Treated aphids

No turns occured with solid silhouettes and probes made by aphids presented with these targets were in all respects distributed similarly to those made by aphids with triommatidia intact (Figs. 63-66). With the series of silhouettes having central white gaps, a group of probes occured about 30-35 mm. from the first three silhouettes presented (solid silhouette and silhouettes with central gaps of 1 mm. and 2 mm) (Fig. 69 a-c). This group became less distinct and eventually disappeared as the width of the central gap increased (Fig. 69 d-f). The group of probes made by entire aphids about 5-10 mm. from the silhouettes with the larger gaps (Fig. 66 c-f), was not apparent. Turns occured immediately before silhouettes with central gaps of 2 mm. or more (Fig. 69 c-f).

With a silhouette composed of four black stripes, very few probes

occured and turns were more numerous than those made by entire aphids, grouped within 10 mm. of the silhouette (Fig. 70).

Visual Changes 2 : Ex-afference

This term describes those visual changes which involved actual movement of objects in the visual field of the aphid (von Holst 1954). The image movement in this case elicited a response only in so far as it differed from the re-afference which would have been produced by the movement of the aphid in stationary surroundings (Hassenstein 1950, 1951, 1961).

Lateral Movement

Visual targets

The following experimental arrangement was used to produce sudden actual lateral movement of an object:

A straight ridge, 10 cm. long, with one standard pillar to each side, at standard distance, mounted on a common axle passing transversely beneath the ridge, so that both pillars could be laid down out of sight and made to suddenly appear or disappear.

Entire aphids

Almost all the aphids probed immediately when the black pillars were made to appear or disappear, irrespective of the position of the pillars in the visual field. This response was apparently not the same

as that made to stationary pillars to either side of the ridge, since it occured when pillars were made to appear in (or disappear from) the dead abeam position. Although the angular acceleration of the images across the eye must have been very high when the pillars were swung up or down, no turns occured.

Treated aphids

Probes were made immediately on the appearance or disappearance of the pillar, as with entire aphids. No turns were made.

Subtended Angle

Visual targets

The experimental arrangement was as follows:

8. A straight wax ridge, 10 cm. long, with at one end, facing the walking aphids, a black silhouette which was partly hidden by white cards, leaving a central vertical black strip which could be suddenly expanded widthways by remote control.

Entire aphids

Sudden expansion of the black strip was followed by immediate probing with most of the aphids tested (Fig. 65 a,b). When the strip was expanded soon after the aphids had started along the ridge, a second group of probes also occurred, further along the ridge where the silhouette subtended about 25° to 30° (Fig. 71). When the strip was not expanded until after a group of probes had been made where

the unexpanded strip subtended 25-30°, a second group of probes still occurred immediately the strip was expanded (Fig. 7lb). The expansion itself was clearly distinct (as a stimulus for probing) from the angle subtended by the silhouette at points along the ridge.

Treated aphids

As with entire aphids, sudden expansion of the black strip elicited probes immediately in a similar distribution along the ridge (as in Fig. 7lb).

Unilaterally Blinded Aphids

Methods

The apparatus and techniques used to extirpate the triommatidia of some aphids were also employed in the unilateral blinding of a further experimental group. Aphids were anaesthetised and mounted on their backs as described earlier. A small speck of hard, black wax was fixed on the end of the cauterising needle and held against the compound eye. The current was switched on very briefly, so that the wax just melted and formed a minute droplet over the entire eye. Aphids were then left to recover for several hours before being used in the experiments. A final examination of each aphid was made immediately prior to use, to ascertain that the wax still covered the compound eye and triommatidium completely and had not flaked off.

Controls

Unilaterally blinded aphids were made to walk along a straight ridge, in a uniformly white environment, with no visual target present. A few random probes were made and no turns (Fig. 72).

Re-afferent Visual Changes

1 : Lateral Movement

With a standard pillar to both sides of a straight ridge, at standard distance, probes and turns were distributed similarly to those made by entire aphids (Fig. 61). As before, probes occurred in two groups, one about 10-20 mm. before the mid-point of the ridge and the other a similar distance after the mid-point. Turns also occurred as before immediately before the midpoint of the ridge, where the angular acceleration of the image reached its highest value.

Re-afferent Visual Changes

2 : Subtended Angle

Aphids presented with a series of black silhouettes having central white gaps (as before) made very few probes with the solid silhouette and the silhouette with the 1 mm. gap. Larger gaps elicited probes about 4 mm. to 10 mm. from the silhouette (Fig. 72 a-f). Turns occurred with silhouettes having central gaps 2 mm. or more in width, in the last few millimetres before the pillar was reached.

Discussion

Where re-afference alone was associated with the lateral movement of an image, probing responses were made by fully sighted and unilaterally blinded aphids, but not by those with extirpated triommatidia. The involvement of the triommatidium in the above responses thus seem probable. The distribution along a ridge of probes made in response to the lateral movement of an image was apparently determined by the angular position of that image in the field of view of the aphid. The absolute angular velocity of the image was not critical, although some movement would have been essential for re-afference to occur.

A response of this type was not apparent when a black pillar was situated between about 57° and 123° to either side of the aphid. Since the triommatidium has no laterally directed facet, it would be reasonable to assume a triommatidial "blind spot" which may have coincided with the above regions of the aphid's horizon. The lack of probes when the pillar was near the dead astern position of an aphid was most likely to have been due to the pillar being obscured by the bulk of the abdomen of the aphid.

Turns were not affected by extirpation of the triommatidia and it is likely that they were made in response to stimuli received by the compound eye. Turns always corresponded to an acceleration in the lateral movement of an image across the eye which exceeded 36 mins. of arc/sec.^{2} (where the aphid walked at 3 mm./sec.) and a stimulus of this type was most likely to have been perceived as flicker across the successive facets of the compound eye.

The angle subtended by a silhouette dead ahead was found to be critical in eliciting a probing response. For most of the aphids tested, this angle was between 27° and 30°, although some groups of probes extended to points where the angle subtended was as small as 19° or as large as 53°. This response depended on the perception of the silhouette by the compound eyes and was not affected by extirpation of the triommatidia; it was absent in unilaterally blinded aphids and may have involved binocular vision. From the morphology of the head of Aphis fabae, it seems likely that a zone of binocular vision covering between 40° and 60° of arc extends directly ahead of the aphid, so that silhouettes would have appeared within this zone when probing occurred.

The speed of reloaction of the edges of the silhouette over the eyes did not appear to be important in eliciting probes in this situation. The apparent angular velocity of the edges of the silhouettes at the position of most frequent probing, was relatively low. Probes occurred several millimetres before the point at which the angular velocity of the pillar would have started a rapid, logarithmic increase towards its maximum value.

The "loom" effect of a solid silhouette, which elicited probes when the silhouette subtended an angle of approximately 30°, apparently inhibited any further response to the relocation of the edges of the silhouette, which may have been expected to occur when the silhouette subtended an angle of approximately 100°.

REORIENTATION AND PROBING AT VARIOUS LIGHT INTENSITIES

Methods

The light intensity under which the preceding experiments were conducted was altered by moving the lamp closer to the experimental arrangements to provide a higher light intensity and by using a rheostat "dimmer" to give lower intensities.

A very strong illumination of 6000 Lux was achieved by bringing the 100 Watt "Atlas Spotlight" bulb to a position 25 cm. above the experimental surface. A glass dish of water was placed immediately beneath the lamp to prevent overheating at the experimental surface. The dimmer was used to provide a moderate light intensity of 250 Lux and a low light intensity of 10 Lux.

Thirty entire aphids, freshly moulted and at 6 and 24 hrs. old, were used in two experimental arrangements. In the first, aphids walked across the flat plate with a standard black pillar at normal distance from the point where the aphids debouched from the causeway. In the second experiment, aphids traversed a straight ridge, 10 cm. long, with the pillar in the same position relative to the aphid at its starting point (standard distance).

Results

Moderate Light Intensity

With illumination of 250 Lux, aphids behaved in all respects

exactly as in the foregoing experiments with illumination of 2800 Lux. On the flat, newly moulted adults made sinuous paths, young adults made orbital paths and old adults made constant angle paths as in (Fig. 24b, e, i). On ridges, probes and turns were again distributed in a typical manner as in Figs. 44a, b, d.

High Light Intensity

At both very high and very low light intensities, the usual patterns of behaviour did not emerge. With illumination of 6000 Lux, aphids tended to walk straight ahead without probing or reorientating towards a pillar. Only two of the old adults tested made "constant angle" paths on the flat and occasional random probes were made on ridges, mainly by newly-moulted aphids (Figs. 73 & 74).

Low Light Intensity

Illumination of 10 Lux likewise prevented characteristic reorientation and probing behaviour. Probing was frequent, both on the flat and on ridges, and was apparently at random. Lateral reorientation towards the pillar did not occur and aphids on the flat either walked straight ahead or wandered at random. Aphids on a ridge frequently climbed down from it, usually after probing, but occasionally without having probed. They moved gradually down onto the sides of the ridge whilst walking forwards and without making sharp turns (Figs. 75 & 76). Presumably even in the absence of a pillar, aphids under "normal"

illumination were orientating visually, since by comparison they walked along straight paths; i.e. they performed something akin to the standard optomotor response to a pattern, which modified into a local directional orientation to a dominant contrast.

Discussion

Rhythmic, spontaneous electrical activity is probably common to all compound eyes and is of ganglionic origin (Roeder 1939, 1940; Autrum 1951, 1952; Burkhardt 1954; Burtt et al 1959a). As was mentioned earlier, in Dytiscus there are actually two such rhythms, one of which occurs only under maximum illumination and was visualised by Adrian (1937) as representing the simultaneous discharge of all the neurones. A system of dual rhythms has since been found in other insects and the amplitude of such rhythms is often related to the intensity of illumination and the degree of adaptation in the eye (Roeder 1939, 1940; Crescitelli et al. 1942; Burkhardt 1954). Light intensity may thus act directly on the eye by altering its sensitivity to stimulation, as well as indirectly by altering the nature of the sensory input.

The stimuli which determined the characteristic reorientation patterns on the flat and the positions of probes and turns on ridges, included the visual contrast between the black pillar and its white background and the speed of translocation of this contrast boundary across the field of view (flicker effect). At very high and very low light intensities, this contrast may have been insufficient to elicit a response,

explaining the absence of the characteristic behaviour patterns.

In addition to the overall intensity, the wavelength composition of incident light is important, since the retina is selectively sensitive to certain wavelengths, which may thus appear to have a higher intensity than others (Ludtke 1953; Heintz 1959). In the present experiments, however, spectral composition could not be guaranteed constant when the intensity was reduced with a dimmer or when a glass dish of water was used as a heat filter.

DISCUSSION

The stimulus-response system in insects has certain unique features which are of importance in any consideration of the role of specific stimuli in determining overt behaviour. A stimulus constitutes a change in the environment which imparts sufficient energy to the receptor to set up a state of local excitation (Dethier et al. 1961). The local excitation in turn generates an action potential which travels along the nerve connecting the receptor to the central nervous system (CNS). Although the receptor may be specific, the information which it sends along the nerve is not. All nerve impulses have the same nature. The total number of impulses reaching the brain is not proportional to the amount of physical energy acting as the stimulus (Fraenkel et al. 1940) and there is no direct energy flow from the stimulus to the response. The stimulus is merely a cue, which releases or inhibits an action or behaviour pattern. The relationship between the stimulus and the

nervous impulses which it generates is neither simple nor constant.

A restricted number of neurones is a characteristic of insect nervous systems (Carthy 1965). Although the axons may be large (so-called "giant fibres"), they conduct much more slowly than vertebrate myelinated nerve fibres. Synapses are often lacking and axons from a group of sense organs may merely fuse to form a nerve leading to the CNS. A reduction in the amount of information contained in the sensory input would almost certainly result from this arrangement (Roeder 1963).

Control of muscular activity occurs peripherally rather than centrally, through the presence of both excitatory and inhibitory efferent fibres. In the stridulation behaviour of crickets, excitation and inhibition of motor commands from the thoracic ganglia are integrated by the corpora pedunculata and transmitted to the muscles via the central body and supra-oesophageal ganglion (Huber 1963).

The simplicity of the nervous system and the slow rate of impulse transmission reduces the possibility of continuously regulating movement by sensory feedback. Many actions, once initiated, invariably continue to their conclusion. The "strike" reaction of mantids and the "open system" turning response of salticid spiders are both responses requiring no sensory feedback (Mittelstaedt 1962; Land 1972). Feedback is important, however, in the maintenance of posture and in course control during locomotion. Sensory feedback from proprioceptors in the halteres of Diptera, for instance, controls the orientation of the flying insect in all three planes (Pringle 1957).

Feedback may be visual as well as proprioceptive. The fly Eristalis, walking past a pattern of black and white vertical stripes, receives a re-afferent visual input. The apparent movement of the stripes is due entirely to the locomotion of the insect and the visual feedback maintains the insect on a constant course, against the apparent movement of the stripes. On the other hand, actual movement of the stripes past a stationary insect causes an optomotor response in which the fly turns with or towards the direction of movement. A possible reason for this apparent contradiction is that locomotion or eye movement automatically inhibits the optomotor response, as was suggested by Palka (1969), with crickets. Against this, when the head of Eristalis is turned through 180° about the long axis so that the order of the visual elements is reversed, the insect no longer reorientates in a normal manner in stationary surroundings, but spins rapidly in tight circles once it begins to move (Mittelstaedt 1962).

To explain this anomaly, it has been supposed that the CNS contains a pattern, to which the pattern of sensory input must correspond for the movement to cease. Von Holst (1954) suggests that the efference leaves an "image" of itself in the CNS, which he calls the "efference copy", to which the re-afference produced by the subsequent action compares as a negative compares to its print. When the re-afference matches the"efference copy" exactly, the "image" disappears and the efference ceases. Re-afference which effectively suppresses a response in this way is called "negative feedback". When the re-afference is inverted, as in an insect with the head reversed, the efference copy is not matched and summation occurs instead. Movement then progressively

increases so that a simple turning action is repeated until the insect is exhausted. This process has been described as "positive feedback".

The initial efferent "command" originates in a higher centre of the brain and the "efference copy" is imprinted in a lower centre (von Holst 1954). In the stridulation behaviour of crickets, commands initiated in the corpora pedunculata are altered in the central body into a pattern of excitation which probably represents the "efference copy". This pattern is passed to the thoracic ganglia and determines the rate of chirping and the sequences in which the chirps are made (Huber 1963). Auditory feedback then augments the co-ordination and control of stridulation.

In locomotion, forward movement and directional orientation are independently varying processes and the concept "taxis" should be confined to the directional component (Koehler 1950; Jander 1963); a particular taxis mechanism may be used for both attitude and locomotory reorientation. Probing aphids were sometimes seen to make adjustments to their posture by sideways movements with their legs, while keeping the rostrum stationary. One and the same taxis may thus control turning in aphids which are moving forwards and attitude changes in aphids which are probing. In aphids, walking, probing and reorientation are all independent processes. Walking and probing are incompatible behavioural mechanisms, only one of which can operate at a time (although protraction of the rostrum may sometimes occur before locomotion has ceased). The taxis mechanism for reorientation, on the other hand, can operate during walking or probing.

It may be useful to briefly summarise the stimuli provided in the above experiments, the responses which they apparently elicited and the receptors which are thought to have been involved. First, the apparent movement of a pillar, when perceived by the compound eye, elicited "constant angle" turning on the flat plate and sudden turns on the ridges. Movement perceived by the triommatidia elicited compensatory turns on the flat and probes on ridges. Second, the "loom" of a silhouette dead ahead, the subtended angle of which increased as the aphid approached it, was probably perceived by the compound eye and elicited a probing response. Third, the probes made in response to sudden actual movement of objects were mediated by the compound eye.

On the flat, considerable behavioural changes occured during the first 24 hours following the final moult, whereas aphids on ridges did not show changes in the type of response during this period, but only a slight apparent drop in overall responsiveness between 12 and 24 hours. If the triommatidium was involved in reorientation behaviour of nymphs and newly-moulted adults on the flat and the compound eye involved in the behaviour of older aphids, compound eye efference may have become more important in determining behaviour as an aphid aged. With 24 hrs. old aphids on ridges, lateral movement of an image due to the aphid's own locomotion may have elicited probes via stimulation of the triommatidia and turns via stimulation of the compound eyes. This suggested that the triommatidium was capable of providing a sensory input and eliciting a behavioural response at least up to 24 hours after the final moult, but that this response was suppressed in aphids over about 8 hours old, on the flat. The compound eye likewise appeared

to elicit responses in recently moulted aphids on ridges, but not on the flat where "constant angle" orientation, apparently attributable to compound eye stimulation, did not appear until about 12 hrs. after moulting and may have been suppressed in younger aphids.

The compound eye and the triommatidium may thus have been involved in functionally independent stimulus-response systems and, on the flat, the responses mediated by each may have been mutually exclusive and, to some degree, antagonistic. The absence of mutual exclusiveness between the systems in aphids on ridges may have been due to the restricting effect imposed by the ridge on the form of efference. On the flat, responses assumed to be mediated by the compound eye and triommatidium respectively (constant angle path and sinuous path) were largely incompatible, both involving fairly gradual directional changes during locomotion and, since two such behaviour patterns could not occur simultaneously unless they were identical, the response mediated by one receptor may have suppressed that mediated by the other. On ridges, probes and turns were compatible, discrete events, which could follow one another in rapid succession or even occur simultaneously.

To describe the responses mediated by the compound eyes and triommatidia as "antagonistic" is not to say that they are classic antagonists in the sense of Sherrington (1947), as are, for example, walking and probing in apterous aphids (Ibbotson et al. 1959) and flight and settling in alates (Kennedy, 1966). The responses did not show sustained alternation under constant conditions and inhibiting one did not automatically elicit the other (or vice versa). Indeed, since

both responses were elicited by a common stimulus perceived by different receptors, the only means of experimentally inhibiting one response would be to block the perception of the stimulus by one receptor, in which case the system would no longer interact.

There was, however, a sufficient degree of mutual exclusiveness to justify a consideration of orbital path orientation in terms of the combination or alternation of the responses which were thought to have involved the compound eyes and triommatidia respectively. In this transitional phase, the compound eye response may have eventually "broken through" (in the phrase of Sherrington) the inhibitory influence of the triommatidial response and established itself as the dominant motor pattern. The observed reorientation behaviour during this transitional stage did not, however, consist of the haphazard turning which might be expected to result from two responses "pulling in opposite directions", tipping the behavioural balance first in one direction and then the other. The orbital paths were as predictable in their general configuration as the sinuous and constant angle paths, indicating that the entire sequence may have been monitored by a higher centre in the brain. Central control may coordinate behaviour where two behavioural patterns are fully antagonistic, the inhibition of a given activity by stimulating its antagonist being due not to any feedback from the performance of the antagonistic activity, but to central inhibition (Kennedy 1966).

Wallace (1962) observed that the reaction of a locust to only one of two visual stimuli is due not to peripheral inhibition of inflow from the receptors, but to a conflict between the motor outputs required for the two responses. The responses concerned were incompatible, but

not true antagonists. Similarly in aphids, the compound eye and triommatidium may both provide action potentials, each input eliciting a corresponding efference. One of the two potential efferences is suppressed and the other is expressed as overt behaviour.

Peripheral control of sensory organs is not unknown, however, and occurs in the crustacean stretch receptor. An efferent inhibitory fibre innervates the receptor and stimulation of this fibre results in repolarisation of the cell membrane of the receptor, abolishing or diminishing the sensory input (Carthy 1965).

Applying the "efference copy" theory of von Holst to the constant angle paths of old adult aphids, the required re-afference which nullified the efference copy would have been the maintenance of a constant visual pattern. Any apparent movement of the pillar would have caused the efference copy to activate the effector muscles in such a way that the walking insect turned to a greater or lesser extent. The sensory cells of the leg muscles also produced a re-afference which may have supplemented that provided by the visual organs. Given the efference copy was coded in terms of walking speed and amplitude of turning response, the resultant afferent action potentials would have represented a constant position of the image on the compound eye and zero angular velocity.

The transmission of neural information is possible only as the transmission of alternatives and a single contingency may be transmitted most efficiently by sending no message at all (Wiener 1948). Thus the command from a higher centre of the brain of an adult aphid, which predisposes the maintenance of a constant visual pattern in the compound

eye and produces an efference copy in a lower centre, may be the basic condition in walking aphids, where continual re-assessment of the visual situation and re-adjustment in the rate of turn of the aphid were necessary.

In newly moulted adult aphids, a new set of efference copy units is present in the CNS. These are open to some adaptation, but without them behaviour would be totally random. These efference copy units constitute the instinctive component of normal adult behaviour.

Physiological changes in the CNS, which bring about behavioural changes in the organism, are frequently influenced by hormones (Highnam 1964). Although the nerve paths responsible for different behaviour patterns may be present in the nerve cords of insects, the presence of hormones determines which paths are activated to cause behavioural changes (Carthy 1965). Hormones apparently act directly on the central integrative processes responsible for the organisation of different patterns of behaviour.

A "compromise" situation, in which a directional response is the mean of two conflicting potential responses, is found in Eristalis. When the insect was placed at the intersection of two horizontal beams of light of equal intensity, which crossed at right angles, its path followed the diagonal, bisecting the angle formed by the beams. If one eye was dark-adapted, the degree of deflection of the path from the diagonal was dependent on the degree of dark adaptation in the one eye (Dolley et al. 1929; Dolley 1930). "Compromise" reorientations also occur with two directional stimuli which are received by different receptors. On an inclined plane, illuminated from one side, Carausius walks in a direction

of compromise between positive phototaxis on the one hand and negative geotaxis on the other. Changing the brightness of the light or the steepness of the slope alters the direction of walking (Jander 1963).

Since only one pattern of stimulation at a time can be conveyed along the neurones (Wiener 1948), compromise reorientation cannot result from the muscle being activated by two different outputs at the same time. The rapid temporal alternation of incompatible efference may be a more feasible explanation. The relative "strength" of one response when compared to the other would then depend solely on the overall duration of transmission of the respective efference.

In constant angle orientation, the angular deviation of the pillar remained constant, while the degree of turning in the path of the aphid increased exponentially. These two re-afferent components, one visual and one proprioceptive, were complementary in nullifying the efference copy. Exponential increase in the turning response was not apparent until the aphid had completed about 70% of its track, irrespective of the size or proximity of the pillar.

In young aphids, deviation from the constant angle path, possibly due to the occasional breakthrough of nymphal behaviour, meant that visual and proprioceptive re-afference diverged progressively further from the efference copy. The image moved across the eye with increasing rapidity, while the curvature of the aphid's path remained constant or even decreased. A point was eventually reached at which the disparity between the actual re-afference and the ideal re-afference needed to nullify the efference copy was sufficiently large to cause an "avoidance reaction" consisting of a sharp, contralateral turn.

The first abrupt turn set the aphid on an orbital path about the pillar and, in this situation, image movement was nil and the visual component of the re-afference matched the efference copy. The proprioceptive component, on the other hand, diverged from the efference copy to a progressively greater extent as the aphid progressed on the orbital path, since no increase in the curvature of the path occurred. A second contralateral "avoidance" turn thus occurred at some point along the orbital path to leave the pillar directly behind the aphid.

Aphids on circular ridges, with a pillar in the centre of the circle, apparently experienced no triommatidial stimulation at all and walked continuously, probing only rarely. Where aphids on ridges received stimuli via both the compound eyes and the triommatidia, the ridge itself prevented nullification of the efference copy, since the progressive turning response dictated by the "constant image" command was blocked by the equally basic dorsal light response, which kept aphids on the ridge. The suppressed efference summated and only found expression in the sudden turns towards the pillar, which occurred when the angular acceleration of the pillar was maximal. Suppression of the "constant image" efference allowed the breakthrough of probing behaviour mediated by the triommatidium, which was particularly apparent where the pillar entered or left the triommatidial field of view.

The limited degree of flicker in triommatidial afference distinguishes it markedly from afference provided by the compound eye and may have been responsible for a subsequent difference in response. In first and second instar nymphs, the triommatidial facets are not mounted on a tubercle, but are all directed laterally and hence capable of

perceiving a greater degree of flicker between them. Experiments with these nymphal stages may reveal behavioural analogies with endopterygote larvae, which orientate in response to flicker across a small number of lateral ocelli (Dethier 1943, 1963). If suitable experimental arrangements could be devised, it would be useful to monitor reorientation behaviour through the nymphal instars, as the triommatidial facets gradually changed their relative positions, from the larval to the adult condition.

In addition to the experiments with Aphis fabae described here, some preliminary experiments were performed using apterous virginoparae of Myzus persicae Sulz., Macrosiphum gei Koch and Sitobion avenae Fab. All these species are gregarious, but none forms such dense aggregates as does A. fabae. The nymphs made sinuous paths, the oldest adults made constant angle paths and at least some of the young adults made orbital paths. In M. gei, orbital paths occurred within an hour of the final moult and lasted until the aphids were about eight hours old. In M. persicae, orbital paths occurred in the same period as for A. fabae and, with S. avenae (in a few individuals only), about six to twelve hours after the final moult.

It would be unwise to attempt to correlate isolated responses observed in the laboratory with insect ethology in the field. One point emerges from these experiments, however, which is worth considering in a wider context. All the directed reorientations were, with one exception, towards the black pillar and, on the flat, usually resulted in the aphid attaining the pillar and climbing up it. The exception was the orbital path in which young adults effectively avoided the pillar.

Recently-moulted adult apterous aphids tended to leave the plants in the stock culture and to undergo a period of locomotory activity during which they could be seen walking over the sides and lids of the cages. This period of photopositive wandering, soon after the final moult, has also been reported from field observations and it has been suggested that it parallels the more spectacular migratory phase of the young adult alates (Kennedy et al. 1959). The effect of orbital path orientation would be to prevent aggregation and aid the dispersal of the aphids to new feeding sites at the time when their reproductive potential was highest.

A specific dispersal mechanism, which operated once in every generation, would be particularly desirable in those plant-sucking insects in which a succession of apterous generations is usual. The triommatidium occurs in the Aphidoidea and Cocoidea, the only groups to have successive generations of apterous females. The secondary loss of wings is often associated with a decrease in the number of facets in the compound eye (Kalmus 1945). In aphids, the consequent loss of visual acuity in the adult may be associated with delayed development of the compound eyes in the nymph. The precociously developing triommatidium would provide the larva with visual organs before the complete development of the compound eye and so make possible reorientation and dispersal in the nymphs. The larvae are the most important dispersal phase in the apterous females of many coccids (Pflugfelder 1939).

More importantly, the incompatibility between the responses

mediated by the compound eyes and triommatidia respectively provides a physiological basis for dispersal behaviour in the adult apterae. Those insects in which the triommatidia are the sole visual organs of the apterae (Coccoidea, Adelgidae, Phylloxeridae, Pemphigus, Tetraneura, Caratovacuna etc.) and those in which the triommatidia are absent (e.g. Subsaltusaphis, Trichocallis, Coloradoa, Capitophorus, Eulachmus, Cinara) may not have a dispersal phase in the newly moulted adult apterae.

In conclusion, the triommatidium is possibly intricately involved in the reorientation and dispersal behaviour of apterous A. fabae and probably many other aphids. It may provide the additional sensory input necessary to establish an antagonistic situation between incompatible efferences, which in turn could constitute the basis for dispersal behaviour in the young adult apterae. In the large amount of literature on the responses of flying aphids, no specific investigation of the role of the triommatidium appears to have been made. In the light of the present work, such an investigation may provide a fresh viewpoint on the migratory behaviour of alate aphids.

SUMMARY

The triommatidium is a group of three ommatidia, mounted on a tubercle and appended to the postero-lateral part of the compound eye in most aphids. It compares with the compound eye in sensory capabilities, with the exception that flicker is limited and motion is

perceived as a vector without spatial connotations. The triommatidium evolves from compound eye facets, differentiates as a functionally independent receptor and is fully developed in the first instar larva, at which stage the compound eye may be rudimentary.

Reorientation and probing in apterous, female A. fabae was examined on the flat and on ridges. With no restraint on lateral reorientation, the aphids' tracks often had common features. On ridges, lateral reorientation was limited to an aphid turning sharply and leaving the ridge. Probing behaviour occurred in both situations.

Nymphs on the flat described sinuous paths towards a black pillar, young adults orbited the pillar and old adults reached the pillar by exponential curves. Extirpation of the triommatidia prevented responses typical of nymphs and young adults. It was assumed that the triommatidium was involved in the release of these responses and that the triommatidia and compound eyes comprised functionally separate systems.

On ridges, aphids reorientated when the angular acceleration of an image across the compound eye reached a critical value. Probing was elicited by movement of an image into or out of the triommatidial field of view, or to the angle subtended at the compound eyes by an image dead ahead. Sudden actual movement of objects also caused probing.

Similar results were obtained with other aphid species and responses observed in A. fabae may be common to many aphids possessing compound eyes and triommatidia.

Responses mediated by the compound eyes and triommatidia respectively were antagonistic and incompatible. Those mediated by the triommatidia prevailed in nymphs, whilst the compound eyes were involved in the behaviour of old adults. Young adults showed "compromise" behaviour, which resulted in their avoidance of objects ahead. This had the effect of dispersing aggregates of young adult aphids and it was inferred that the triommatidium plays an important role in the dispersal mechanism of apterous aphids.

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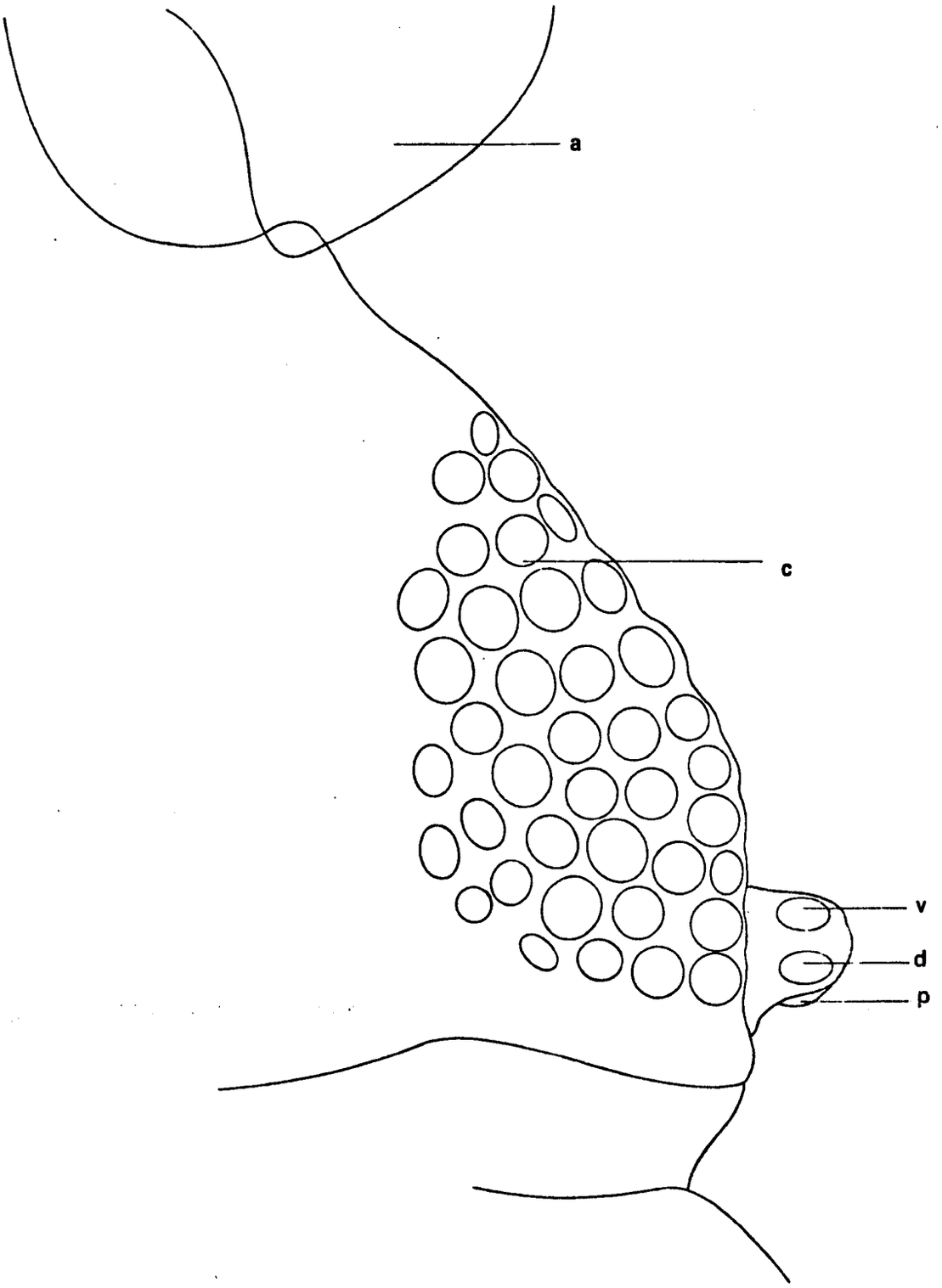


Fig. 1. Aphis fabae Scop., apterous, virginoparous female. The visual organs of the right hand side, seen from above. (Original).
a = antenna, c = compound eye, d, v & p = dorsal, ventral and posterior facets of the triommatidium respectively.

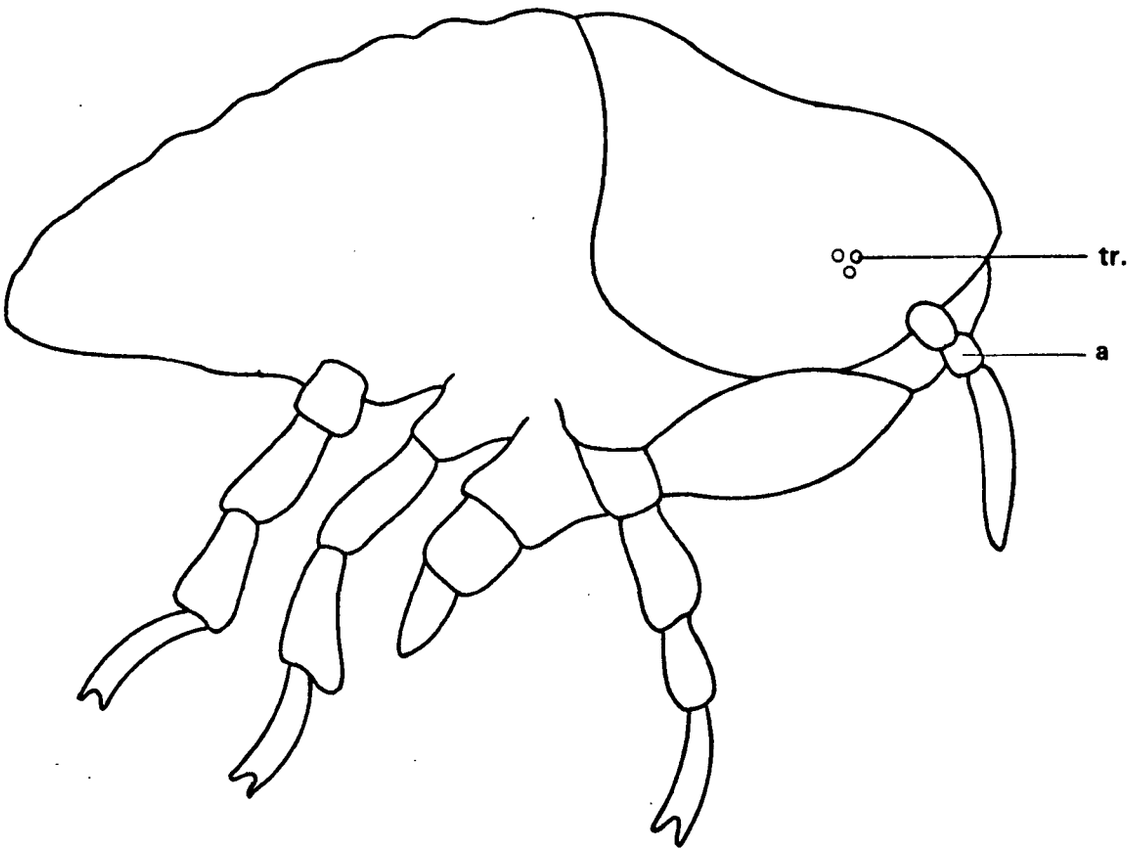


Fig. 2. Adelges laricis Vallot, first instar apterous virginopara, showing the position of the triommatidium. Redrawn after Borner.
a = antenna, tr. = triommatidium.

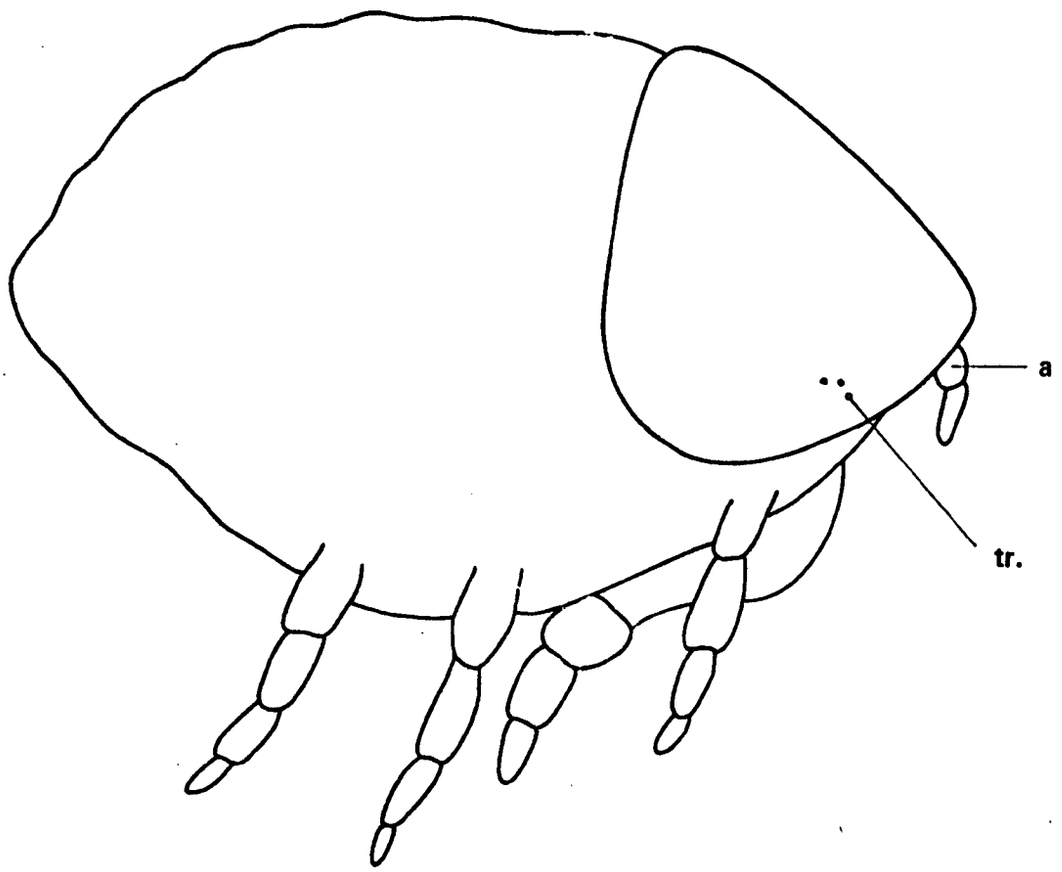


Fig. 3. Pineus pini Gmelin, first instar apterous virginopara, showing the position of the triommatidium. Redrawn after Borner. a = antenna, tr. = triommatidium.

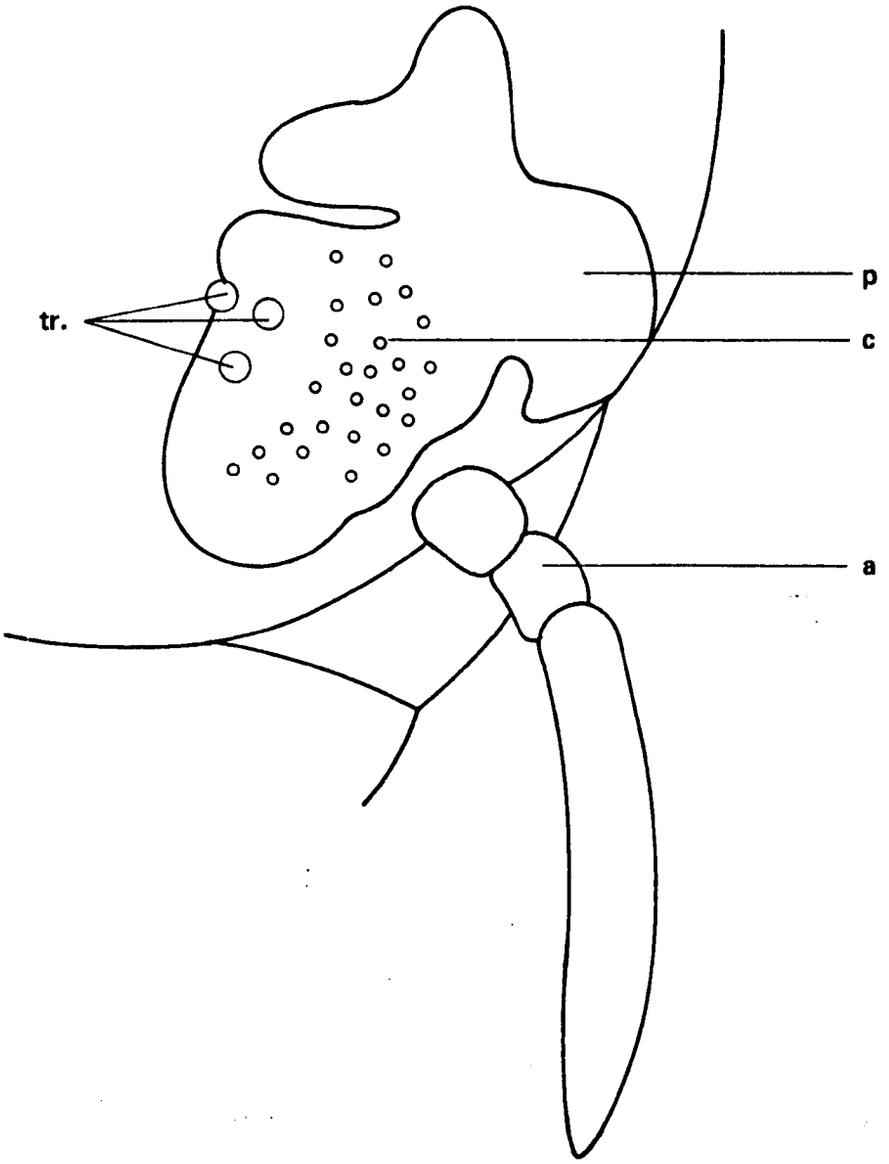


Fig. 4. Adelges laricis Vallot, alate sexupara nymph. Triommatidium and rudimentary compound eye. Redrawn after Borner. a = antenna, c = compound eye, p = pigmented area, darker in colour than the surrounding cuticle, tr. = facets of the triommatidium.

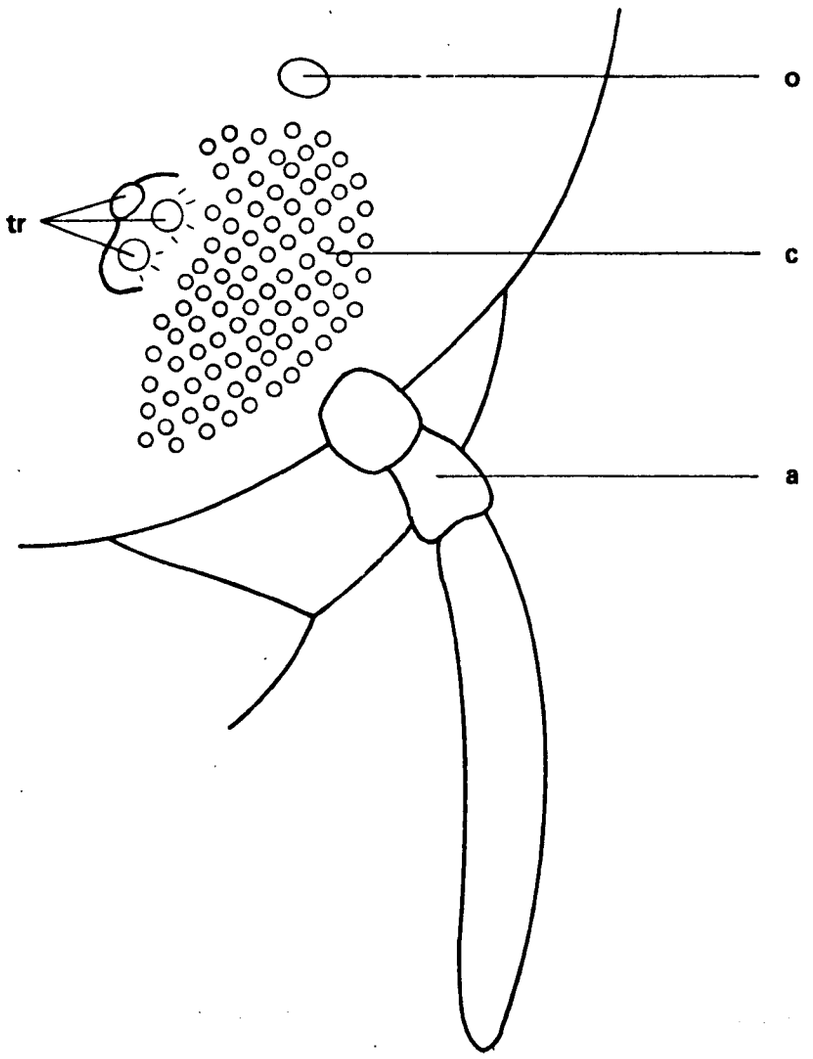
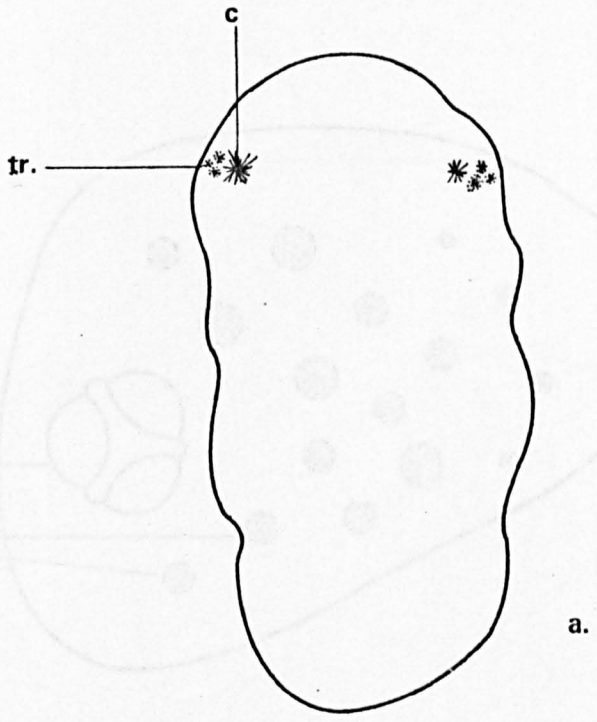


Fig. 5. Adelges laricis Vallot, alate sexupara adult. Triommatidium and fully developed compound eye. Redrawn after Borner. a = antenna, c. = compound eye, o = ocellus, tr. = facets of the triommatidium.



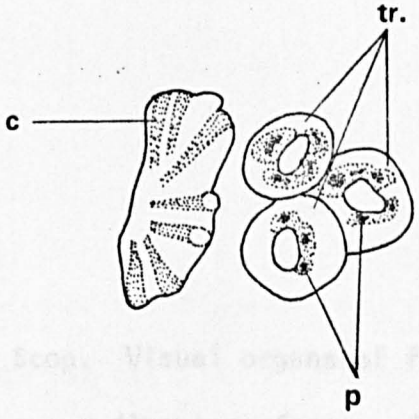


Fig. 6. Macrosiphum gei Koch. a) Embryo taken from apterous virginoparous female (x 100). b) The visual organs on the right hand side (x 1000). c = compound eye rudiments, p = pigment cells within the triommatidium, tr. = facets of the triommatidium. (Original).

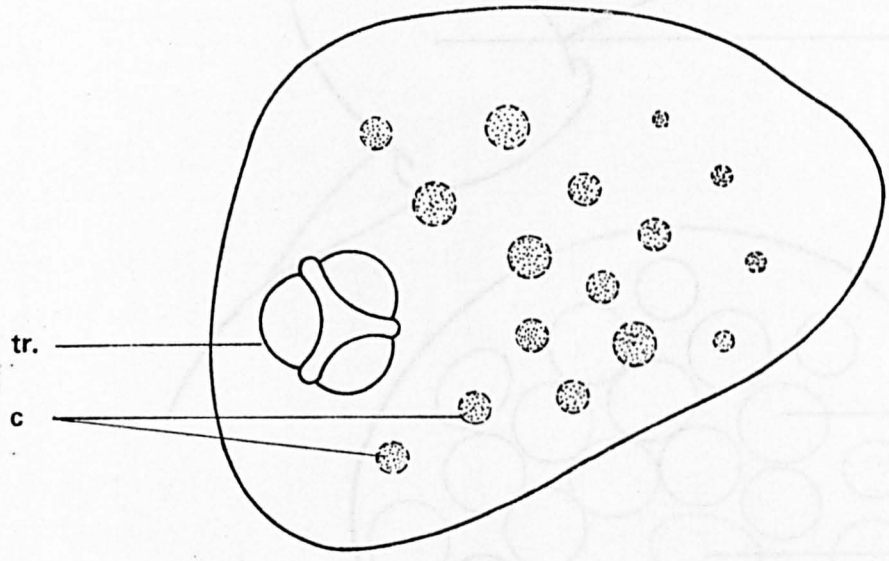


Fig. 7. Aphis fabae Scop. Visual organs of first instar apterous virginopara. c = rudimentary facets of compound eye, tr. = triommatidium. (Original).

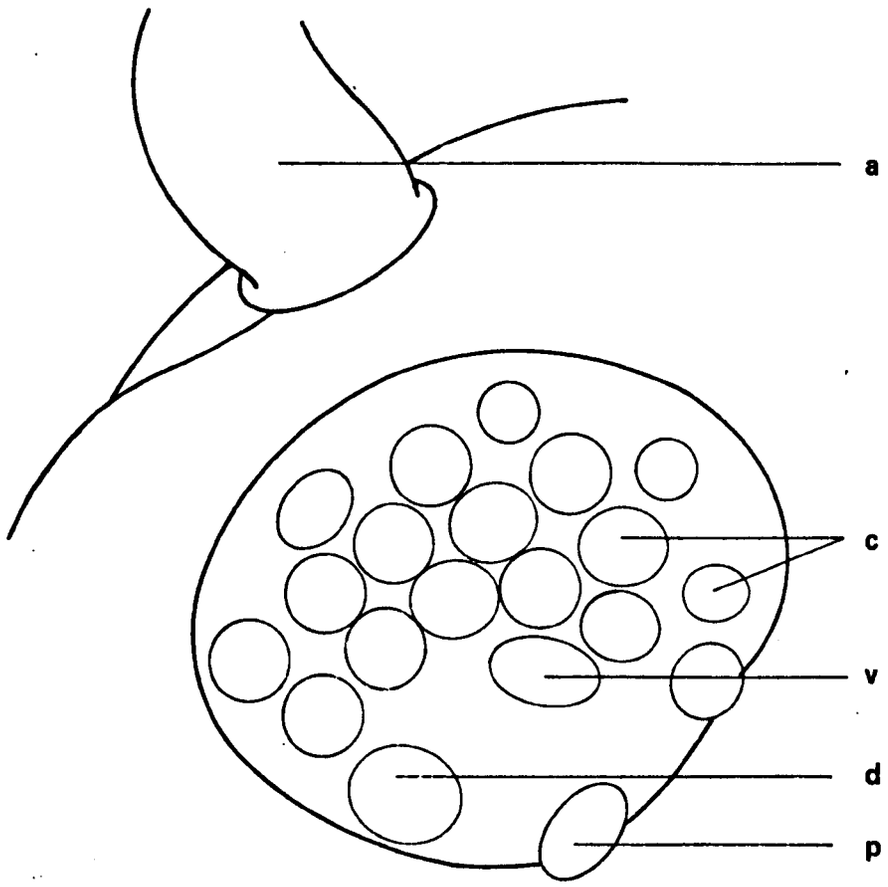


Fig. 8. Myzus persicae Sulz. Visual organs of first instar larva hatching from overwintering egg. Redrawn from a photograph by Watase. a = antenna, c = facets of the developing compound eye, d = dorsal facet of the triommatidium, p = posterior facet, v = ventral facet.

Table 1. Dimensions of the compound eye and triommatidium in larvae hatching from overwintering eggs(μm). (After Watase)

Species of aphid	triommatidium				compound eye		
	major diameter of tubercle	facet size (major diam.x minor)			major diam. of compound eye	No. of facets	size of facets (major diam. x minor diam.)
		dorsal	ventral	posterior			
A. distylii	20-22	8x8	8x8	10x10	—	—	—
C. nekiashi	34	8x8	8x8	8x8	—	—	—
C. hippaphaes	—	—	—	—	44-46	16-23	8x8-12x8
L. tropicalis	36-48	12x10.8	15.2x12	16x12	136-148	62-58	12x12-14x12
E. thunbergii	—	—	—	—	80-86	32-40	11.2x10.4-12x12
C. pineti	—	—	—	—	80-84	32-36	12x10-12x12
D. nishiyae	30.5	8x8	8x7.2	10x10	—	—	—
C. saliapterus	24-26	12x12	13.2x12	14x13.2	56-60	16-18	8.8x8-10x10
A. pomi	20-24	10x10	10x10	12x12	52-56	15-19	8.4x8-10x10
M. persicae	22	11x11	11x11	11x11	56	15-17	8x8-8.4x8.4
T. piricola	28	12x12	12x12	10.4x10.4	56-64	15-21	8.8x8.8-10x10
T. ulmi	30	8x8	10x8	11.2x8	—	—	—
Macrosiphum sp.	20-22	10x10	10x10	12x10	52-56	14-19	8x8-10x10
M. rosae ibarae	24	12x12	14x14	16x16	84	30-36	10x10
A. corni	32.5	10.4x10.4	10.8x10.8	11.6x11.6	—	—	—
A. gossypii	20-24	12x10	12x11	12x12	48-52	10-15	8x8-10x10
P. californensis	20-30	11.2x10	11.6x10.6	12x12	44	5-7	8x8-10x8.8
Periphyllus sp.	30x32	15.2x11	16x14.4	20x16	68	12-15	11.2x11.2-12x12

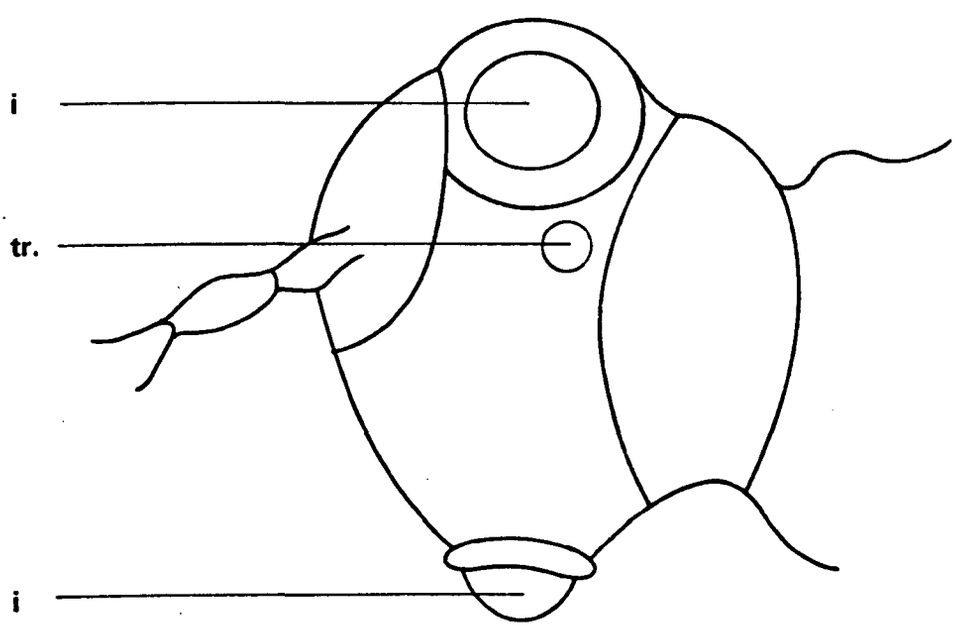


Fig. 9. Parthenolecanium corni (Bouche), adult male. Lateral view of head showing imaginal eyes (secondarily divided compound eye) and triommatidium. After Pflugfelder.

i = imaginal eye, tr. = triommatidium.

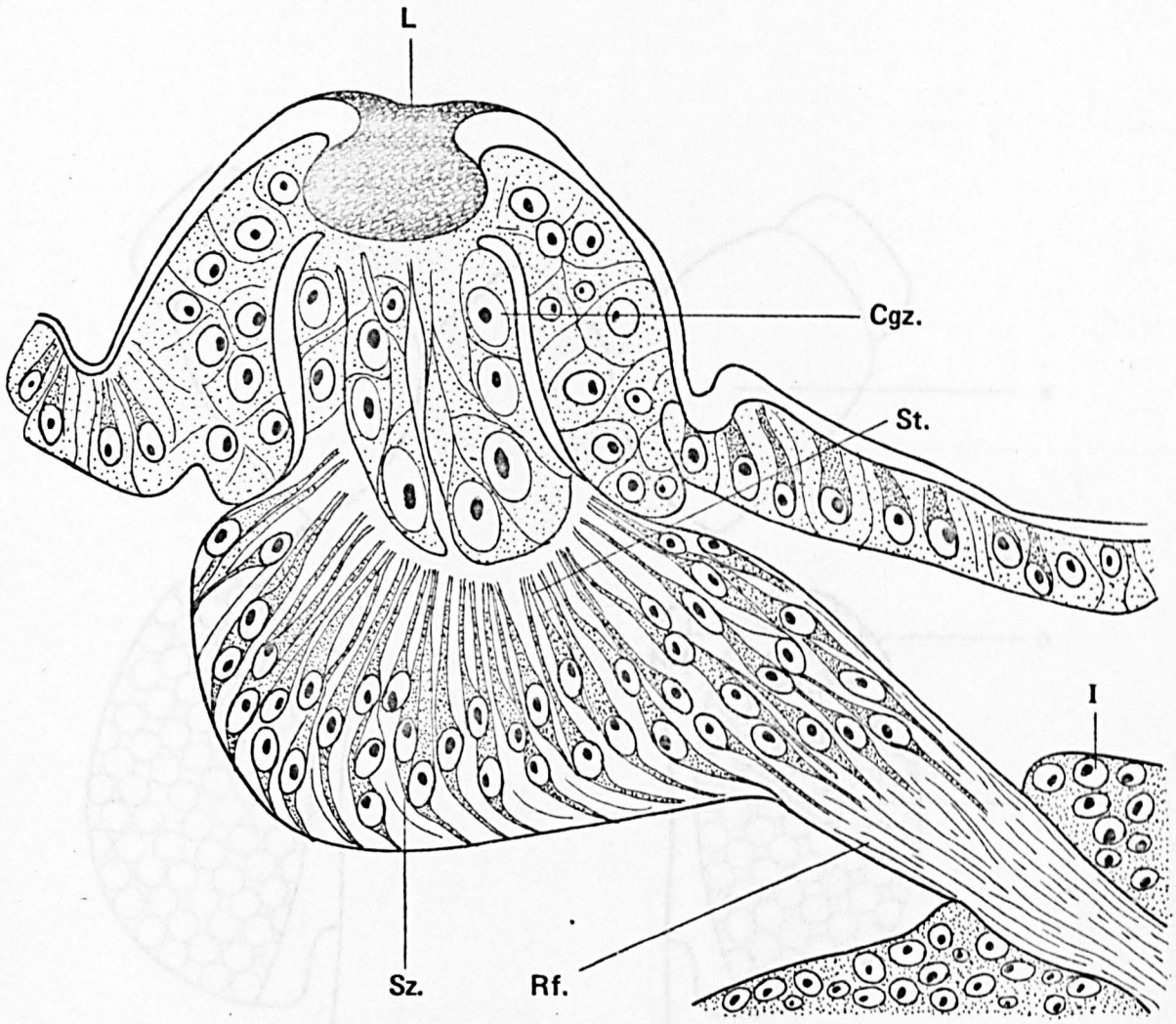


Fig. 10. Parthenolecanium corni (Bouche), adult male. Section through imaginal eye. After Pflugfelder.

Cgz. = crystalline cone cells, L = lens, Rf. = retinal fibres, St. = rhabdoms, Sz. = sense cells (retinular cells).

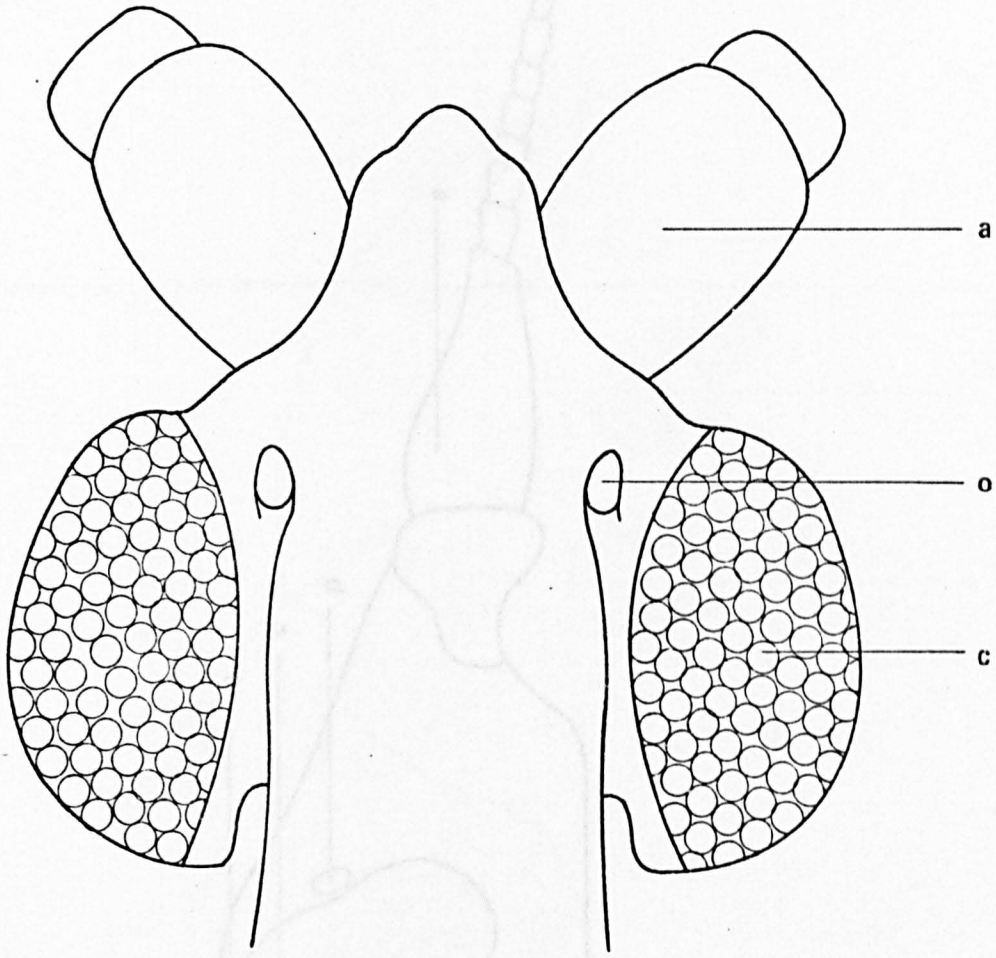


Fig. 11. Drosicholdes haemoptera, adult male. Dorsal view of head. Redrawn after Weber. a = antenna, c = compound eye, o = ocellus.

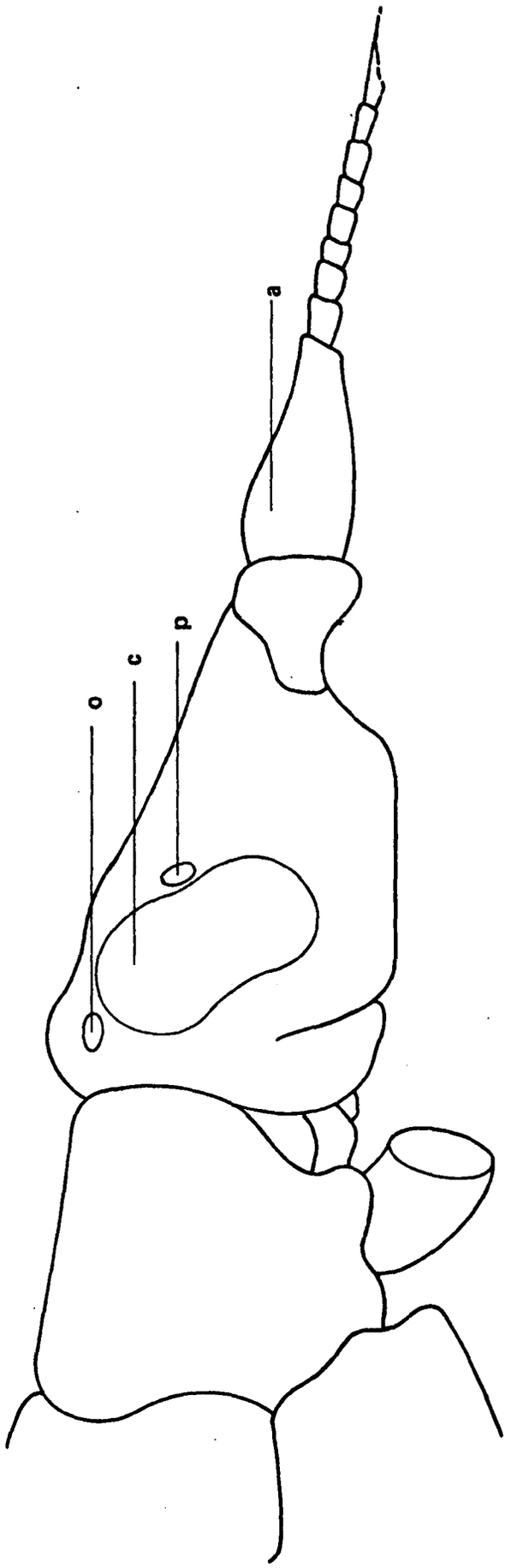


Fig. 12. Livia juncorum Latreille. Lateral view of head to show the position of the "pre-ocular tubercle". After Crawford, a = antenna, c = compound eye, o = ocellus, p = pre-ocular tubercle.

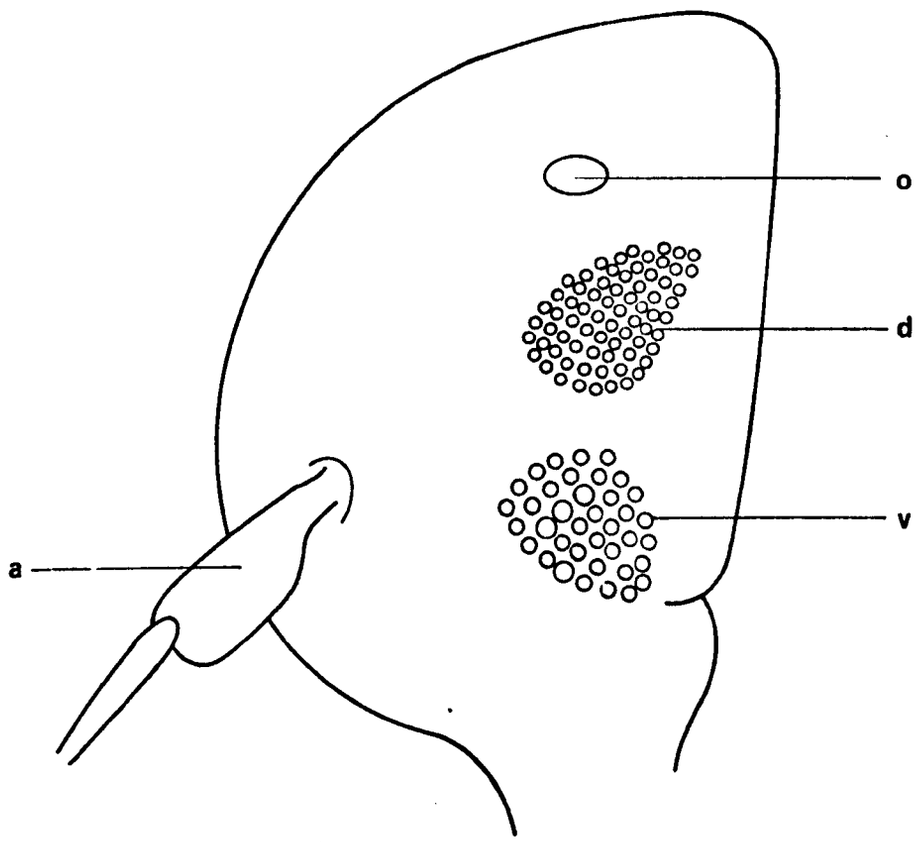


Fig. 13. Aleyrodes sp., adult male. Lateral view of head to show division of compound eye. Redrawn after Grasse.

a = antenna, d = dorsal part of compound eye, o = ocellus, v = ventral part of compound eye.

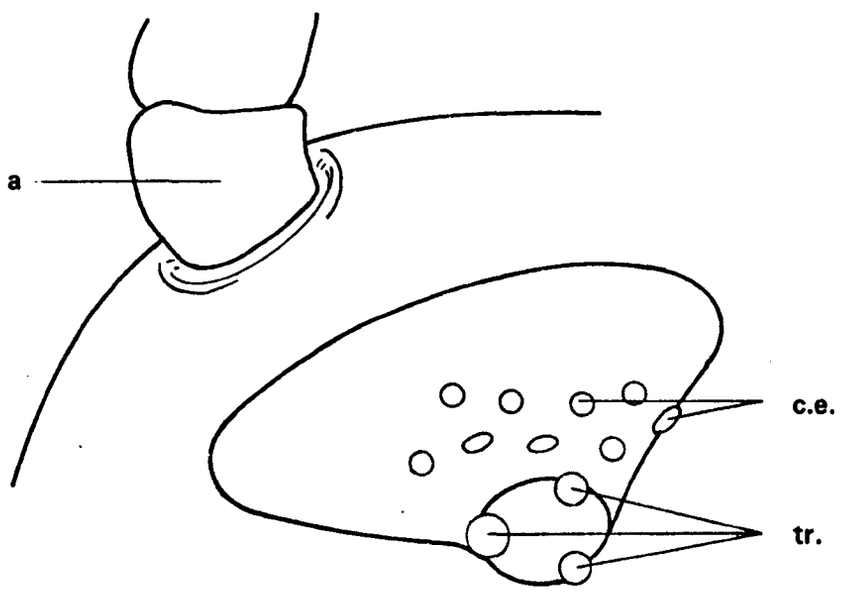


Fig. 14. Aphis gossypii Glover. Visual organs of first instar larva hatching from overwintering egg. Redrawn from a photograph by Watase. a = antenna, c.e. = facets of developing compound eye, tr. = triommatidium.

Table 2. The major diameter of the facets of the compound eye and triommatidium in Anoecia corni Fab. (μm)

(After Watase)

Form	hatching from overwintering eggs				apterous female on winter host				apterous female on summer host			
	triommatidium			compound	triommatidium			compound	triommatidium			compound
Stage	dor.	ven.	pos.	eye	dor.	ven.	pos.	eye	dor.	ven.	pos.	eye
Apterous												
1st instar	10.4	10.8	11.6	--	10	10	12	--	11.2	11.2	12	--
2nd instar	12	12	12	--	12	12	13.6	--	12	12	14	--
3rd instar	12	12	14	--	12	14	14	8	12	12	14.4	--
4th instar	16	16	16	--	14	14	16	8.8	16	16	16	6
adult	16	16	20	--	16	16	20	10	18	20	20	12
Alate												
1st instar	12	12	12	--	12	12	12	--	10.8	11.2	14.4	--
2nd instar	14	14	14	--	12	12	16	--	12.8	12.8	14.4	--
3rd instar	14	14	16	8	12	12	20	10	14	14	15.2	6
4th instar	16	16	20	10	16	16	20	12	20	20	20	8.8
adult	16	16	20	12	16.3	16.3	21.1	12	16	18	20	10

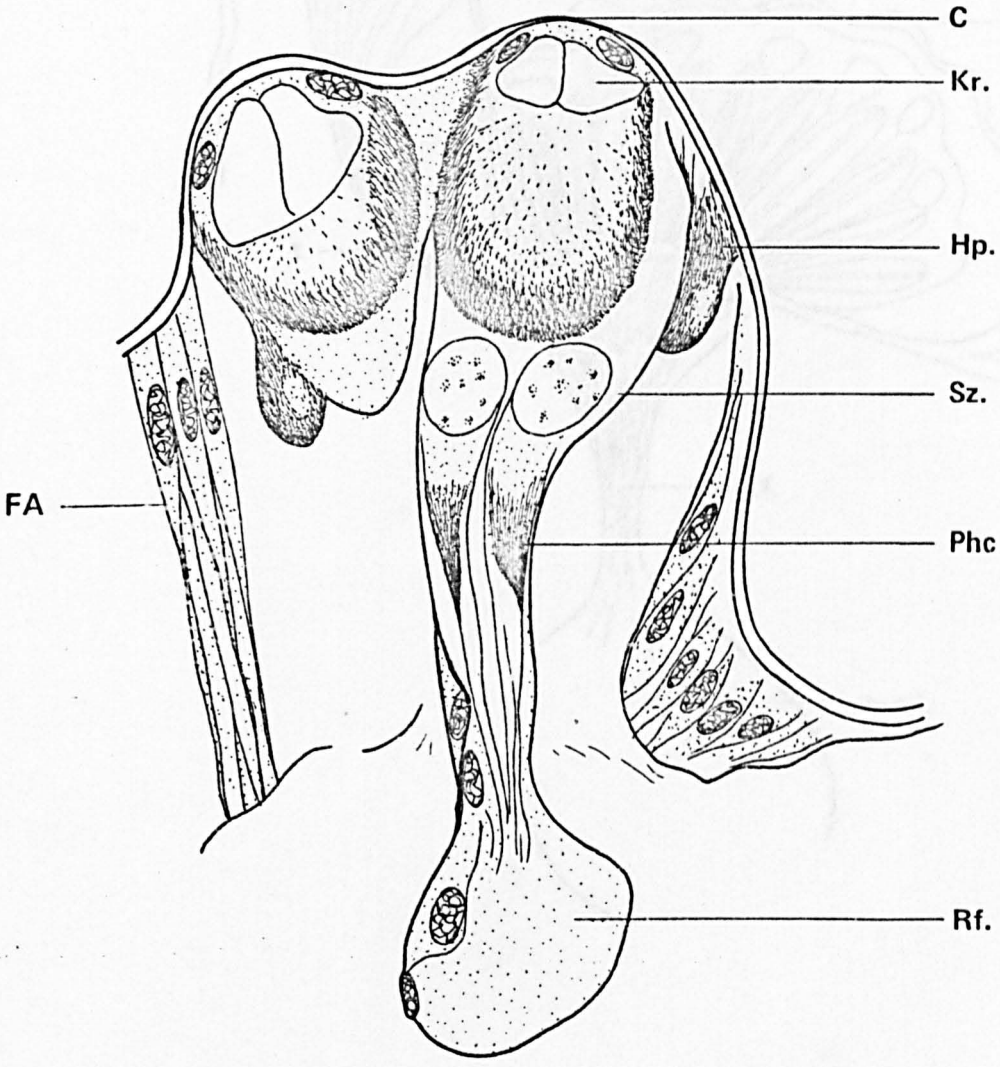


Fig. 15. Pemphigus sp., adult, alate female. Longitudinal section through triommatidium. After Pflugfelder.

C = cornea, FA = compound eye, Hp. = primary pigment cell, Kr. = crystalline cones, Phc. = phaeoconus, Rf. = retinal fibres, Sz. = sense cells (retinular cells).

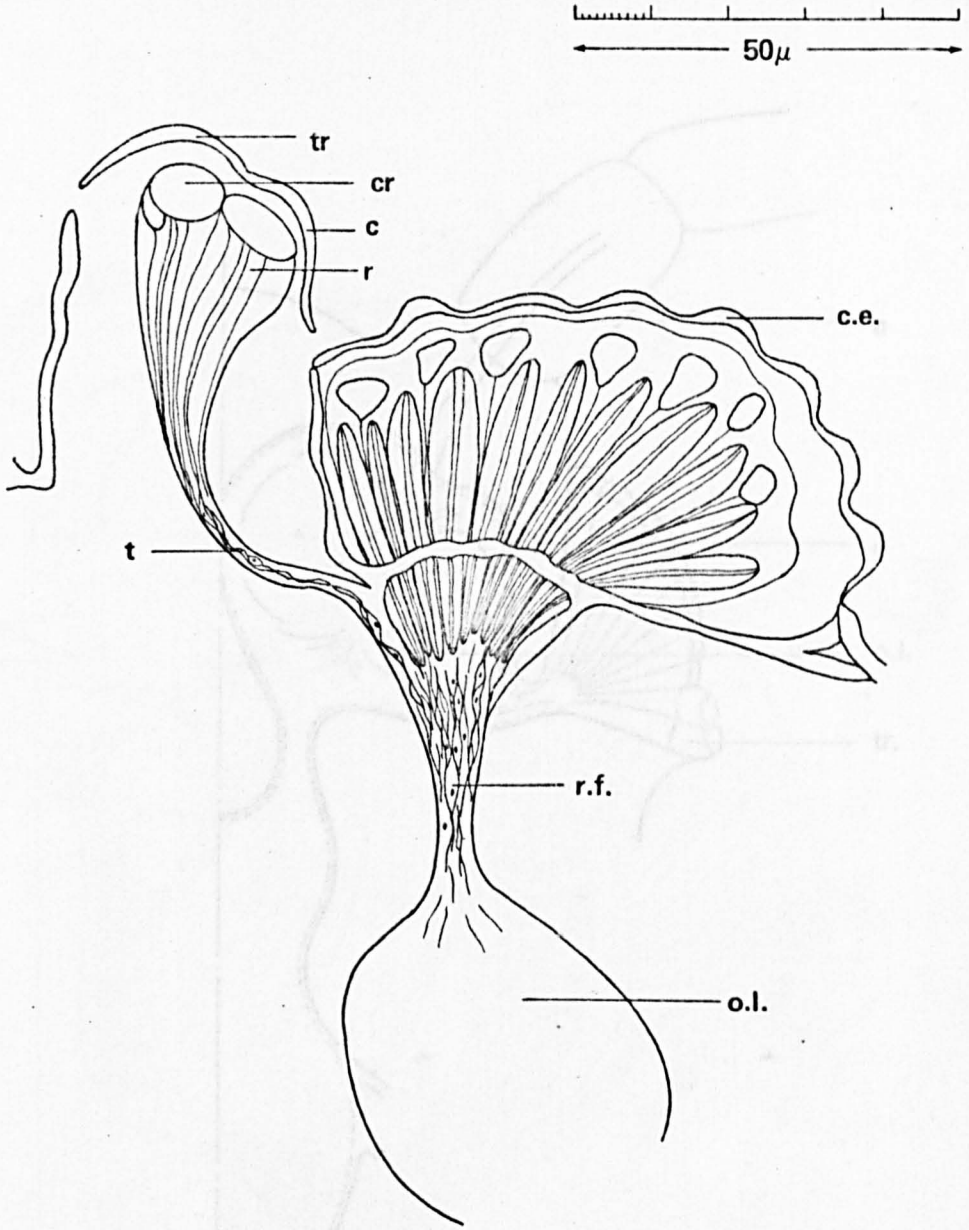


Fig. 16. Aphis fabae Scop., sagittal section through the compound eye and triommatidium of an apterous female (original).

c = cornea; c.e. = compound eye; cr. = crystalline con ; tr.= triommatidium; c.l. = olfactory lobe of brain; r = retinular cells of triommatidium; r.f. = retinal fibres of compound eye; t = triommatidial nerve.

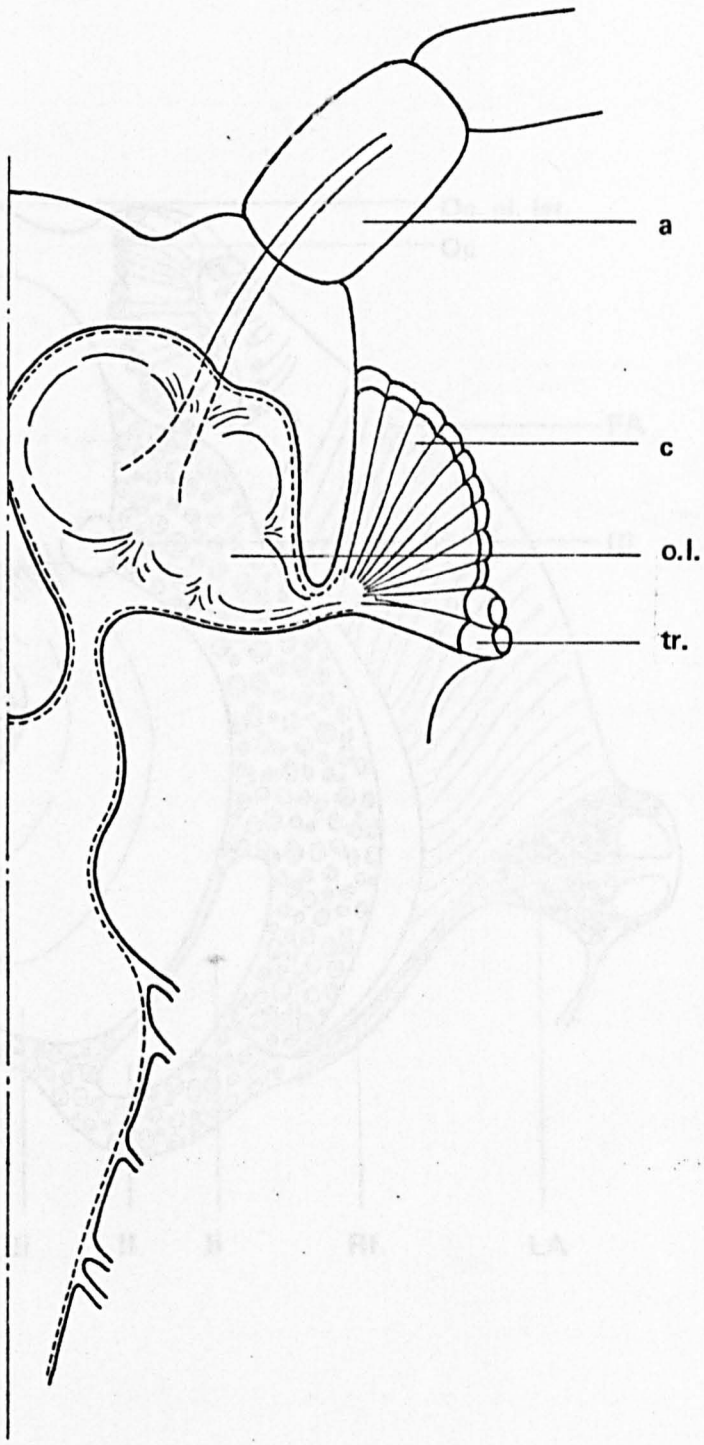


Fig. 17. Aphis pelargonii (Kalt.). The innervation of the visual organs of the right hand side. Redrawn after Witlaczil.
a = antenna, c = compound eye, o.l. = optic lobe of brain, tr. = triommatidium.

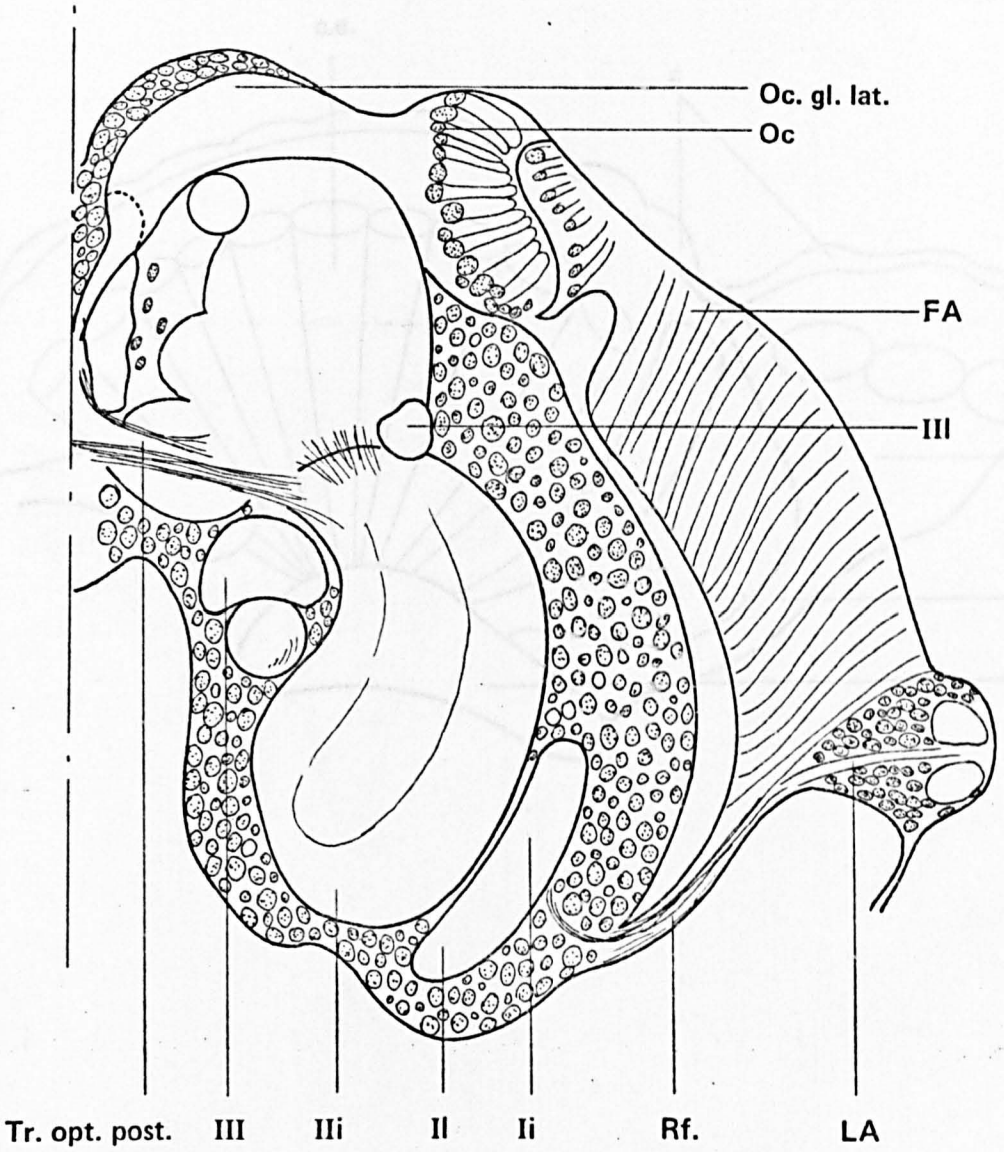


Fig. 18. Pemphigus sp., alate female. Sagittal section through right side of brain to show innervation of visual organs. After Pflugfelder. FA = compound eye, LA = triommatidium, Oc. = ocellus, Rf. = retinal fibres, II & III = optic lobe.

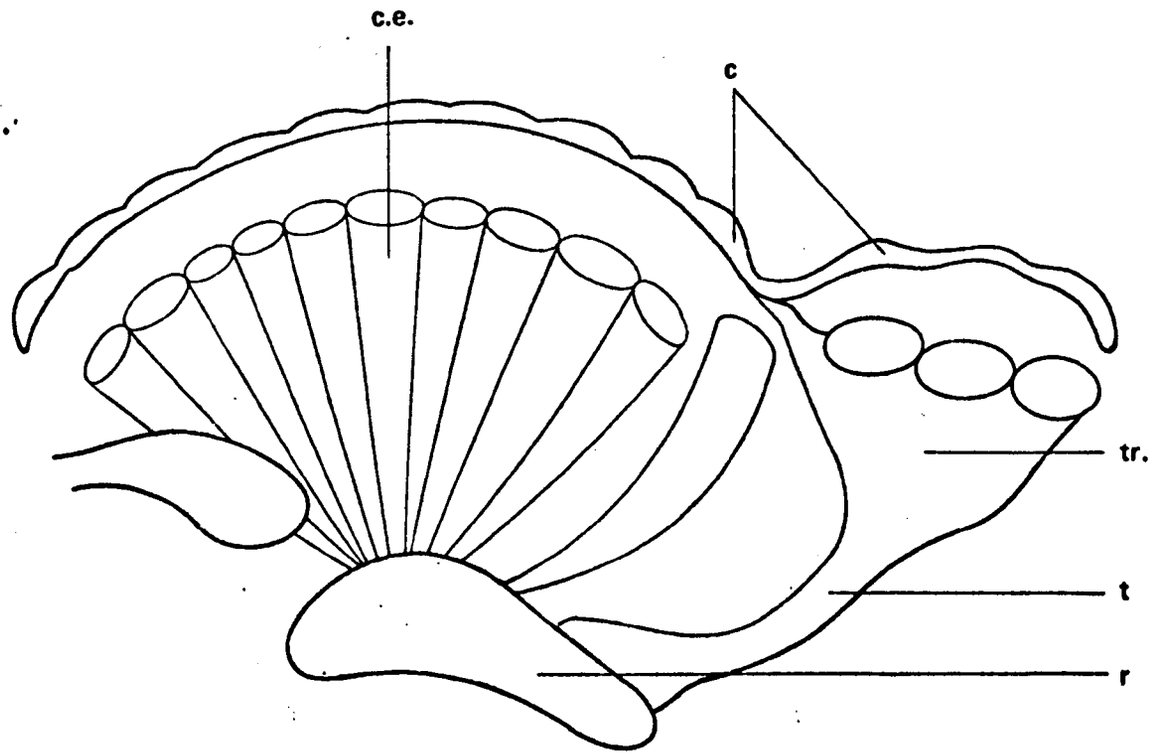


Fig. 19. Anoecia corni (Fab.), alate male. Section through visual organs. Redrawn from a photograph by Watase.

c = cornea, c.e.= ommatidia of the compound eye, r = retinal fibres leading to the optic lobe of the brain, tr. = triommatidium, t = triommatidial nerve.

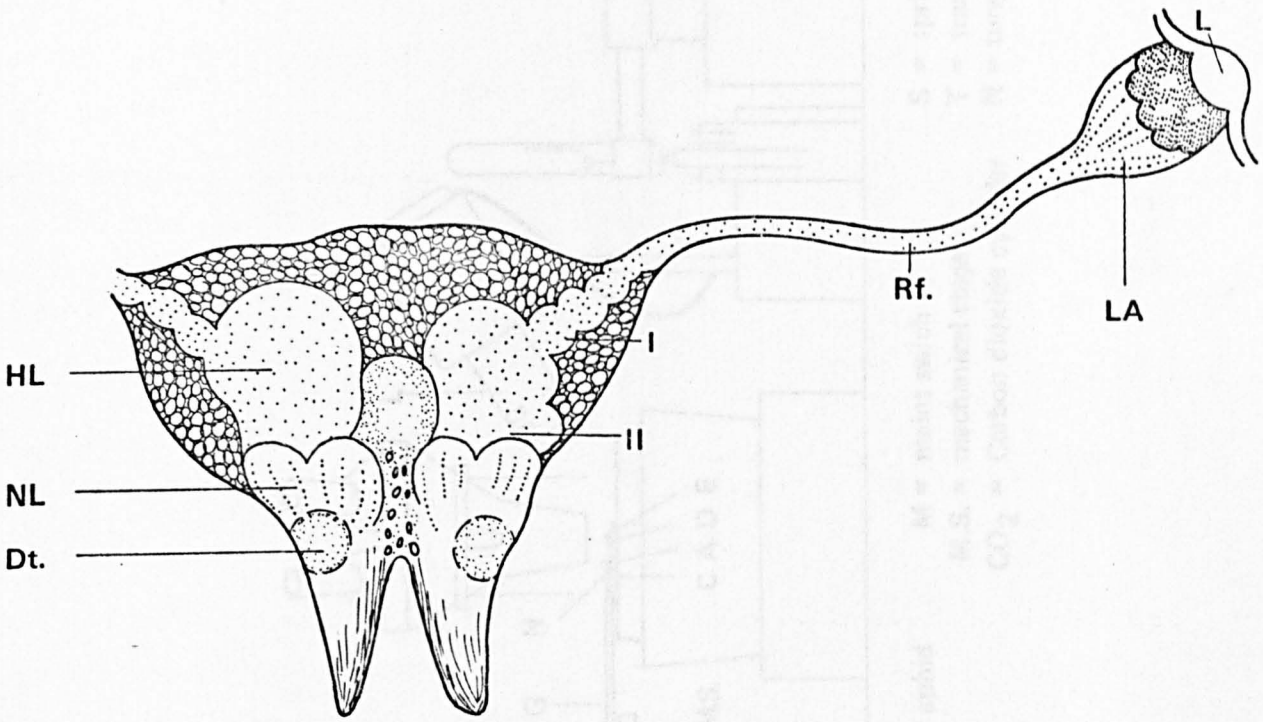
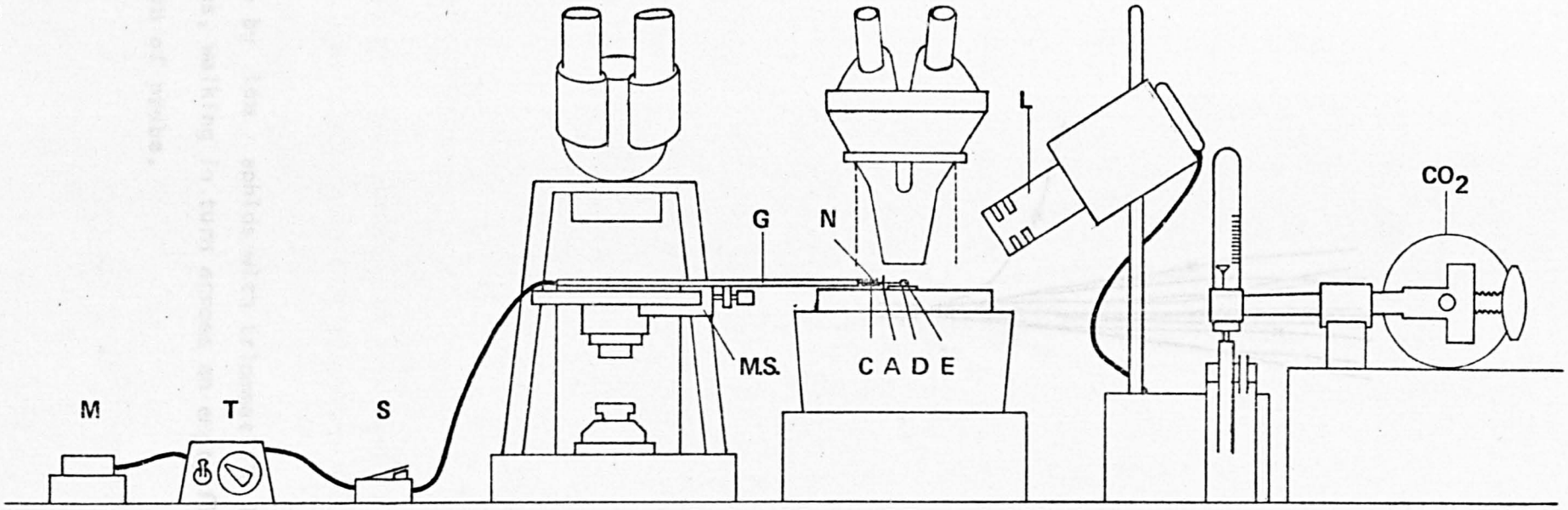


Fig. 20. Parthenolecanium corni (Bouche), adult female. Section through brain and triommatidium. After Pflugfelder. L = lens, LA = fused ommatidia of triommatidium, Rf. = retinal fibres, I & II = optical ganglia, Dt. = deuterocerebrum.

Fig. 21. Diagram of the apparatus used to cauterise the triommatidium in aphids. See text for details.



A = asbestos shield
C = coil of nichrome wire
D = disk of cork
E = experimental aphid
G = glass rod
L = lamp
M = mains swich
M.S. = mechanical stage
CO_2 = Carbon dioxide cylinder
S = spring loaded switch
T = transformer
N = tungsten needle

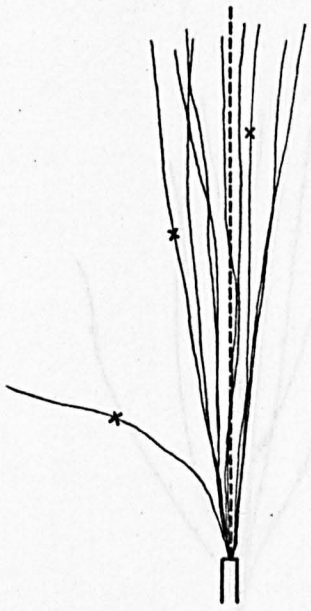


Fig. 22. Tracks made by ten aphids with triommatidia intact and of various ages, walking in turn across an empty flat wax plate.
x = position of probe.

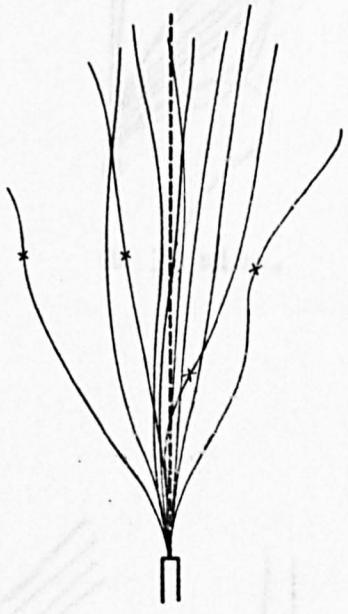


Fig. 23. Tracks made by ten aphids with triommatidia extirpated and of various ages, walking in turn across an empty flat wax plate.

x = position of probe.

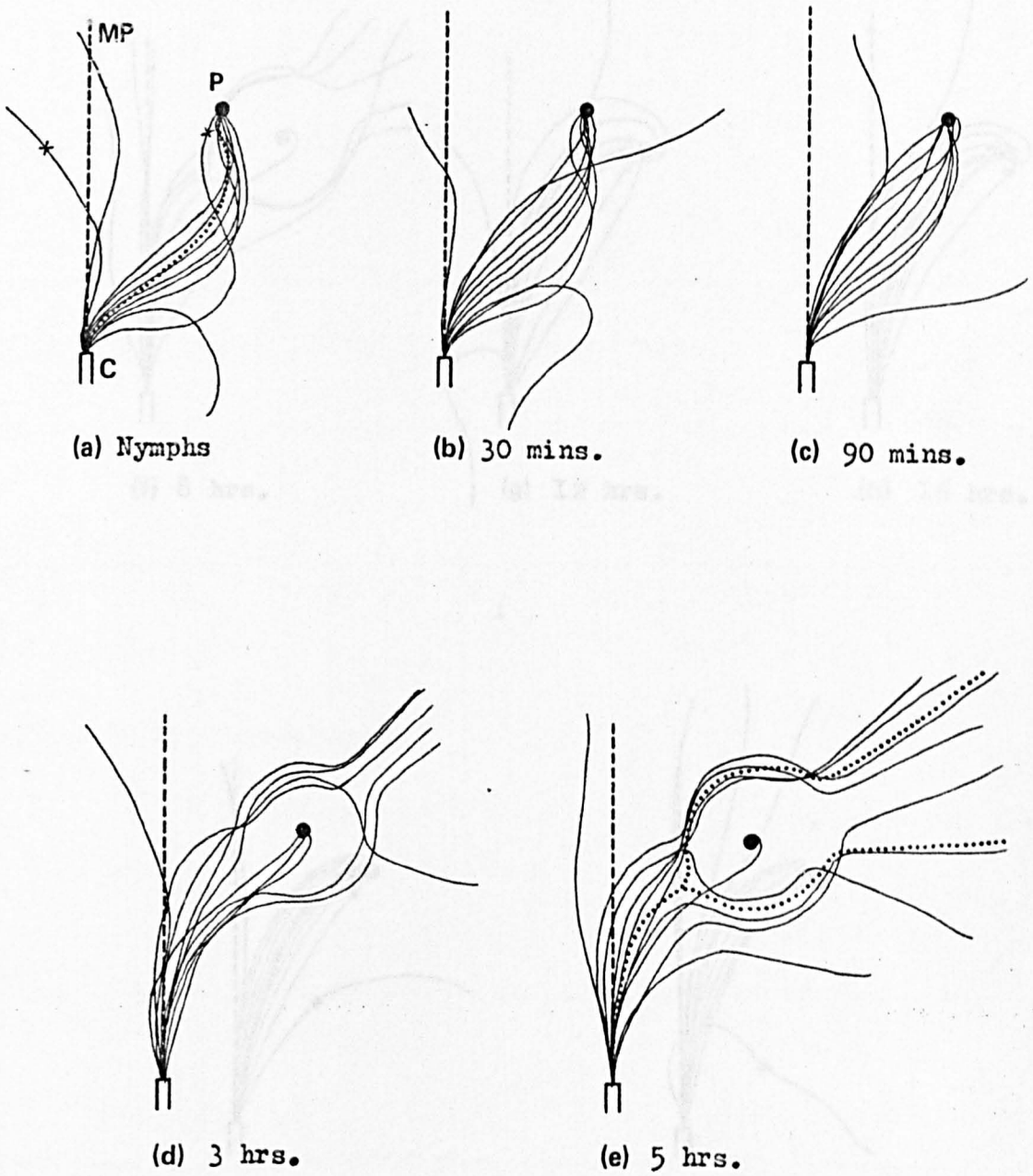
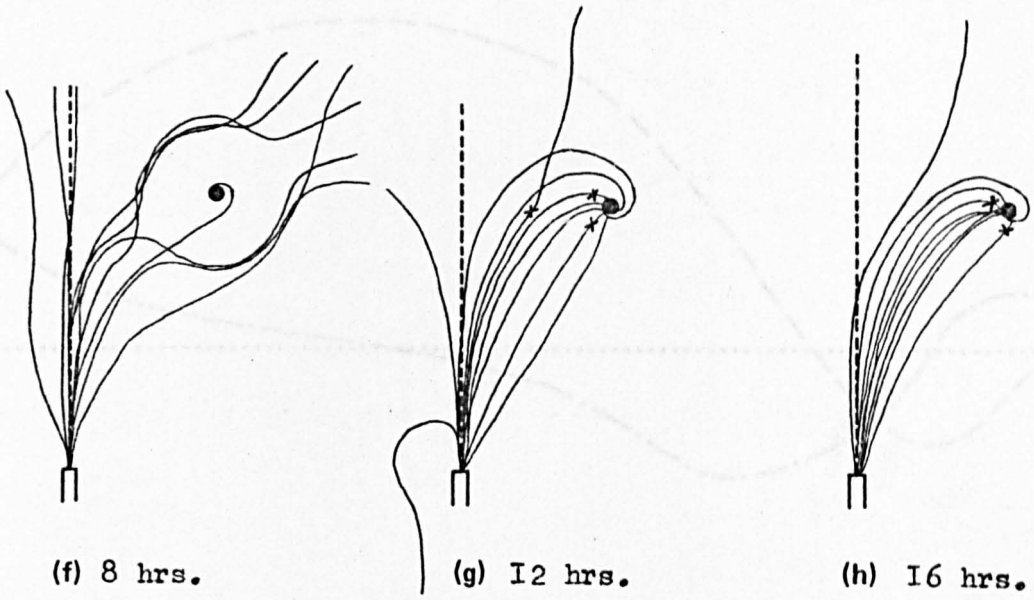
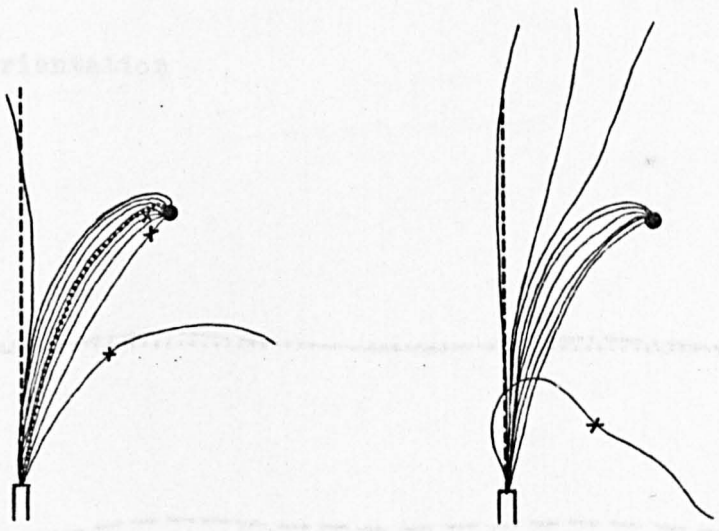


Fig. 24. Ten representative tracks from a total of thirty made by entire aphids of different ages walking towards a "standard" black pillar (2mm. wide and 30mm. high) situated at "normal" distance (30mm.) and at "standard" angle (30^{o}) to the median line (dashed). Dotted tracks are mean tracks, computed from the original 30 in each case. x = position of probe.



(f) 8 hrs. (g) I2 hrs. (h) I6 hrs.



(i) 24 hrs. (j) 48hrs.

Fig. 24. (cont.).

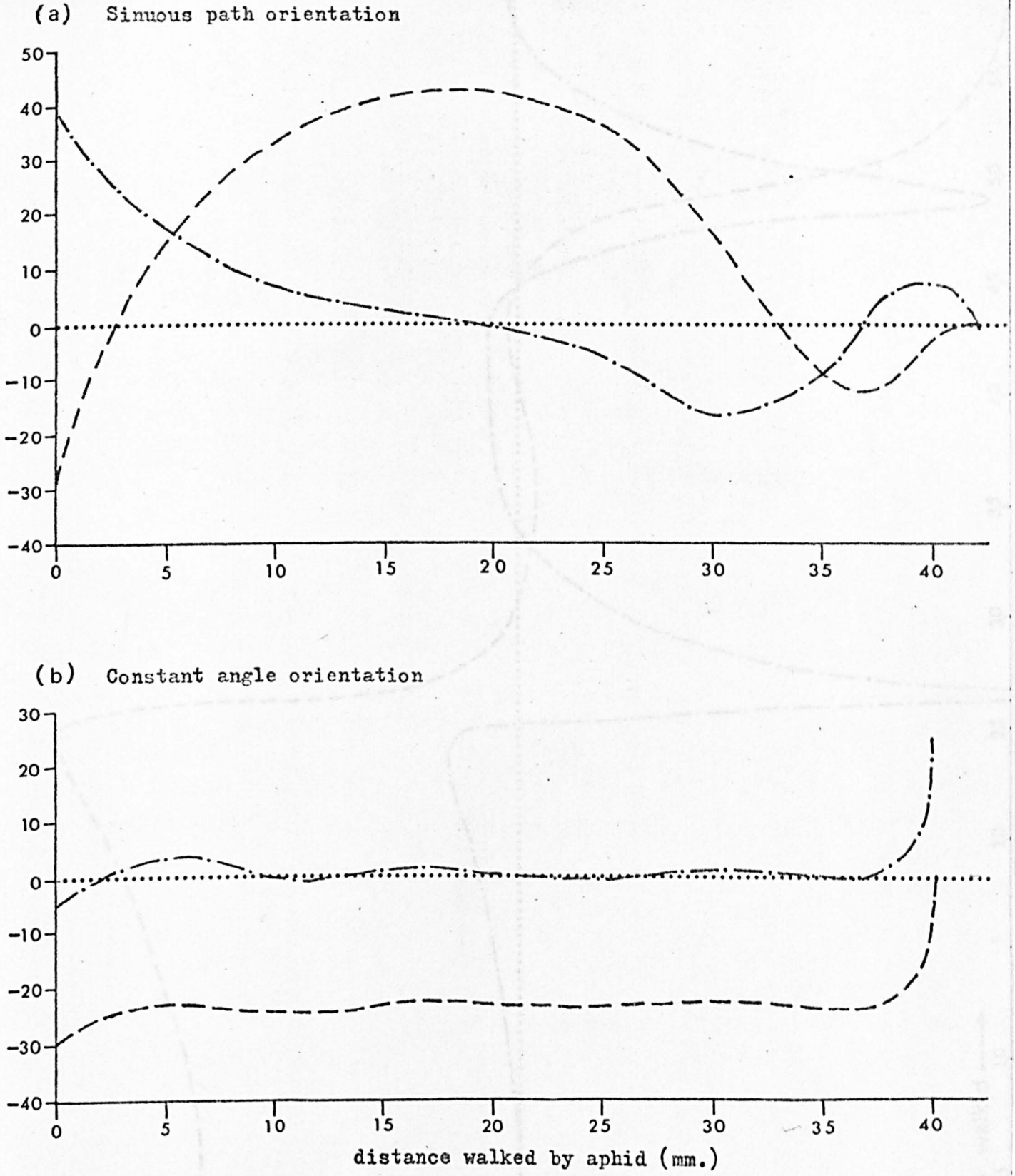


Fig 25 (a) & (b). Graphs to show the angular deviation and angular velocity of a pillar, at successive points along the aphid's path. In each case, a "standard" pillar at "normal" distance and "standard" angle was used. Data averaged over 30 tracks.

— — — — angular deviation (degs.; positive values = to right, negative = to left. —·—·— angular velocity (degs/sec.; positive values = movement to right, negative = movement to left).

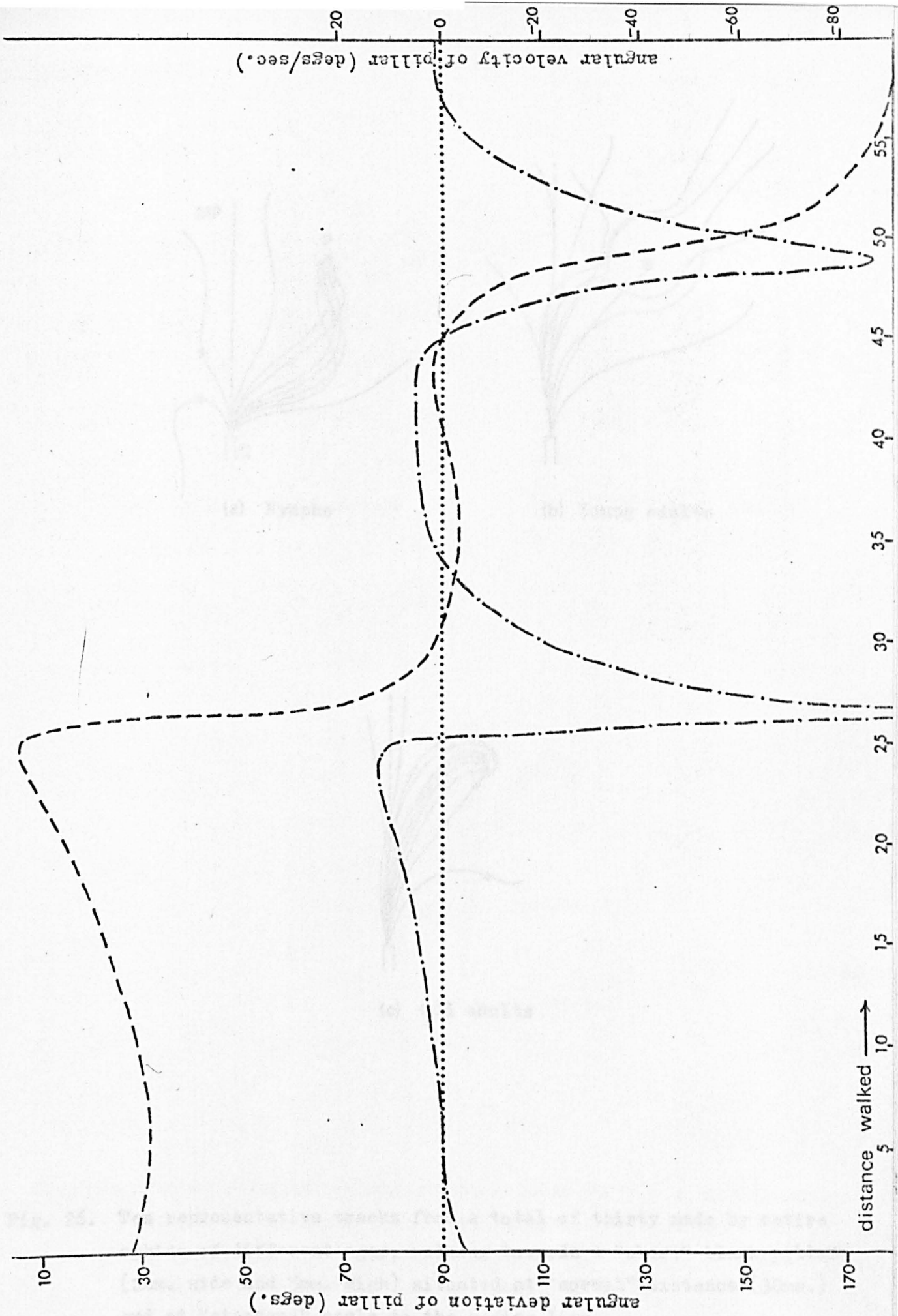


Fig. 25 (c). Orbital path orientation. Legend as for Fig. 25 (a) & (b).

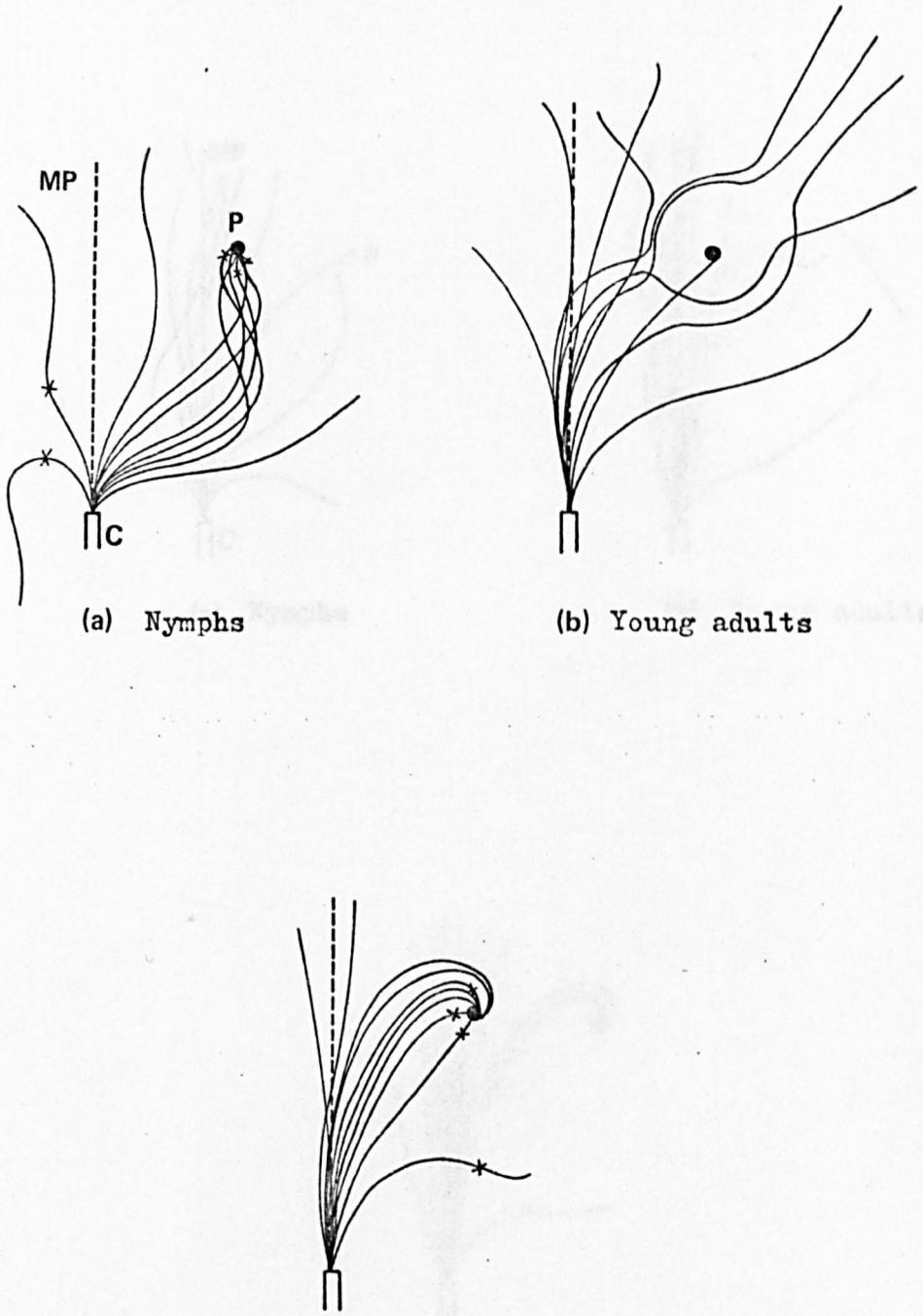


Fig. 26. Ten representative tracks from a total of thirty made by entire aphids of different ages, walking towards a "short" black pillar (2mm. wide and 5mm. high) situated at "normal" distance (30mm.) and at "standard" angle to the median line.

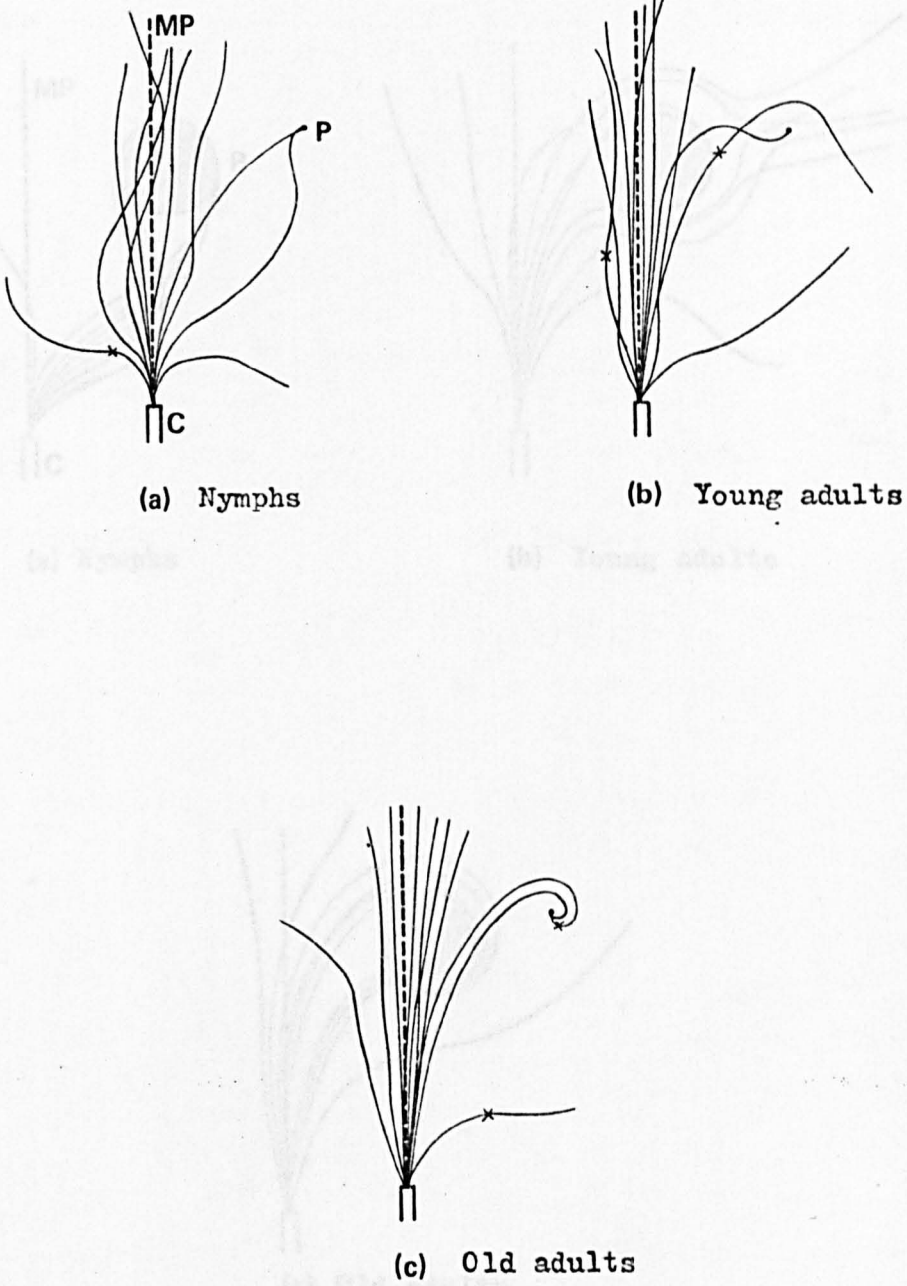


Fig. 27. Ten representative tracks from a total of thirty made by entire aphids of different ages, walking towards a "narrow" black pillar (0.5mm. wide and 30mm. high) situated at "normal" distance (30mm.) and at "standard" angle to the median line.

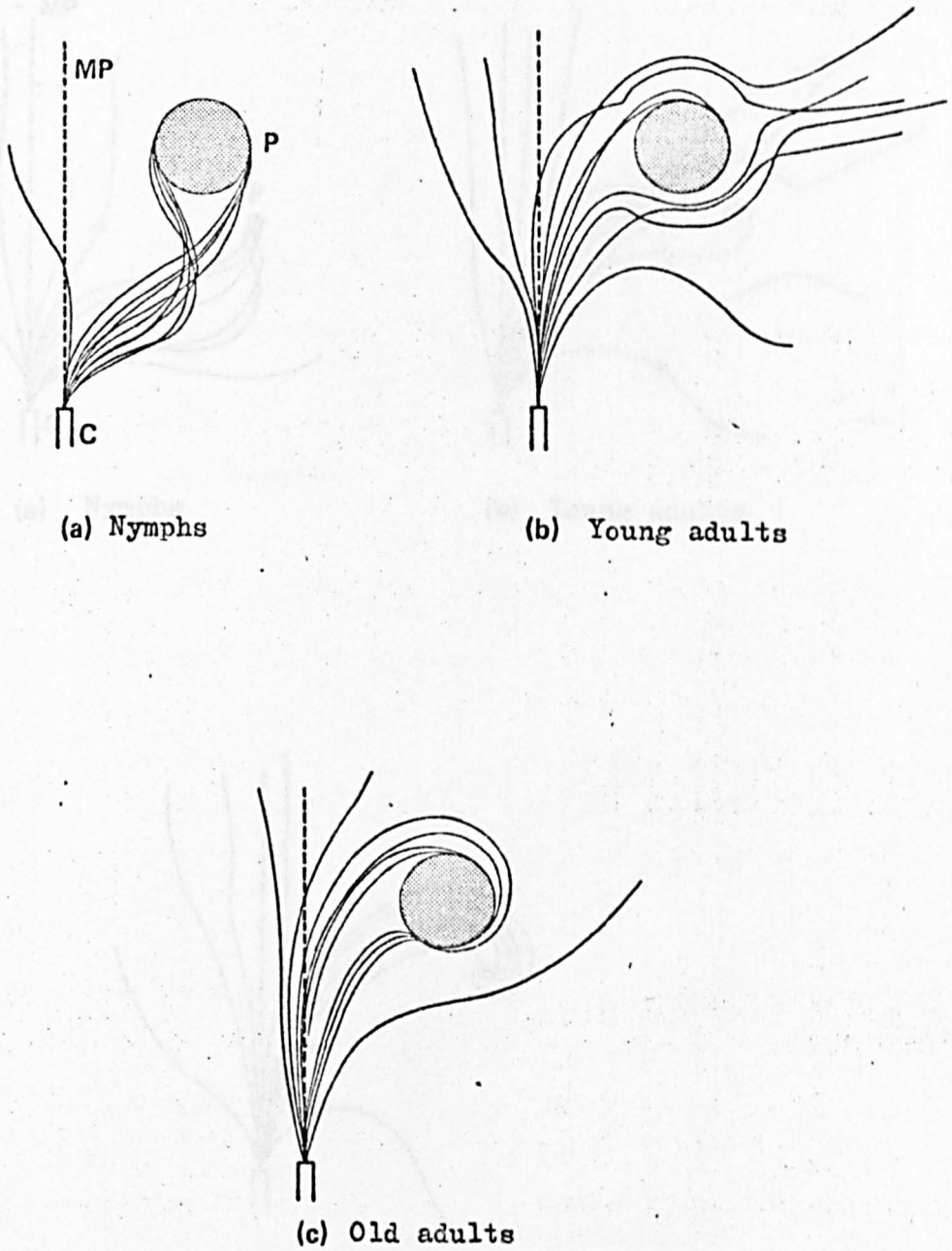
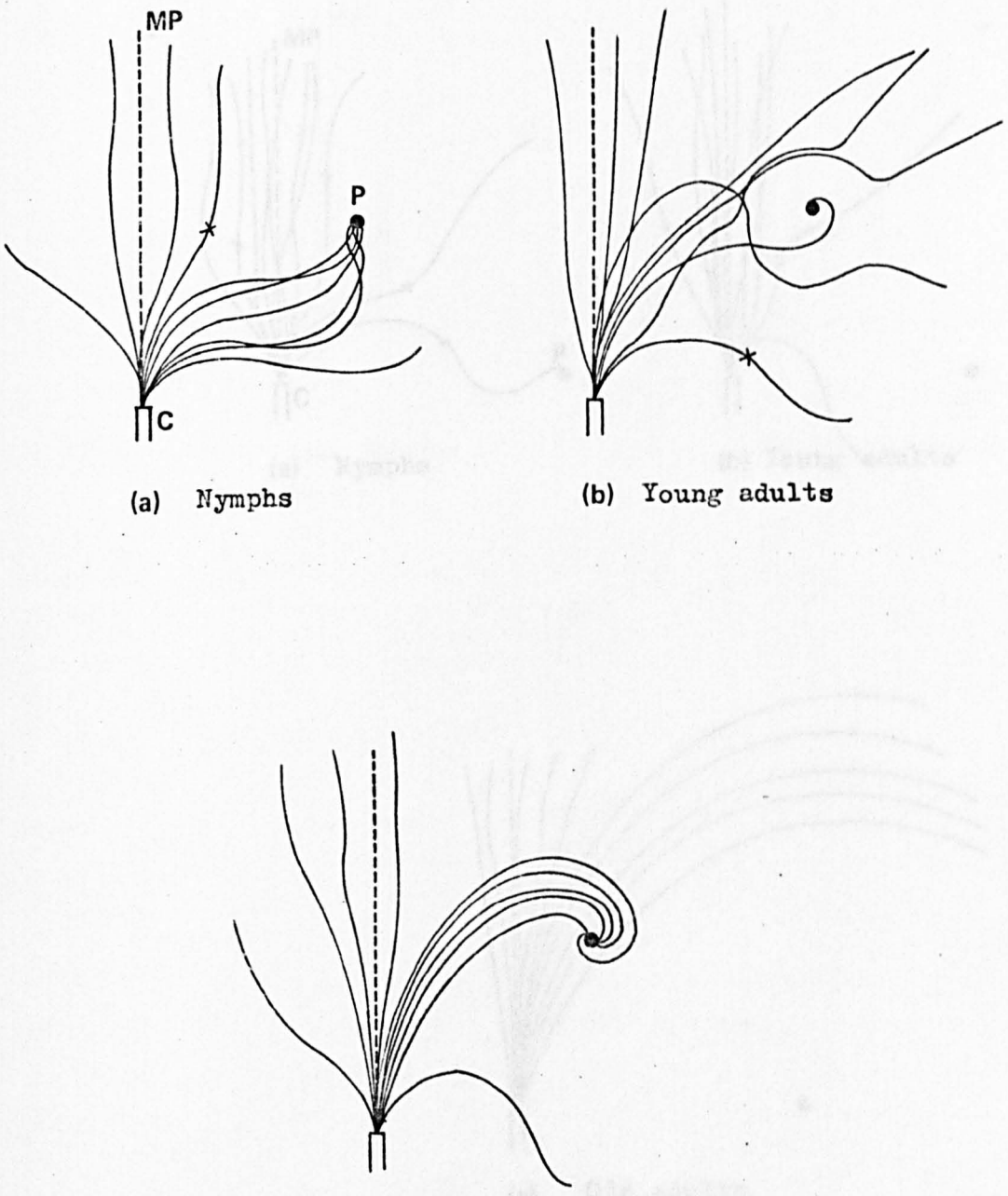


Fig. 28. Ten representative tracks from a total of thirty made by entire aphids of different ages, walking towards a "wide" black pillar (I2mm. wide and 30mm. high) situated at "normal"distance (30 mm.) and at "standard" angle to the median line.



(a) Nymphs

(b) Young adults

(c) Old adults

Fig. 29. Ten representative tracks from a total of thirty made by entire aphids of different ages, walking towards a "standard" black pillar (2mm. wide and 30mm. high) situated at "normal" distance (30mm.) and at "wide" angle (50^{o}) to the median line.

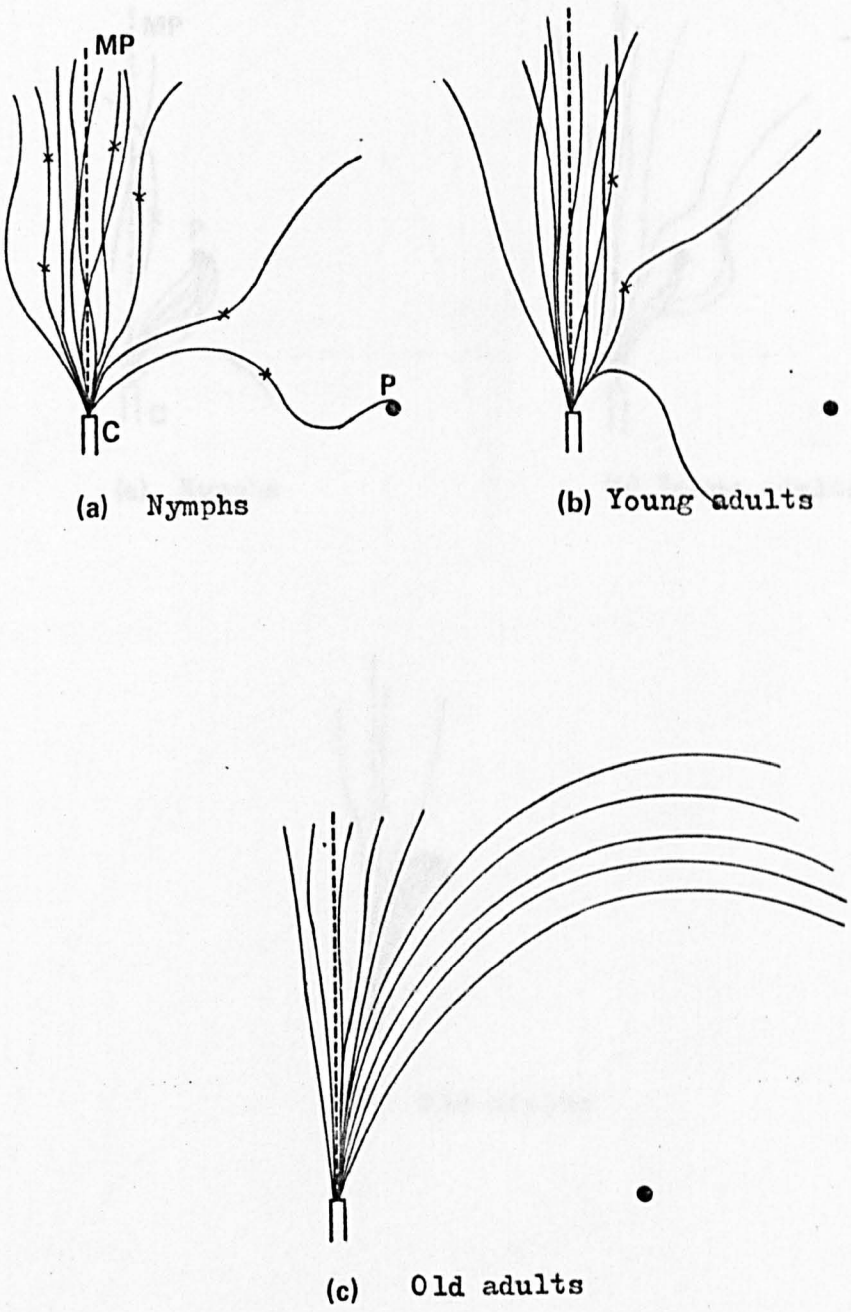
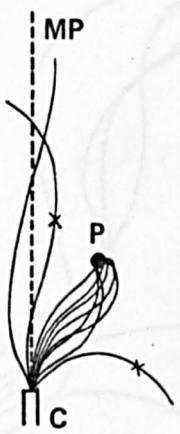
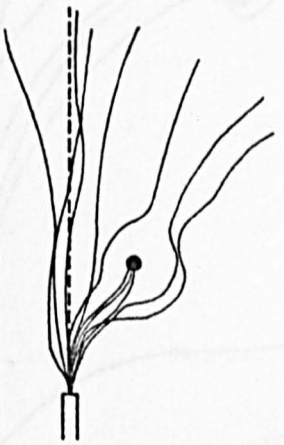


Fig. 30. Ten representative tracks from a total of thirty made by entire aphids of different ages, walking towards a "standard" black pillar (2mm. wide and 30mm. high) situated at "normal" distance (30mm.) and at right angle (90^{o}) to the median line.



(a) Nymphs



(b) Young adults

(c) Old adults

Fig. 31. Ten representative tracks from a total of thirty made by entire aphids of different ages, walking towards a "standard" black pillar (2mm. wide and 30mm. high) situated at "near" distance (15mm.) and at "standard" angle (30°) to the median line.

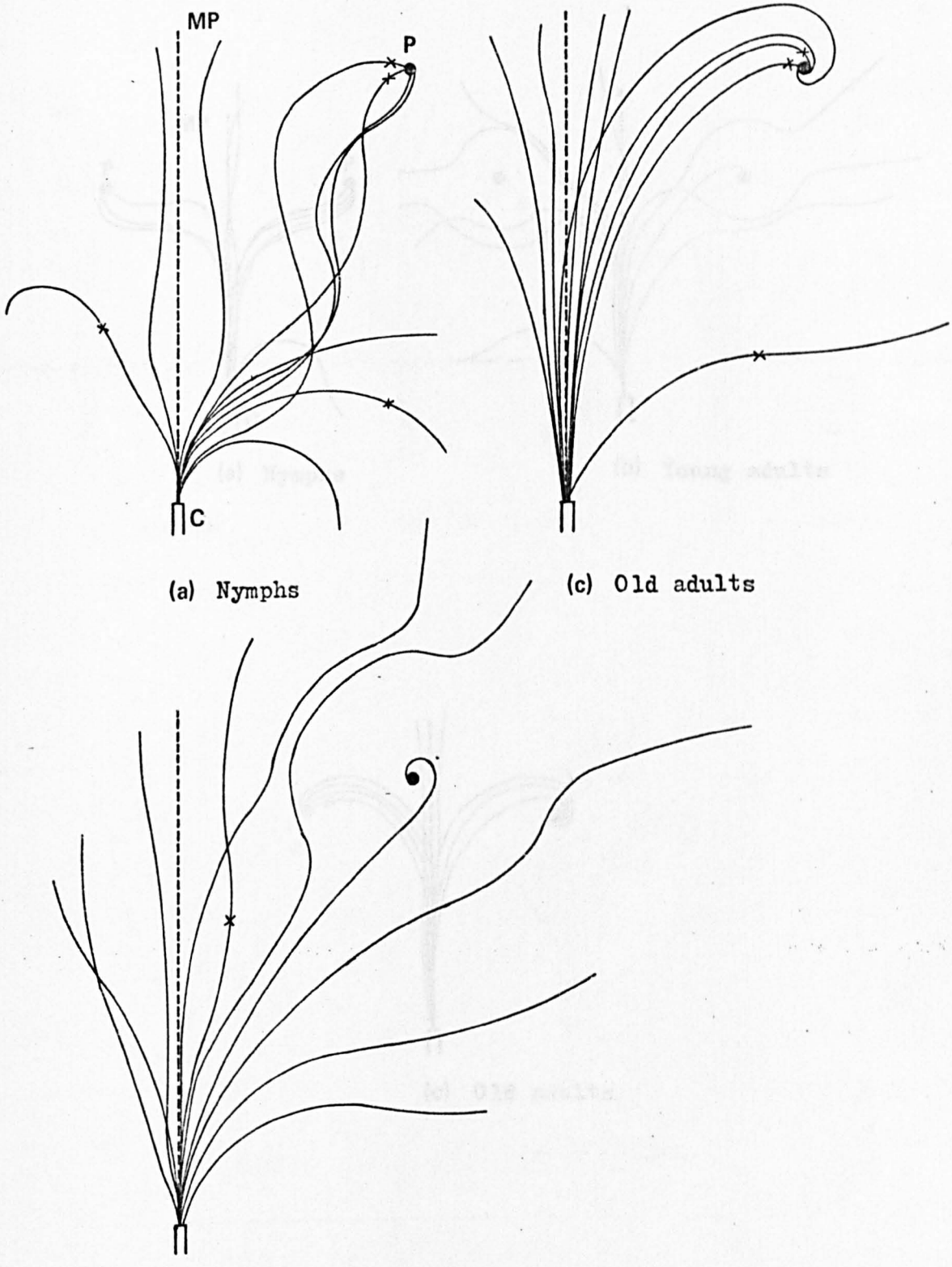


Fig. 32. Ten representative tracks from a total of thirty made by entire aphids of different ages, walking towards a "standard" black pillar (2mm. wide and 30mm. high) situated at "far" distance (60mm.) and at "standard" angle (30°) to the median line.

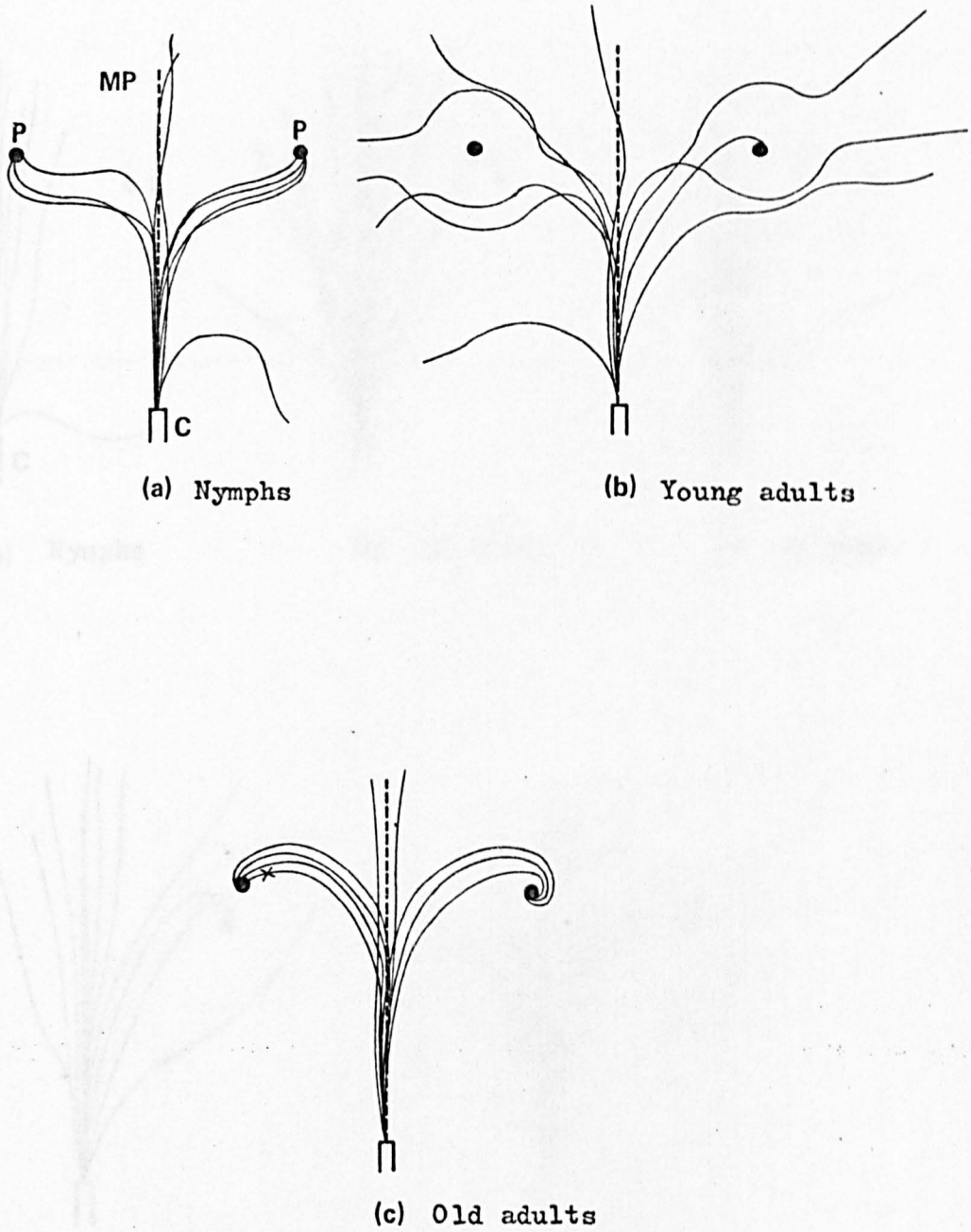


Fig. 33. Ten representative tracks from a total of thirty made by entire aphids of different ages, walking towards two "standard" black pillars (2mm. wide and 30mm. high) situated at "normal" distance (30mm.) and at "standard" angle (30°) to each side of the median line.

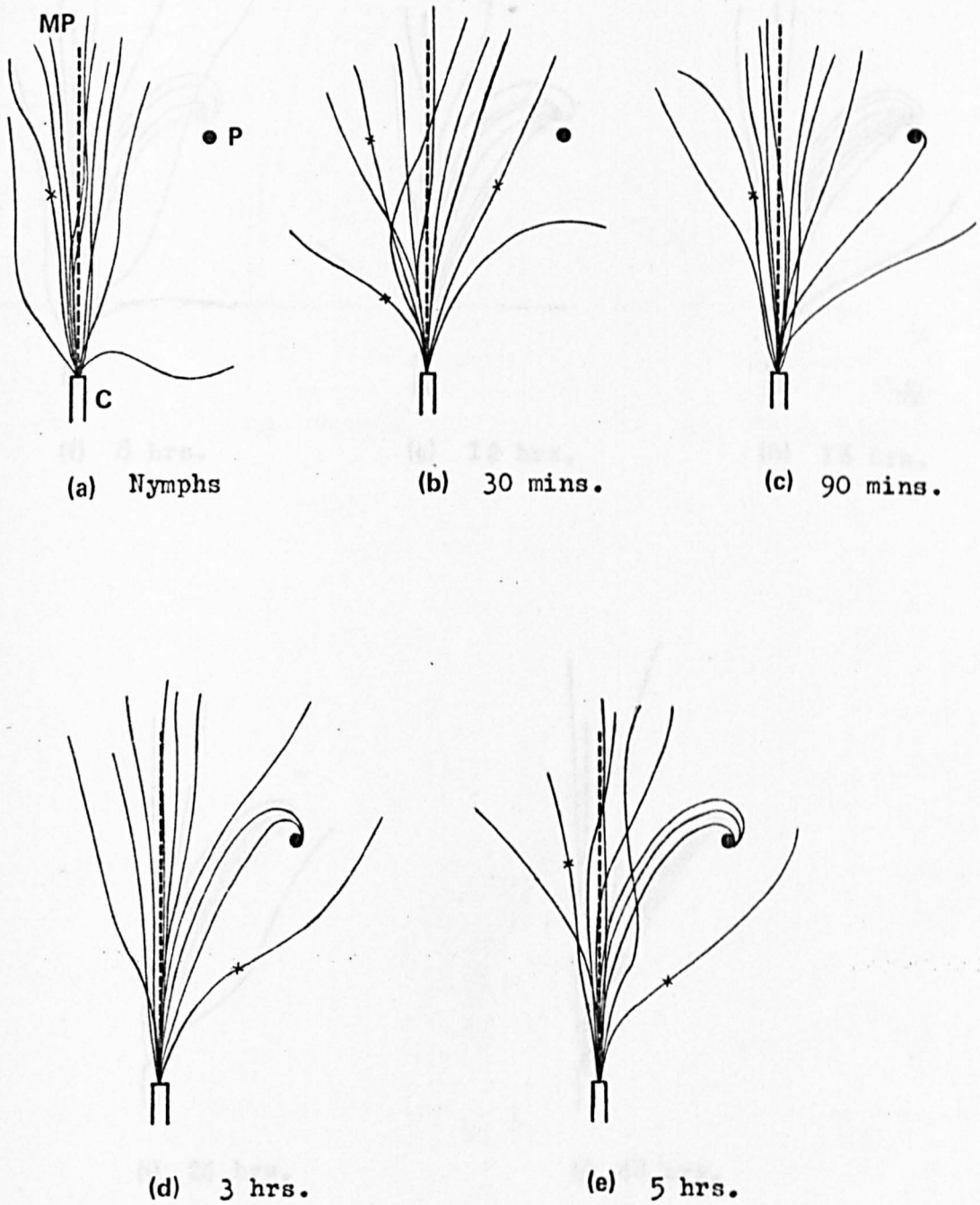
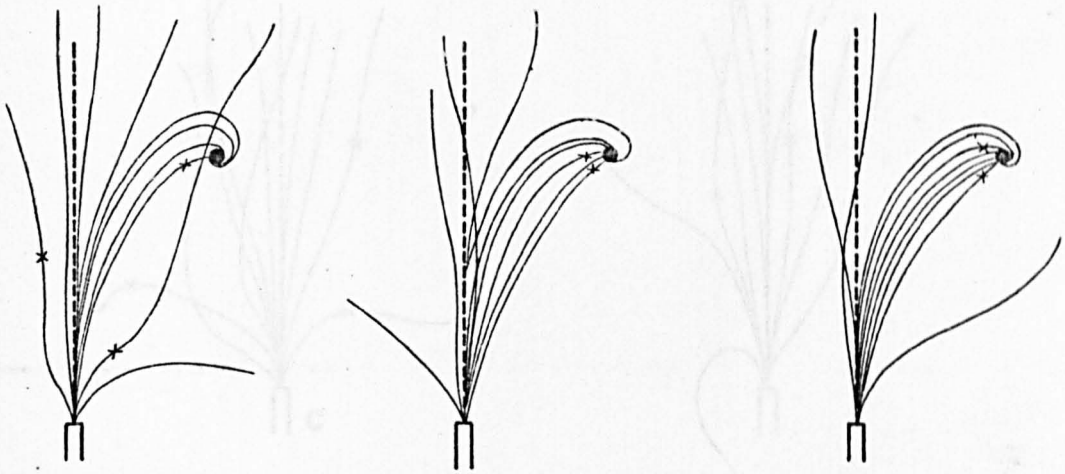
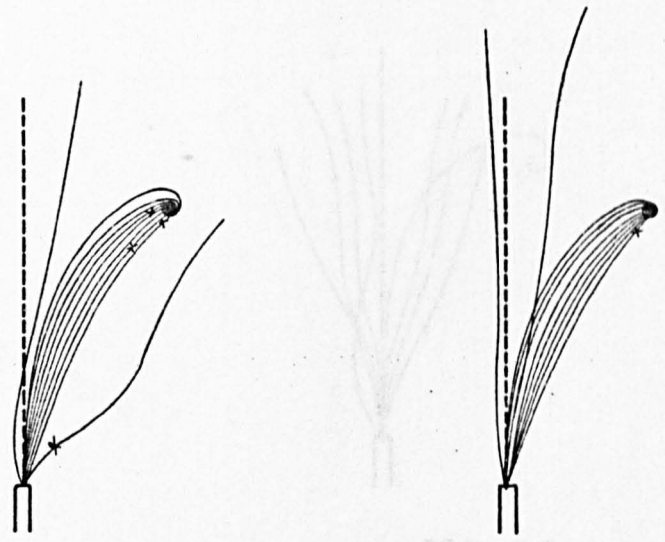


Fig. 34. Ten representative tracks from a total of thirty made by aphids of different ages, with triommatidia extirpated, walking towards a "standard" black pillar (2mm. wide and 30mm. high) situated at "normal" distance (30mm.) and at "standard" angle (30°) to the median line.



(f) 8 hrs. (g) I2 hrs. (h) I6 hrs.



(i) 24 hrs. (j) 48 hrs.

Fig. 34. (cont.).

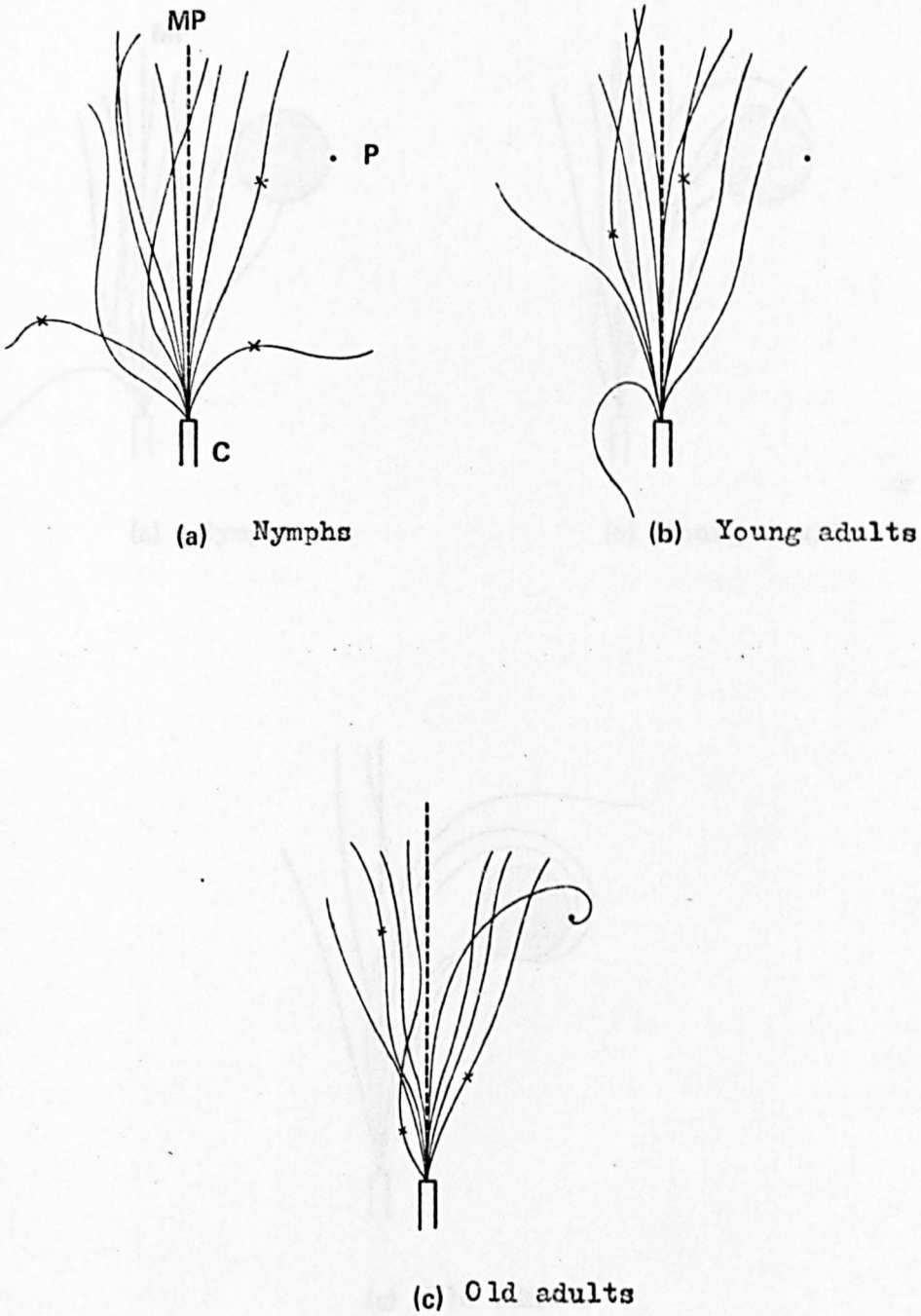
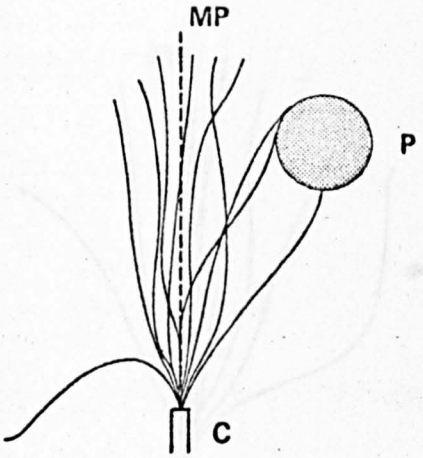
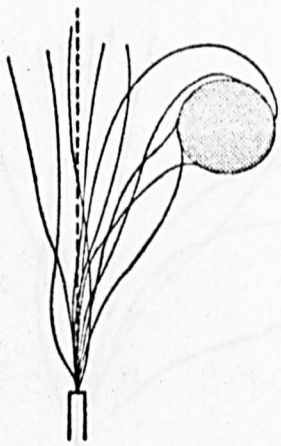


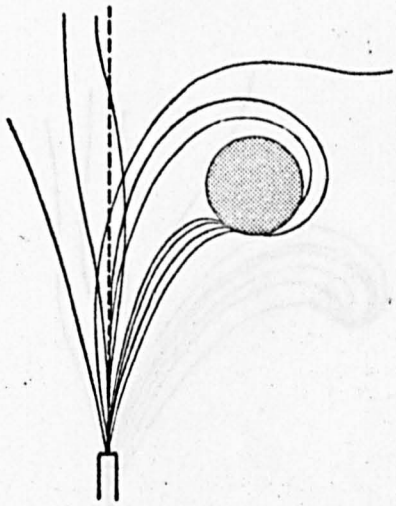
Fig. 35. Ten representative tracks from a total of thirty made by aphids of different ages, with triommatidia extirpated, walking towards a "narrow" black pillar (0.5mm. wide and 30mm. high) situated at "normal" distance (30mm.) and at "standard" angle (30°) to the median line.



(a) Nymphs

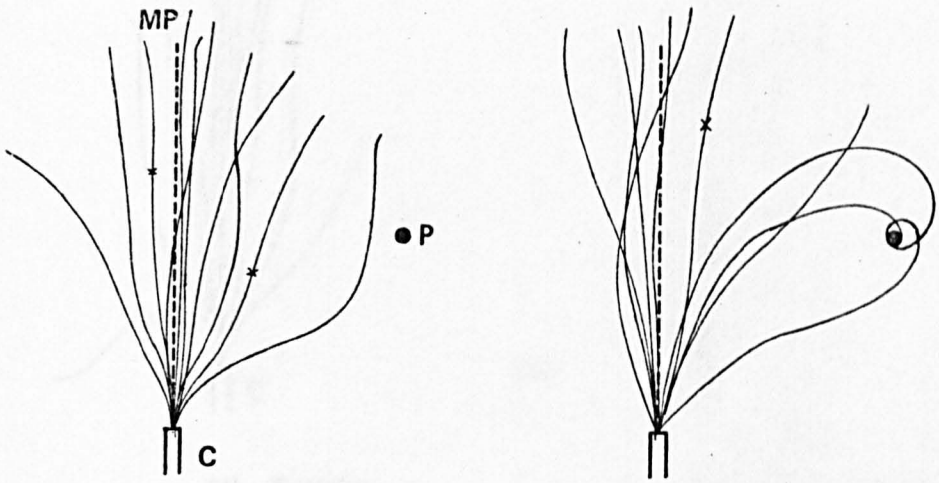


(b) Young adults



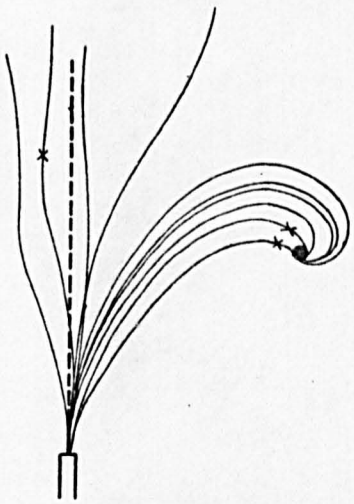
(c) Old adults

Fig. 36. Ten representative tracks from a total of thirty made by aphids of different ages, with triommatidia extirpated, walking towards a "wide" black pillar (I2mm. wide and 30mm. high) situated at "normal" distance (30mm.) and at "standard" angle (30°) to the median line.



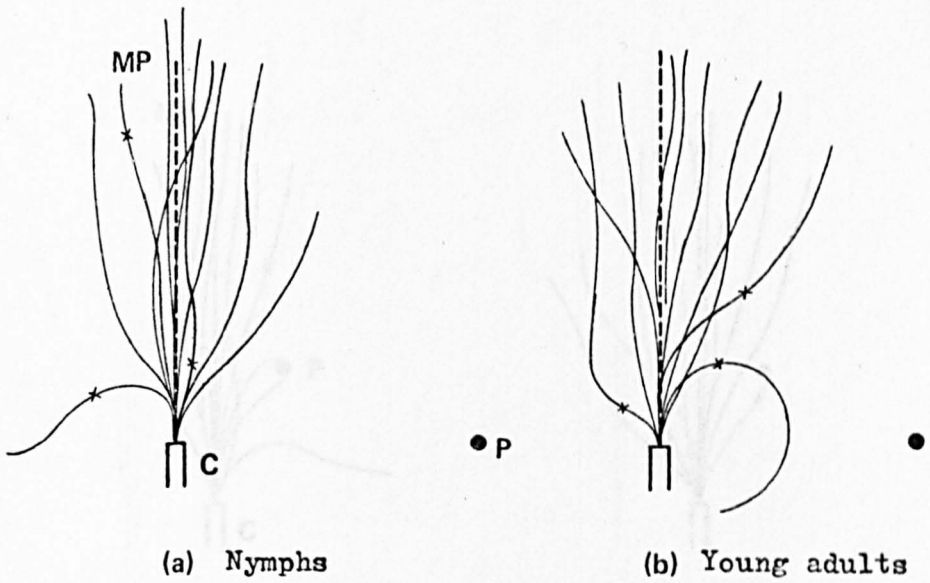
(a) Nymphs

(b) Young adults

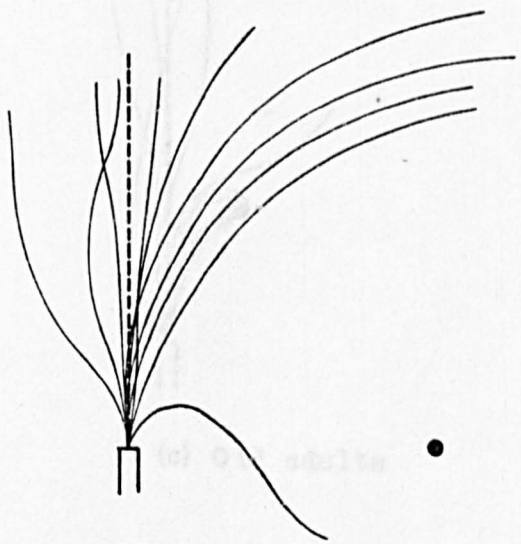


(c) Old adults

Fig. 37, Ten representative tracks from a total of thirty made by aphids of different ages, with triommatidia extirpated, walking towards a "standard" black pillar (2mm. wide and 30mm. high) situated at "normal" distance (30mm.) and at "wide" angle (50°) to the median line.



(a) Nymphs (b) Young adults



(c) Old adults

Fig. 38. Ten representative tracks from a total of thirty made by aphids of different ages, with triommatidia extirpated, walking towards a "standard" black pillar (2mm. wide and 30mm. high) situated at "normal" distance (30mm.) and at right angle (90°) to the median line.

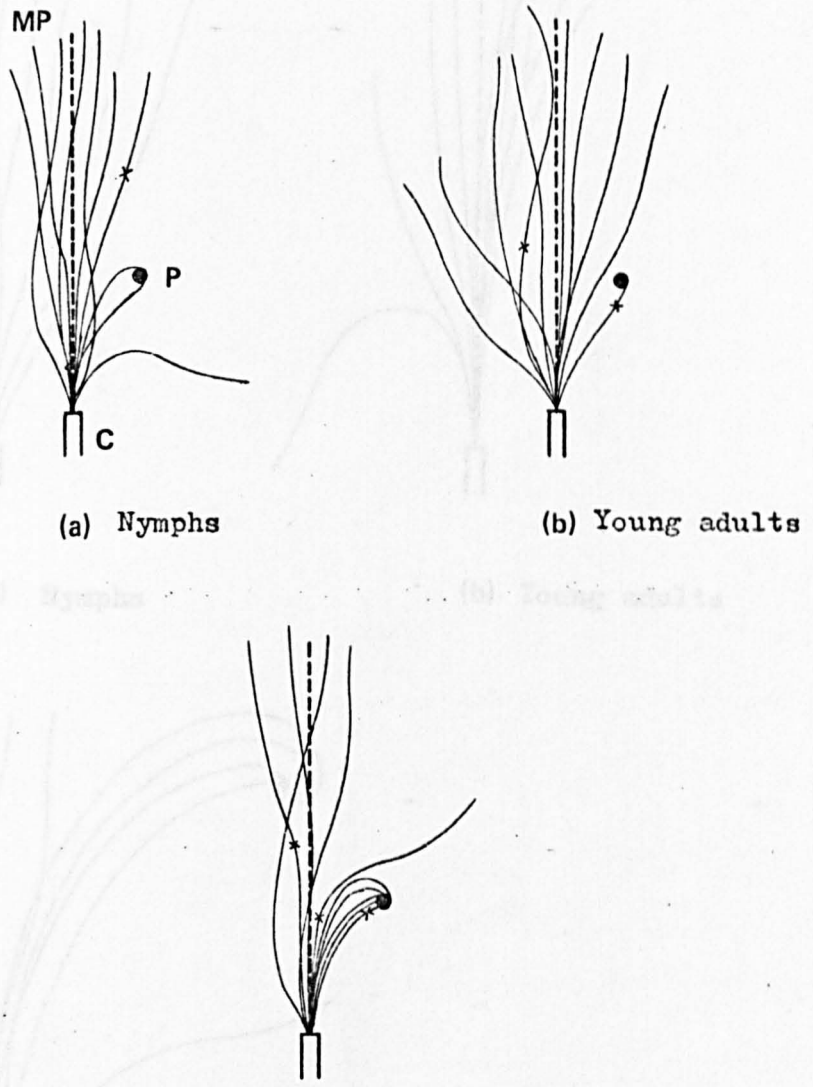
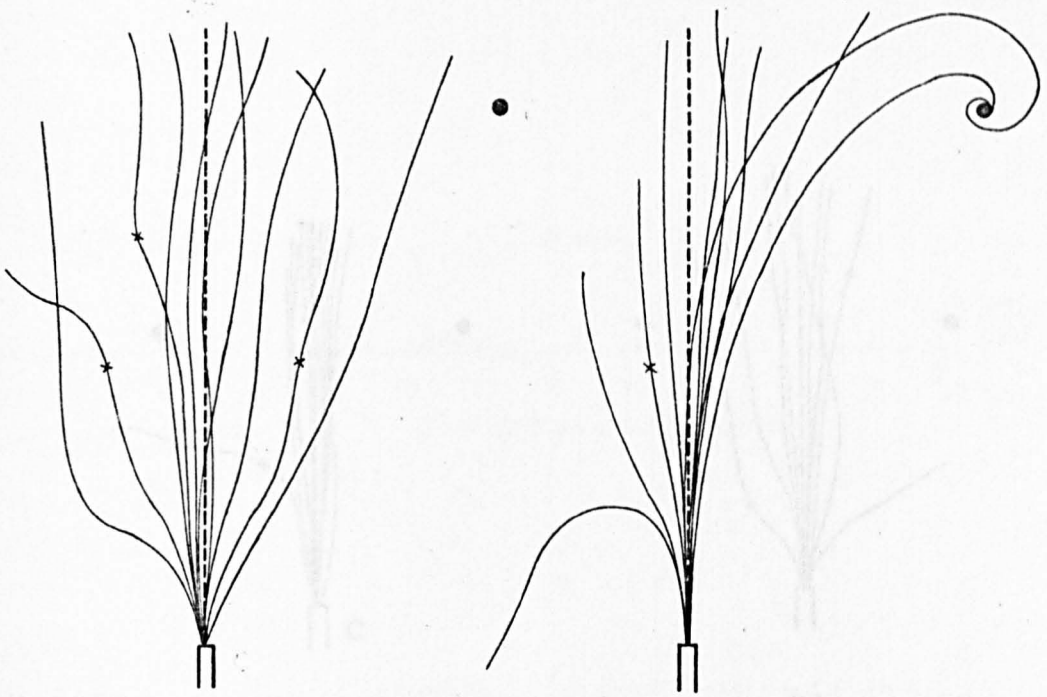


Fig. 39. Ten representative tracks from a total of thirty made by aphids of different ages, with triommatidia extirpated, walking towards a "standard" black pillar (2mm. wide and 30mm. high) situated at "near" distance (15mm.) and at "standard" angle (30°) to the median line.

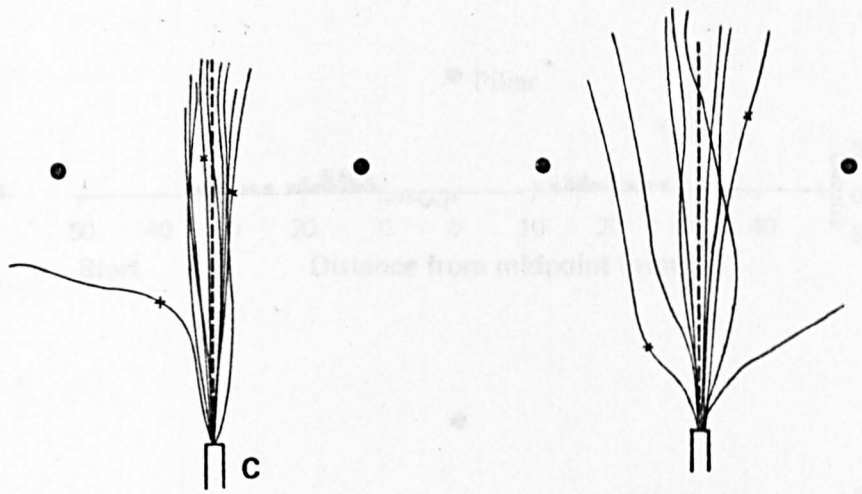


(a) Nymphs

(b) Young adults

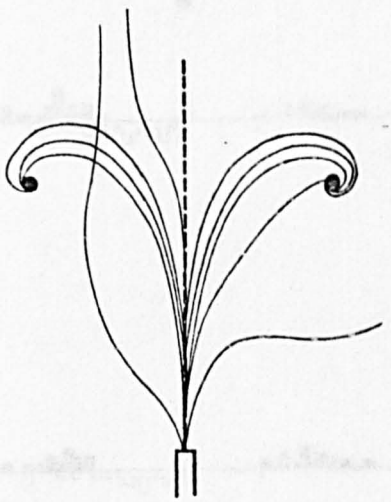
(c) Old adults

Fig. 40. Ten representative tracks from a total of thirty made by aphids of different ages, with triommatidia extirpated, walking towards a "standard" black pillar (2mm. wide and 30mm. high) situated at "far" distance (60mm.) and at "standard" angle (30°) to the median line.



(a) Nymphs

(b) Young adults



(c) Old adults

Fig. 4I. Ten representative tracks from a total of thirty made by aphids of different ages, with triommatidia extirpated, walking towards two "standard" black pillars (2mm. wide and 30mm. high) situated at "normal" distance (30mm.) and at "standard" angle (30°) to each side of the median line.

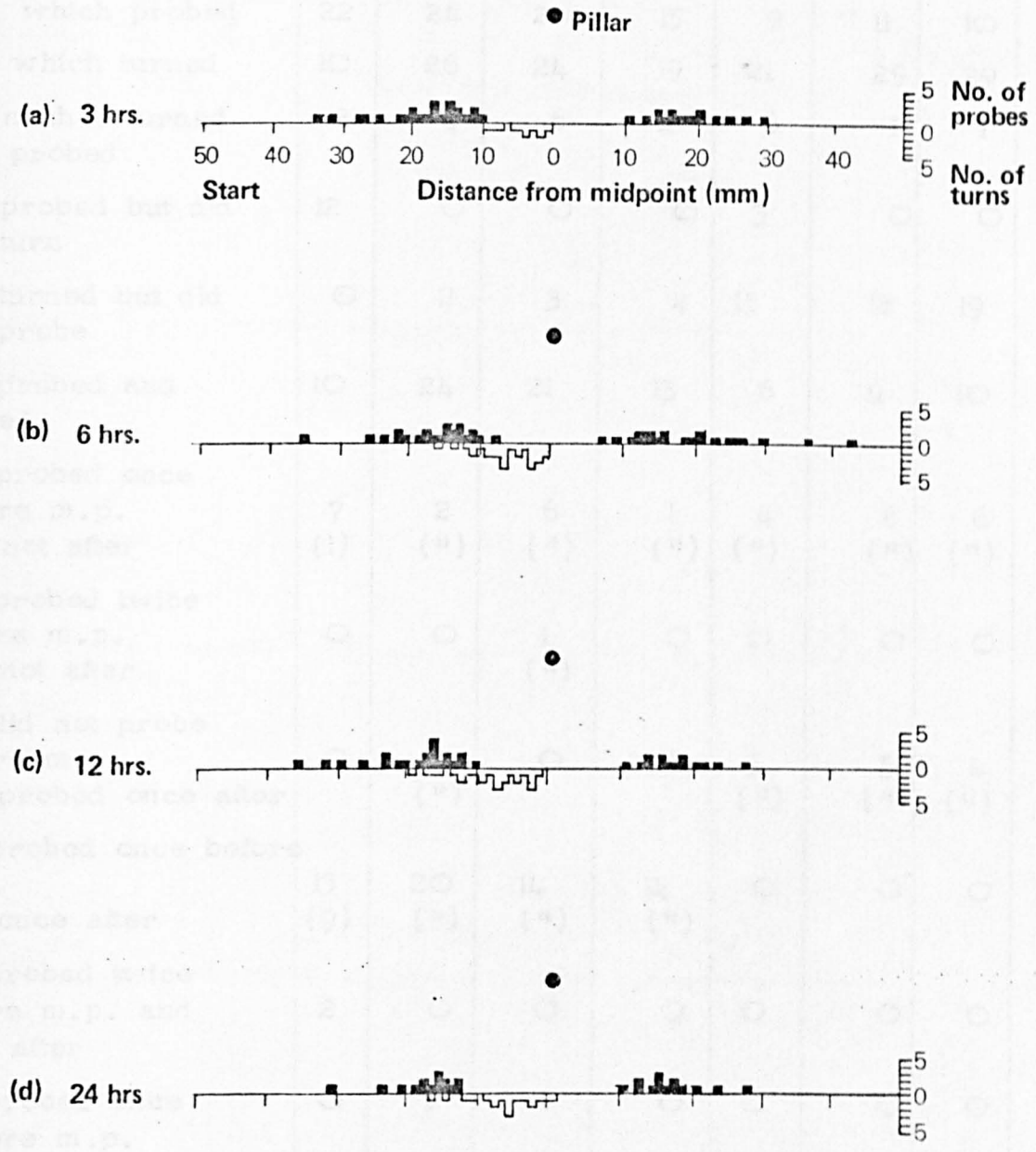


Fig. 42 Distribution along a straight wax ridge of probes and turns made by 30 aphids at ages indicated, walking in turn past a single black pillar situated at right angles to the mid point of the ridge and 15 mm. from it. Aphids with triommatidia intact.

	Triommatidia entire				Triommatidia extirpated			
	Young		Old		Young		Old	
	3h.	6h.	12h.	24h.	3h.	6h.	12h.	24h.
No. of aphids tested	30	30	30	30	30	30	30	30
No. which probed	22	24	21	15	9	11	10	8
No. which turned	10	26	24	19	21	29	29	26
No.neither turned nor probed	8	4	6	11	6	1	1	3
No.probed but did not turn	12	0	0	0	3	0	0	1
No.turned but did not probe	0	2	3	4	15	18	19	19
No.probed and turned	10	24	21	15	6	11	10	7
No.probed once before m.p. and not after	7 (1)	2 (")	6 (")	1 (")	4 (")	6 (")	6 (")	4 (3)
No.probed twice before m.p. and not after	0	0	1 (")	0	0	0	0	0
No.did not probe before m.p. and probed once after	0	1 (")	0	0	5 (")	5 (")	4 (")	4 (")
No.probed once before m.p. and once after	13 (9)	20 (")	14 (")	14 (")	0	0	0	0
No.probed twice before m.p. and once after	2	0	0	0	0	0	0	0
No.probed once before m.p. and twice after	0	1 (")	0	0	0	0	0	0
Total probes before m.p.	24	23	22	15	4	6	6	4
Total probes after m.p.	15	23	14	14	5	5	4	4
Total turns	10	26	24	19	21	29	29	26

Table 3. Distribution between individual aphids of turns and probes made on a straight wax ridge by aphids walking in turn past a single black pillar situated at right angles to the midpoint of the ridge and 15mm. from it (see Figs.44 & 45). Figures in parentheses are the numbers of aphids which turned in each of the groups listed on the left.

m.p. = midpoint of the ridge.

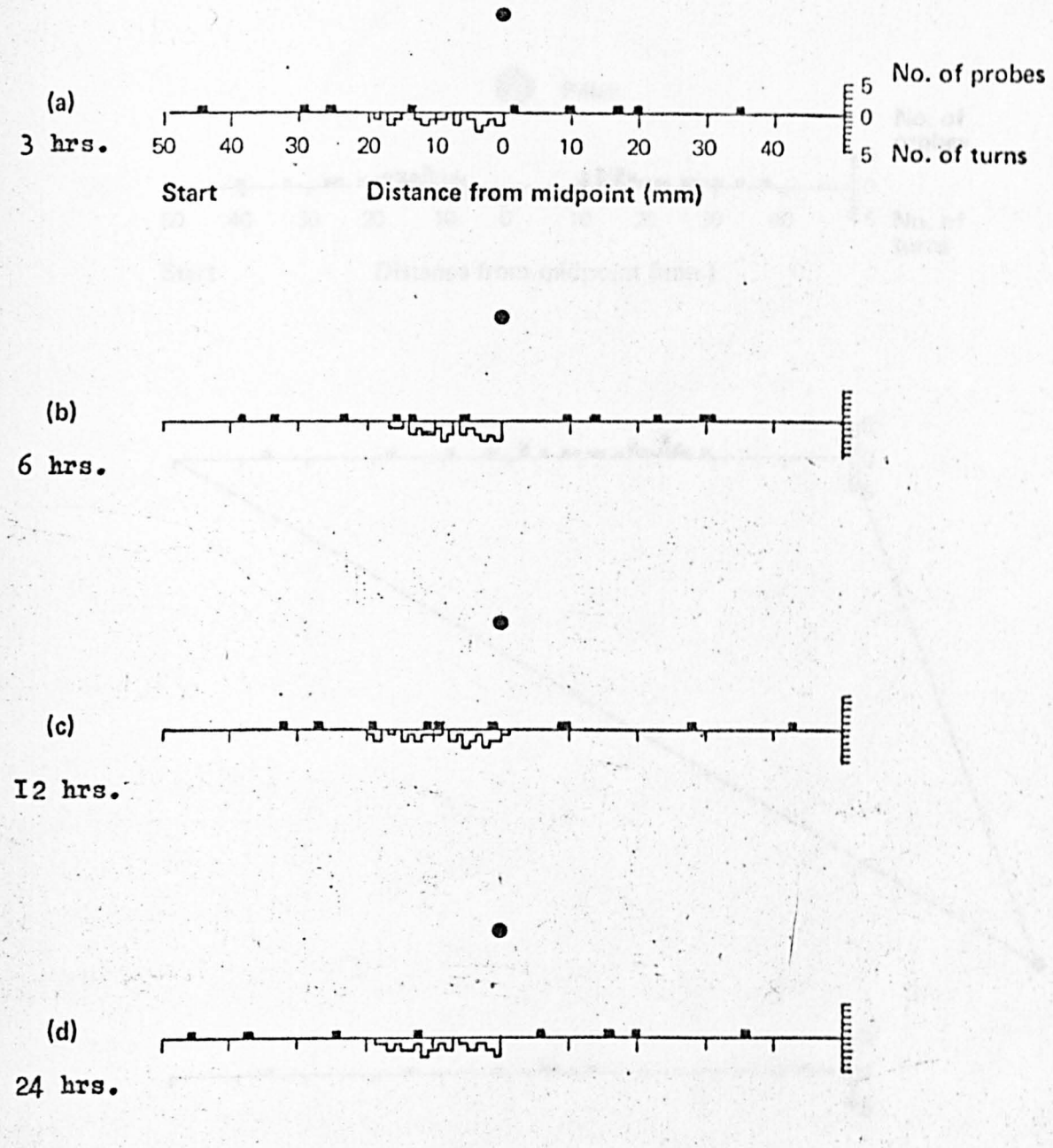
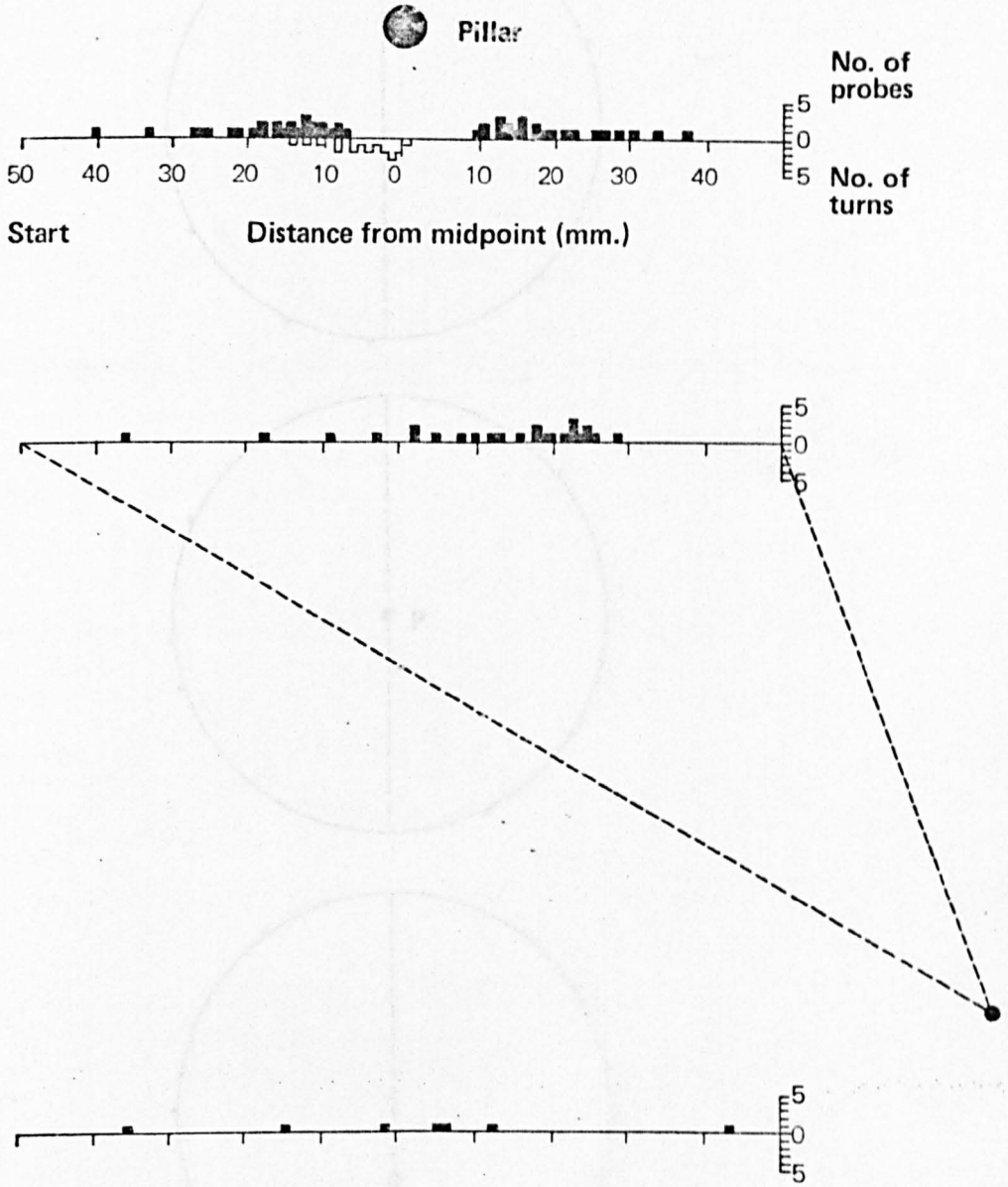


Fig. 43 Distribution along a straight wax ridge of probes and turns made by aphids with triommatidia extirpated and at ages indicated, walking in turn past a single black pillar situated at right angles to the mid point of the ridge and 15mm. from it.



Figs. 44–46. Distribution along a straight wax ridge of probes and turns made by 30 aphids at 12 hrs. old, walking in turn:

Fig. 44. past a black pillar 6 mm. wide and 30 mm. high, situated at right angles to the midpoint of the ridge and 15 mm. from it;

Fig. 45. towards a black pillar 2 mm. wide and 30 mm. high, situated as shown, 15 cm. from the proximal end of the ridge and 8 cm. from the distal end;

Fig. 46. along the empty ridge when no pillar was present.

Aphids with triommatidia intact.

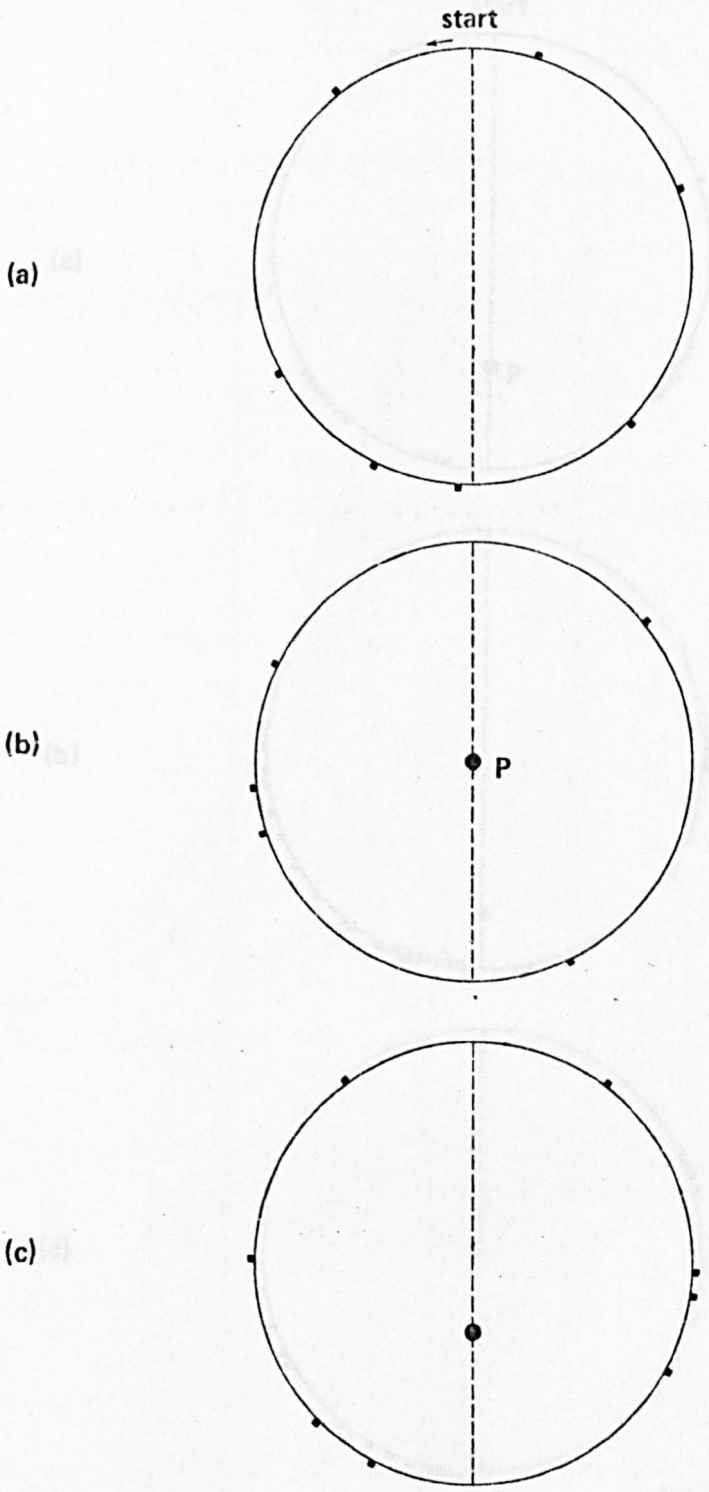


Fig. 47a-c Distribution round a circular wax ridge of probes and turns made by 30 aphids at 12 hours old, walking in turn:
a) round the empty ridge when no pillar was present,
b) past a black pillar 2 mm. x 30 mm. situated at the centre
c) past a black pillar situated 3 cm. inside the rim, the aphids starting from the point where the pillar was farthest from them and in the dead abeam position.
Aphids with triommatidia intact.

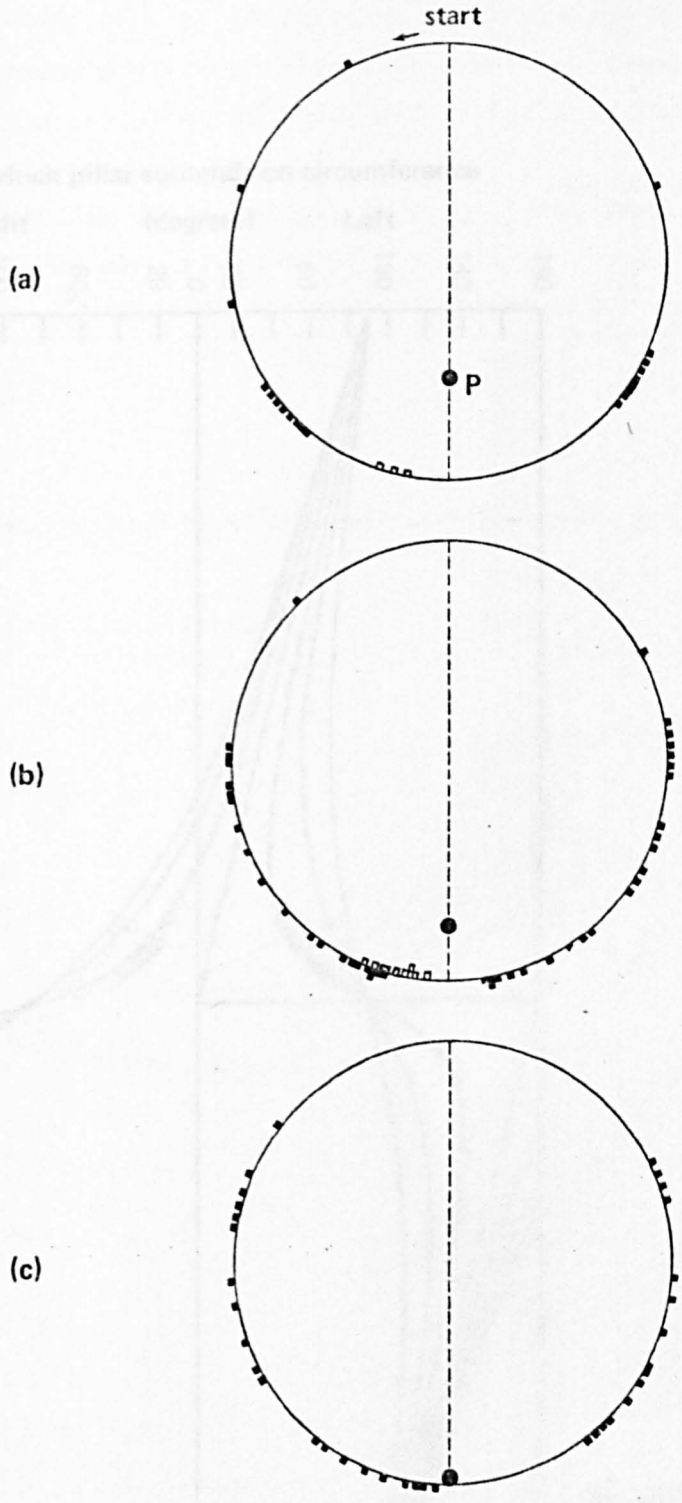


Fig. 48a-c Distribution round a circular wax ridge of probes and turns made by 30 aphids at 12 hours old, walking in turn:
a) past a black pillar 2 mm. x 30 mm. situated 2 cm. inside the rim , the aphids starting from the point where the pillar was farthest from them and in the dead abeam position,
b) as (a), with the pillar 1 cm. inside the rim,
c) with the pillar on the ridge itself.

Aphids with triommatidia intact.

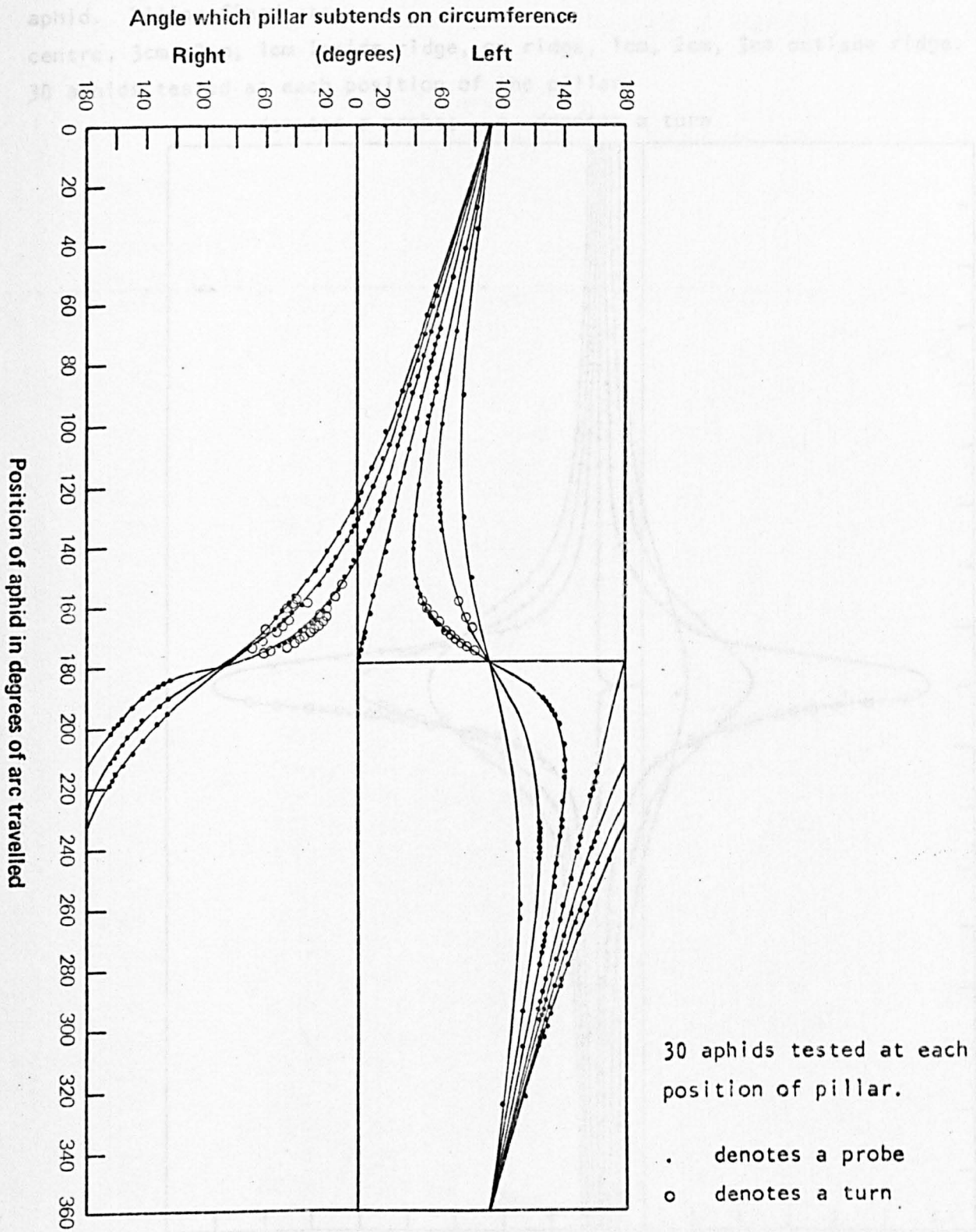


Fig.. 50. Apparent position of pillar (angle subtended) to an aphid walking anticlockwise round a circular ridge, starting with pillar 90° left and at furthest point from aphid. Pillar fixed at: centre, 3 cm, 2 cm, 1 cm inside ridge, on ridge, 1cm, 2cm, 3cm outisde ridge.

Fig. 5I. Apparent angular velocity of pillar to aphid walking anticlockwise round a circular ridge, at a uniform speed of 3mm/sec, starting with the pillar at 90° left and at furthest point from the aphid. Pillar fixed at:
centre, 3cm, 2cm, 1cm inside ridge, on ridge, 1cm, 2cm, 3cm outisde ridge.
30 aphids tested at each position of the pillar.

. denotes a probe; o denotes a turn

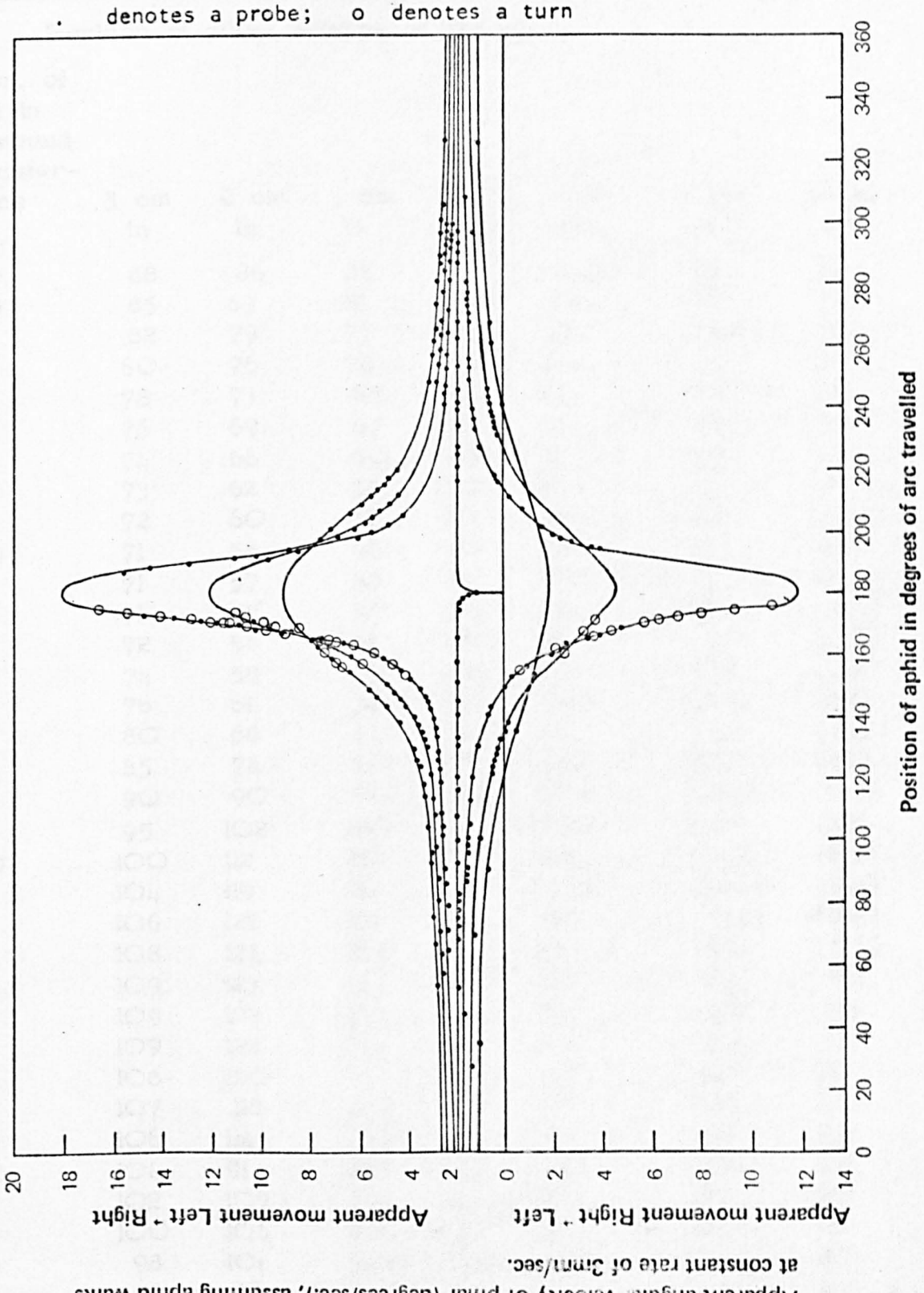


Table 4. The position of a black pillar in the visual field of an aphid at successive 10° positions of the aphid around a circular ridge, with the pillar situated at the left hand dead abeam position and at its furthest from the aphid at the starting point. Unbracketed figures = degrees to the left of dead ahead; bracketed figures = degrees to the right of dead ahead.

Apparent position of pillar (degrees)

Postn. of aphid in dgs. round circumference	Position of pillar relative to the ridge						
	3 cm in	2 cm in	1 cm in	on rim	1 cm out	2 cm out	3 cm out
10	88	86	85	85	84.5	84	84
20	85	83	81	80	79	78	77
30	82	79	77	75	73	71.5	70
40	80	76	72	70	67	65	64
50	78	73	68	65	62	60	58
60	76	69	63	60	57	54	52
70	74	66	60	55	51	47	45
80	73	62	56	50	45	41	37
90	72	60	52	45	39	35	31
100	71	58	48	40	33	27	23
110	71	57	45	35	27	21	15
120	71	57	43	30	20	12	6
130	72	56	41	25	13	4	(3)
140	74	58	39	20	5	(7)	(15)
150	76	61	39	15	(5)	(20)	(28)
160	80	68	44	10	(18)	(35)	(45)
170	85	78	60	5	(42)	(59)	(67)
180	90	90	90	0	(90)	(90)	(90)
190	95	102	120	175	(138)	(121)	(113)
200	100	112	136	170	(162)	(145)	(135)
210	104	119	141	165	(175)	(160)	(152)
220	106	122	141	160	175	(173)	(165)
230	108	124	139	155	167	176	(177)
240	109	123	137	150	160	168	174
250	109	123	135	145	153	159	165
260	109	122	132	140	147	153	157
270	108	120	128	135	141	145	149
280	107	118	124	130	135	139	143
290	106	114	120	125	129	133	135
300	104	111	117	120	123	126	128
310	102	107	112	115	118	120	122
320	100	104	108	110	113	115	116
330	98	101	103	105	107	108.5	110
340	95	97	99	100	101	102	103
350	92	94	95	95	95.5	96	96
360	90	90	90	90	90	90	90

Table 5. The apparent angular velocity of a black pillar across the field of view of an aphid at successive 10° positions of the aphid around a circular ridge, assuming the aphid travels at a constant 3mm./sec., with the pillar situated at the left hand dead abeam position and at its furthest from the aphid at the starting point.

Apparent angular velocity of pillar (degrees/sec.)

Postn. of aphid in dgs. round circumference	Position of pillar relative to the ridge						
	3cm in	2 cm in	1 cm in	on rim	1 cm out	2 cm out	3 cm out
10	1.00	1.35	1.75	1.85	2.10	2.30	2.50
20	1.00	1.35	1.75	1.85	2.10	2.30	2.50
30	1.00	1.35	1.75	1.85	2.10	2.30	2.50
40	1.00	1.35	1.75	1.85	2.10	2.30	2.50
50	0.95	1.30	1.70	1.85	2.15	2.35	2.55
60	0.85	1.25	1.65	1.85	2.175	2.375	2.60
70	0.75	1.20	1.60	1.85	2.20	2.40	2.65
80	0.65	1.10	1.50	1.85	2.25	2.45	2.70
90	0.55	0.95	1.40	1.85	2.30	2.50	2.80
100	0.35	0.80	1.30	1.85	2.35	2.60	2.90
110	0.15	0.65	1.25	1.85	2.40	2.75	3.05
120	0.00	0.40	1.15	1.85	2.50	2.90	3.25
130	0.30	0.15	1.00	1.85	2.65	3.25	3.65
140	0.75	0.45	0.70	1.85	2.85	3.85	4.35
150	1.15	1.35	0.20	1.85	3.45	4.65	5.35
160	1.50	2.50	1.85	1.85	5.15	6.15	7.25
170	1.80	3.85	5.65	1.85	9.60	9.00	8.65
180	2.00	4.65	11.95	0.00	17.90	12.00	9.00
190	1.80	3.85	5.65	1.85	9.60	9.00	8.65
200	1.50	2.50	1.85	1.85	5.15	6.15	7.25
210	1.15	1.35	0.20	1.85	3.45	4.65	5.35
220	0.75	0.45	0.70	1.85	2.85	3.85	4.35
230	0.30	0.15	1.00	1.85	2.65	3.25	3.65
240	0.00	0.40	1.15	1.85	2.50	2.90	3.25
250	0.15	0.65	1.25	1.85	2.40	2.75	3.05
260	0.35	0.80	1.30	1.85	2.35	2.60	2.90
270	0.55	0.95	1.40	1.85	2.30	2.50	2.80
280	0.65	1.10	1.50	1.85	2.25	2.45	2.70
290	0.75	1.20	1.60	1.85	2.20	2.40	2.65
300	0.85	1.25	1.65	1.85	2.175	2.375	2.60
310	0.95	1.30	1.70	1.85	2.15	2.35	2.55
320	1.00	1.35	1.75	1.85	2.10	2.30	2.50
330	1.00	1.35	1.75	1.85	2.10	2.30	2.50
340	1.00	1.35	1.75	1.85	2.10	2.30	2.50
350	1.00	1.35	1.75	1.85	2.10	2.30	2.50
360	1.00	1.35	1.75	1.85	2.10	2.30	2.50

Fig. 52.

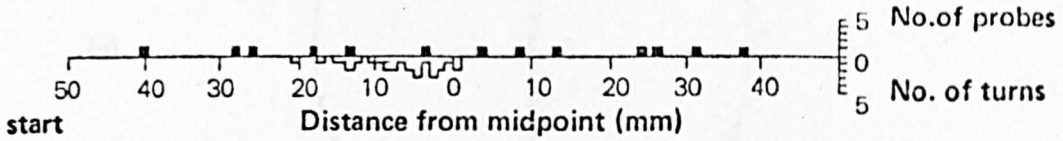
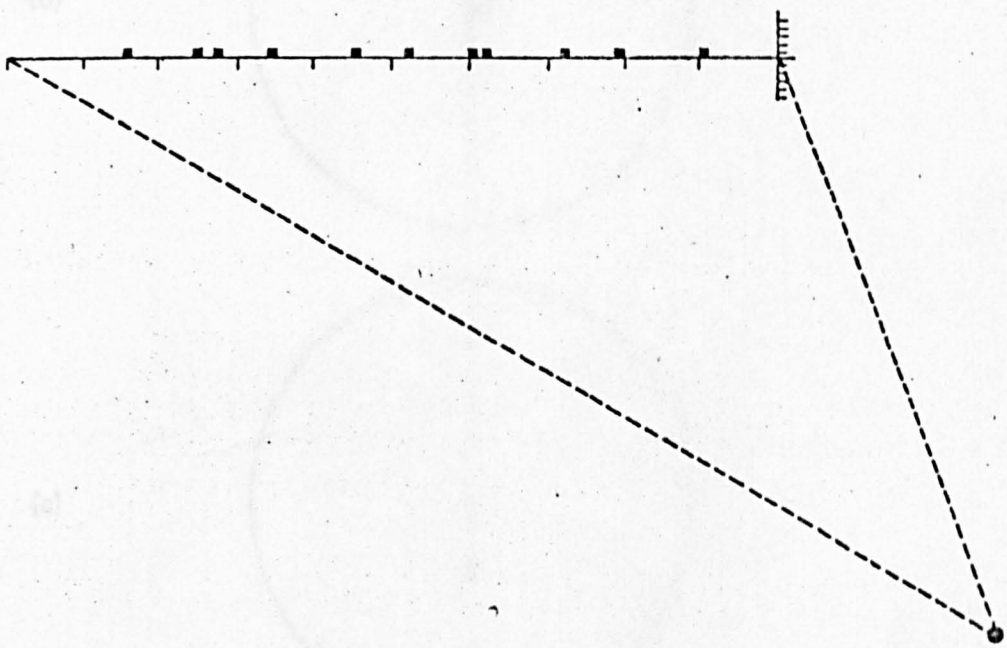


Fig. 53.



Figs. 52 & 53 Distribution along a straight wax ridge of probes and turns made by 30 aphids at 12 hours old, with triommatidia extirpated, walking in turn:

Fig. 52 past a black pillar 6mm. wide and 30mm. high, situated at right angles to the midpoint of the ridge and 15mm. from it.

Fig. 53 towards a black pillar 2mm. wide and 30mm. high, situated as shown, 15cm. from the proximal end of the ridge and 8cm. from the distal end.

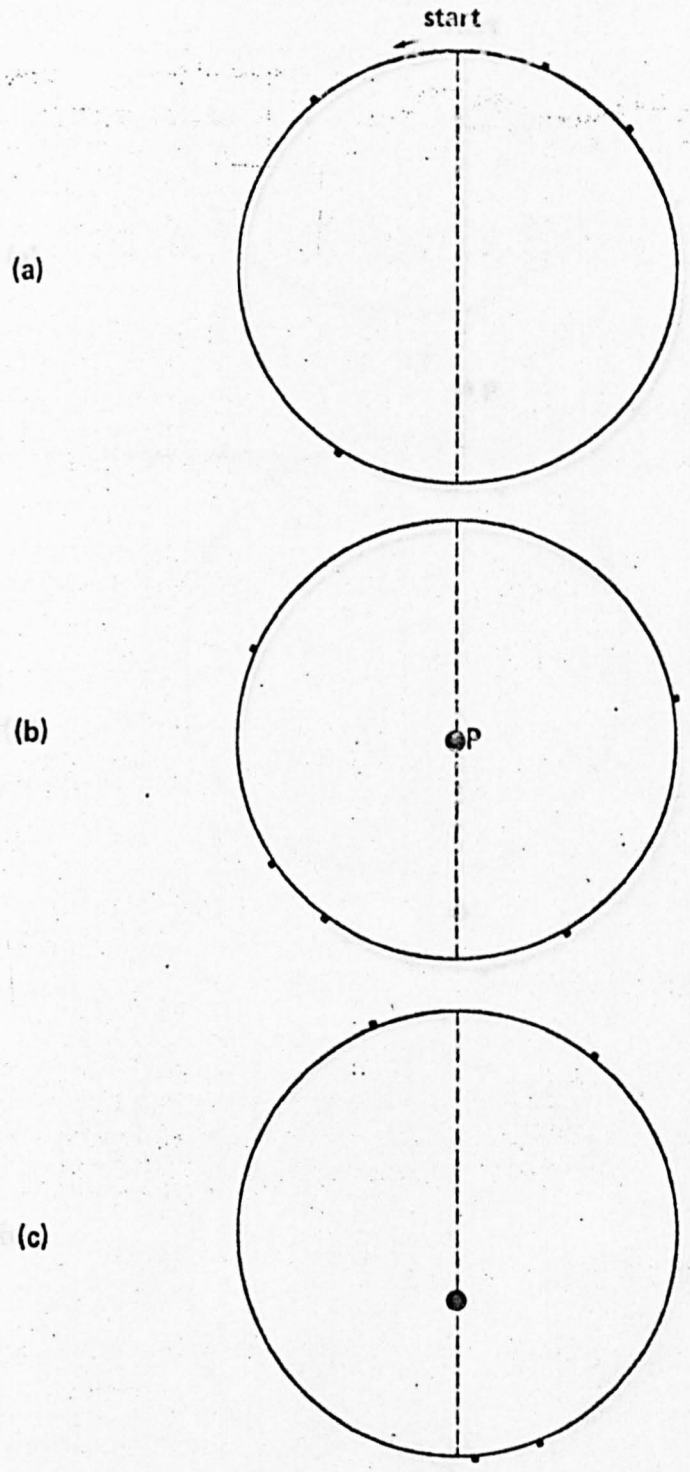


Fig. 54 a-c Distribution round a circular wax ridge of probes and turns made by 30 aphids at 12 hours old, with triommatidia extirpated, walking in turn:

a) round the empty ridge when no pillar was present,

b) past a black pillar 2mm. x 30mm. situated at the centre,

c) past a black pillar situated 3cm. inside the rim, the aphids starting from the point where the pillar was farthest from them and in the dead abeam position.

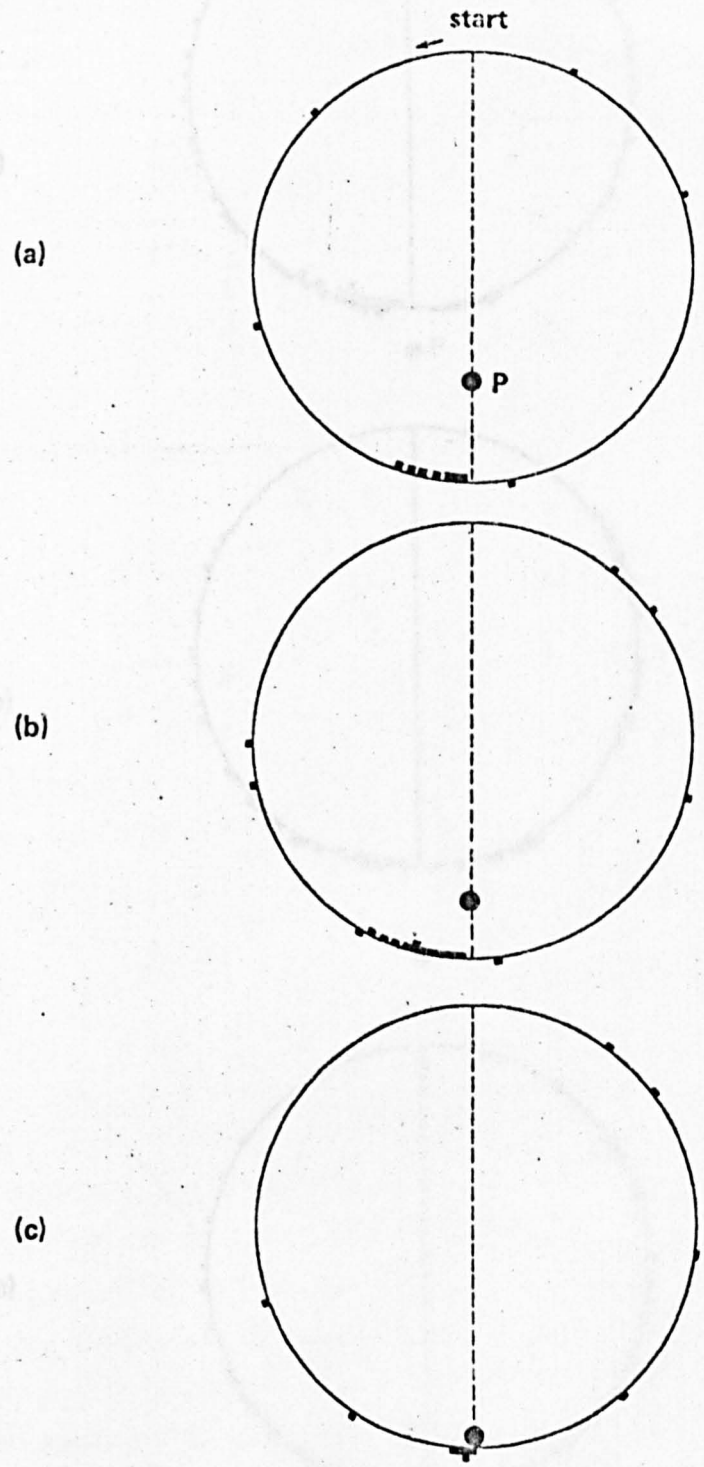


Fig. 55a-c Distribution round a circular wax ridge of probes and turns made by 30 aphids at 12 hours old, with triommatidia extirpated, walking in turn:

a) past a pillar 2mm. x 30 mm. situated 2mm. inside the rim, the aphids starting from the point where the pillar was farthest from them and in the dead abeam position,

b) as in (a), but with the pillar 1cm. inside the rim,

c) as in (a), but with the pillar on the ridge itself.

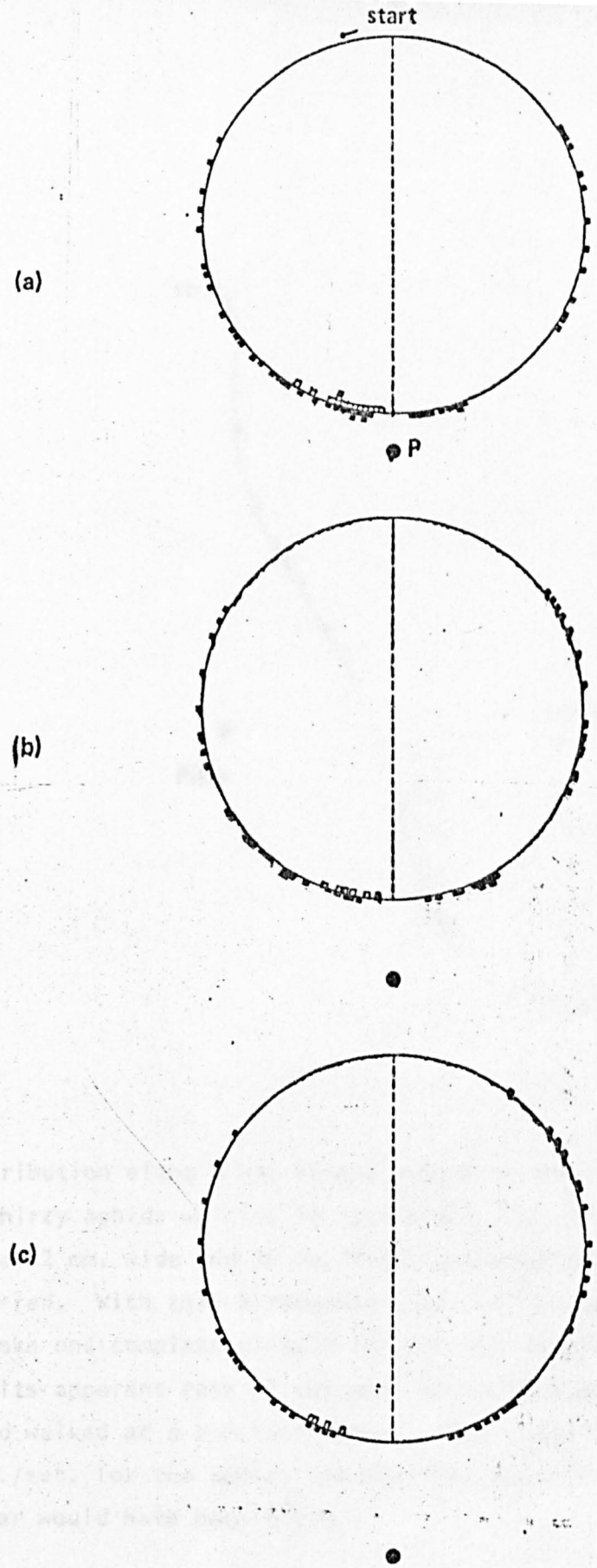


Fig. 56a-c Distribution round a circular wax ridge of probes and turns made by 30 aphids at 12 hours old, walking in turn:
a) past a black pillar 2 mm. x 30 mm., situated 1 cm. outside the rim, the aphids starting from the point where the pillar was farthest from them and in the dead abeam position;
b) as (a), with the pillar 2 cm. outside the rim
c) as (a), with the pillar 3 cm. outside the rim.
Aphids with triommatidia intact.

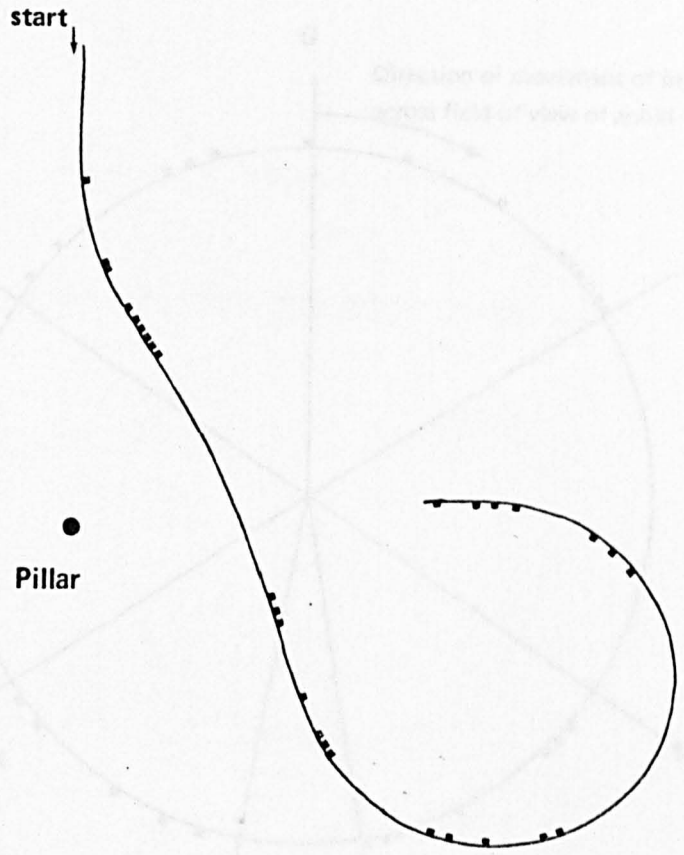


Fig. 57. Distribution along a wax ridge, shaped as shown, of probes made by thirty aphids walking in turn along the ridge past a black pillar 2 mm. wide and 30 mm. high, situated as shown. No turns occu-red. With this arrangement, the pillar would have appeared to make one complete circuit through the visual field of the aphid and its apparent rate of movement would have been constant if the aphid walked at a constant speed. Assuming a walking speed of 3 mm./sec. for the aphid, the apparent angular velocity of the pillar would have been 8^{o}/sec.

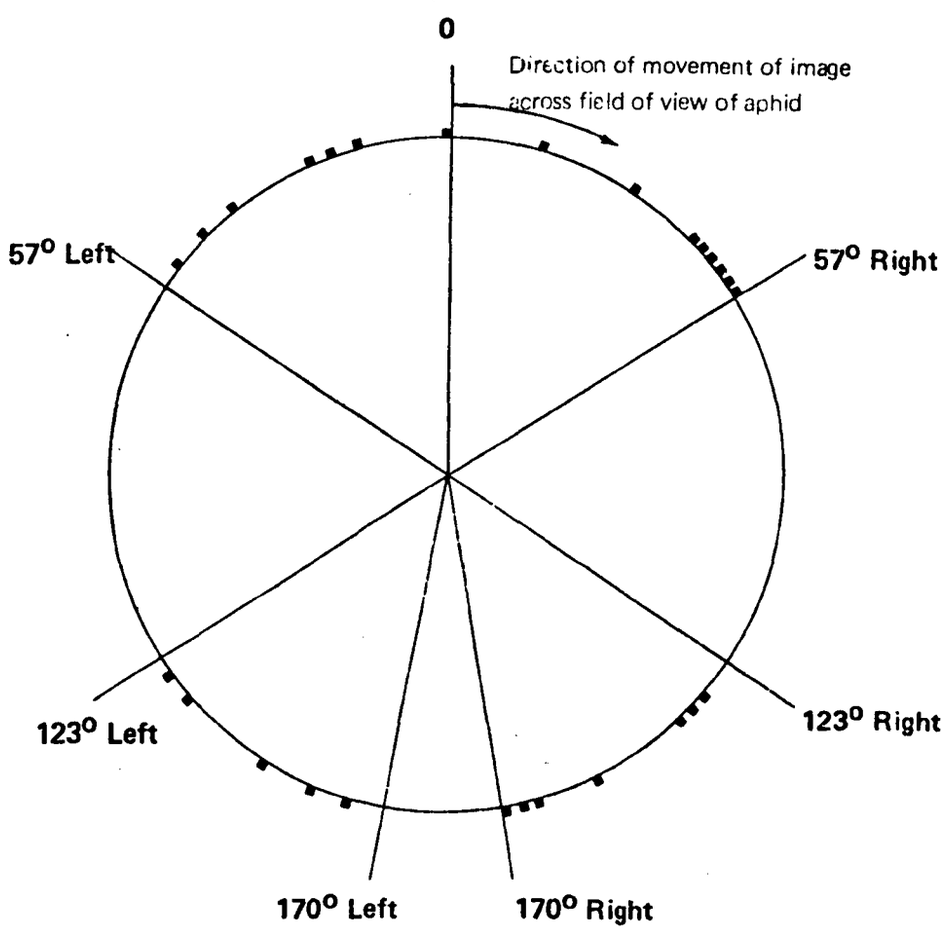


Fig. 58. The distribution of probes shown in Fig. 57, to show the position of the black pillar in the visual field of the aphid at the moment of probing.

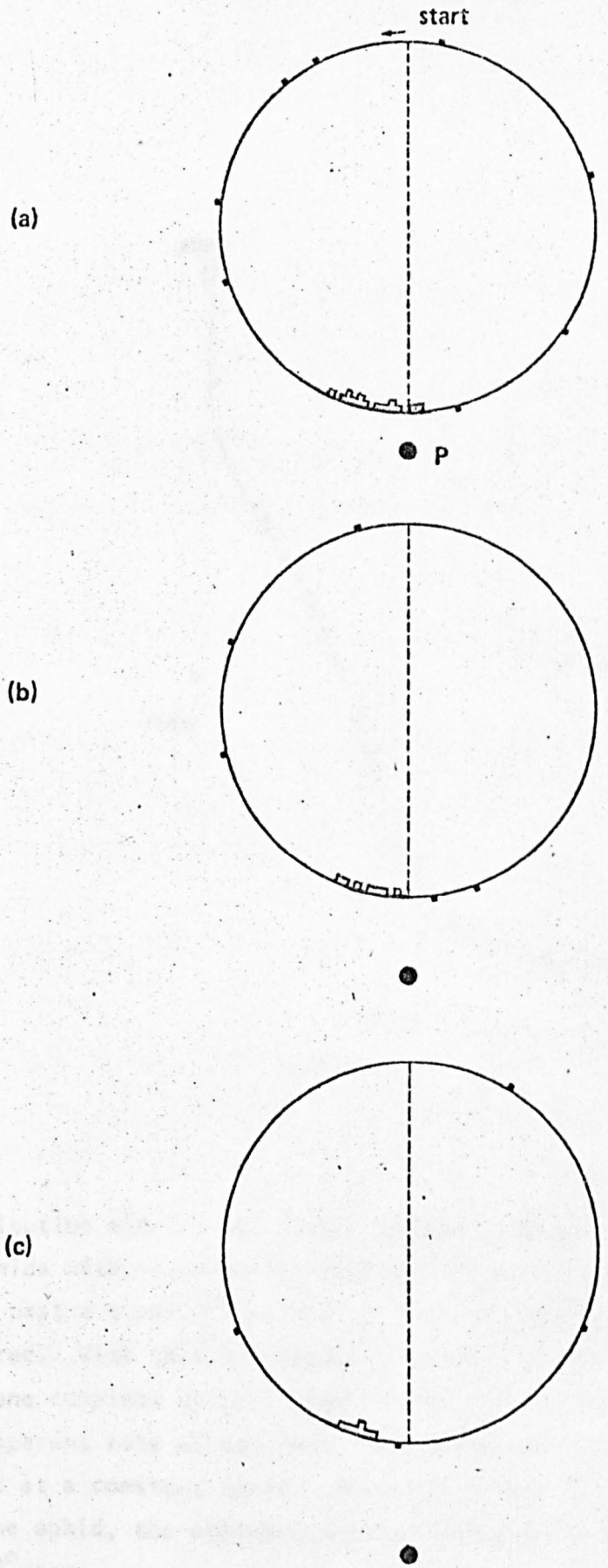


Fig. 59a-c Distribution round a circular wax ridge of probes and turns made by 30 aphids at 12 hours old, with triommatidia extirpated, walking in turn:

a) past a black pillar 2mm. x 30mm. situated 1cm. outside the rim, the aphids starting from the point where the pillar was farthest from them and in the dead abeam position.

b) as in (a), but with the pillar 2cm. outside the rim,

c) as in (a), but with the pillar 3cm. outside the rim.

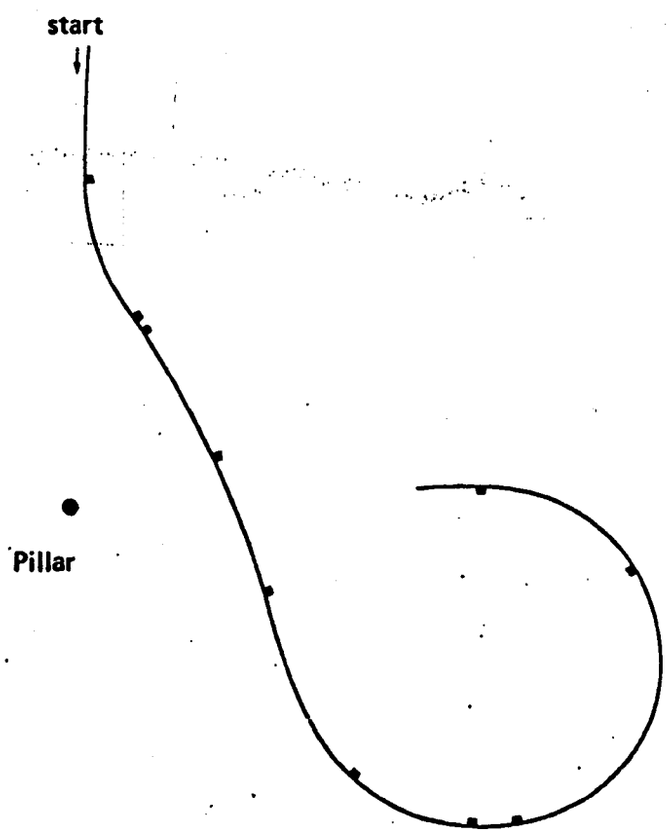


Fig. 60. Distribution along a wax ridge, shaped as shown, of probes made by 30 aphids with triommatidia extirpated, walking in turn along the ridge past a black pillar 2mm. x 30mm. situated as shown. No turns occurred. With this arrangement, the pillar would have appeared to make one complete circuit through the visual field of the aphid and its apparent rate of movement would have been constant if the aphid walked at a constant speec. Assuming a walking speed of 3mm./sec. for the aphid, the apparent angular velocity of the pillar would have been 8^{o}/sec.

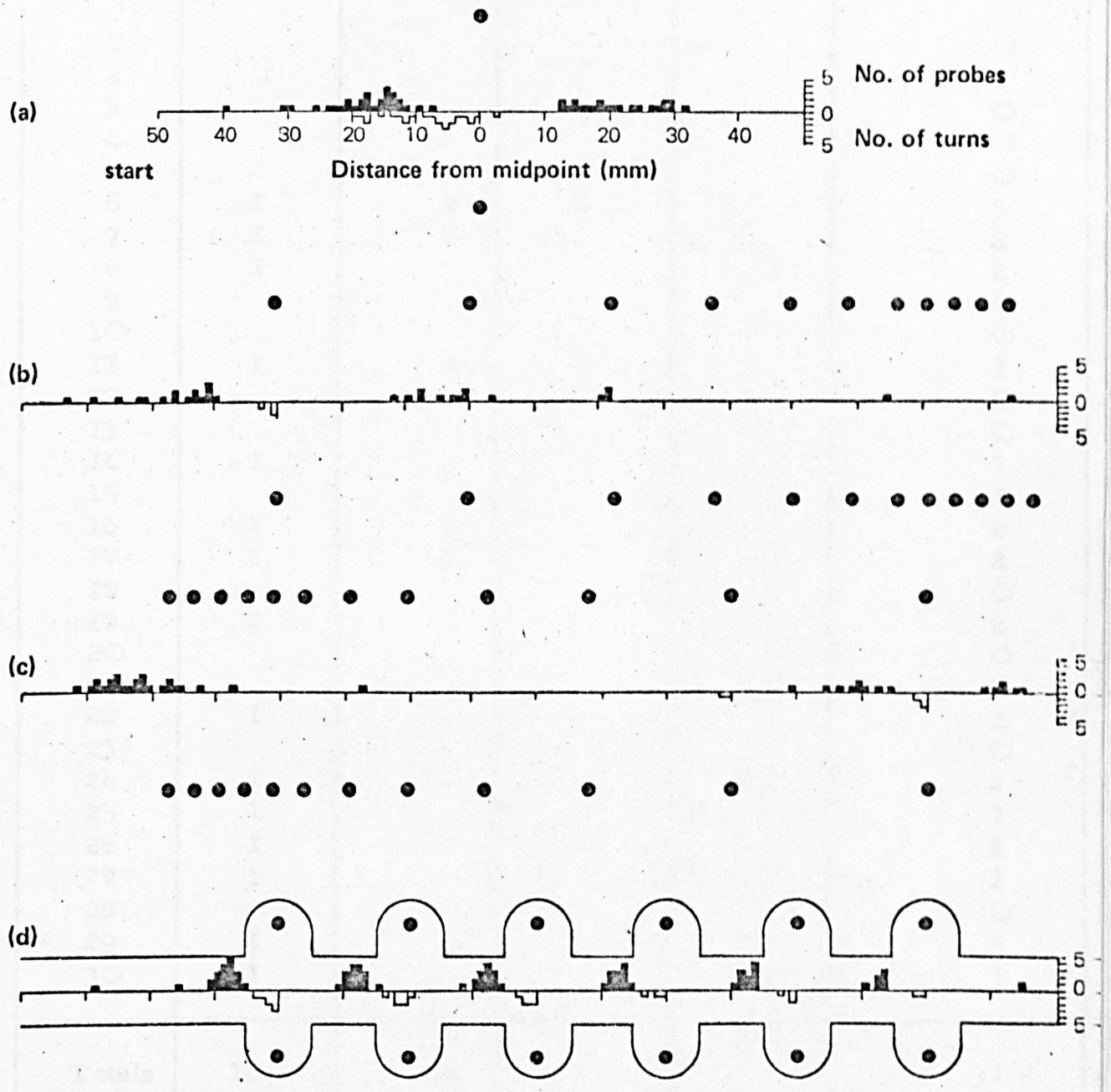


Fig. 6Ia-d Distribution along a straight wax ridge of probes and turns made by 30 aphids with triommatidia intact at 12 hours old, walking in turn along the ridge past the pillars indicated and, in (d), white cardboard screens situated as shown.

Aphid	Position of probe in mm. from aphid's starting point.				Total probes per aphid
	0-40	40-70	70-90	Other	
1					0
2	1				1
3					0
4					0
5					0
6	1	1	1		3
7	1	1			2
8	1			1	2
9					0
10					0
11	1	1	1		3
12					0
13					0
14	1				1
15				1	1
16	1	1			2
17	1	1			2
18					0
19	1	1			2
20					0
21		1			1
22	1				1
23					0
24	1	1			2
25	1				1
26	1	1			2
27	1				1
28					0
29	1	1	1		3
30	1				1
Totals	16	10	3	2	31

Table 6. The distribution of probes made by individual aphids along the wax ridge shown in Fig. 61(b).

Aphid	Position of probe in mm. from aphid's starting point.				Total probes per aphid
	0-40	40-70	70-90	Other	
I	I				I
2	I				I
3		I			I
4			I		I
5	I				I
6					0
7	2	I			3
8	I			I	2
9	2				2
I0					0
II	I	I	I		3
I2					0
I3	I	I	I		3
I4					0
I5	3	I			4
I6	I		I		2
I7				I	I
I8					0
I9	3				3
20					0
2I					0
22	I	I			2
23					0
24	2		I		3
25					0
26	I	I			2
27	2				2
28		I	I		2
29	I				I
30				I	I
Totals	24	8	6	3	4I

Table 7. The distribution of probes made by individual aphids along the wax ridge shown in Fig. 58(c).

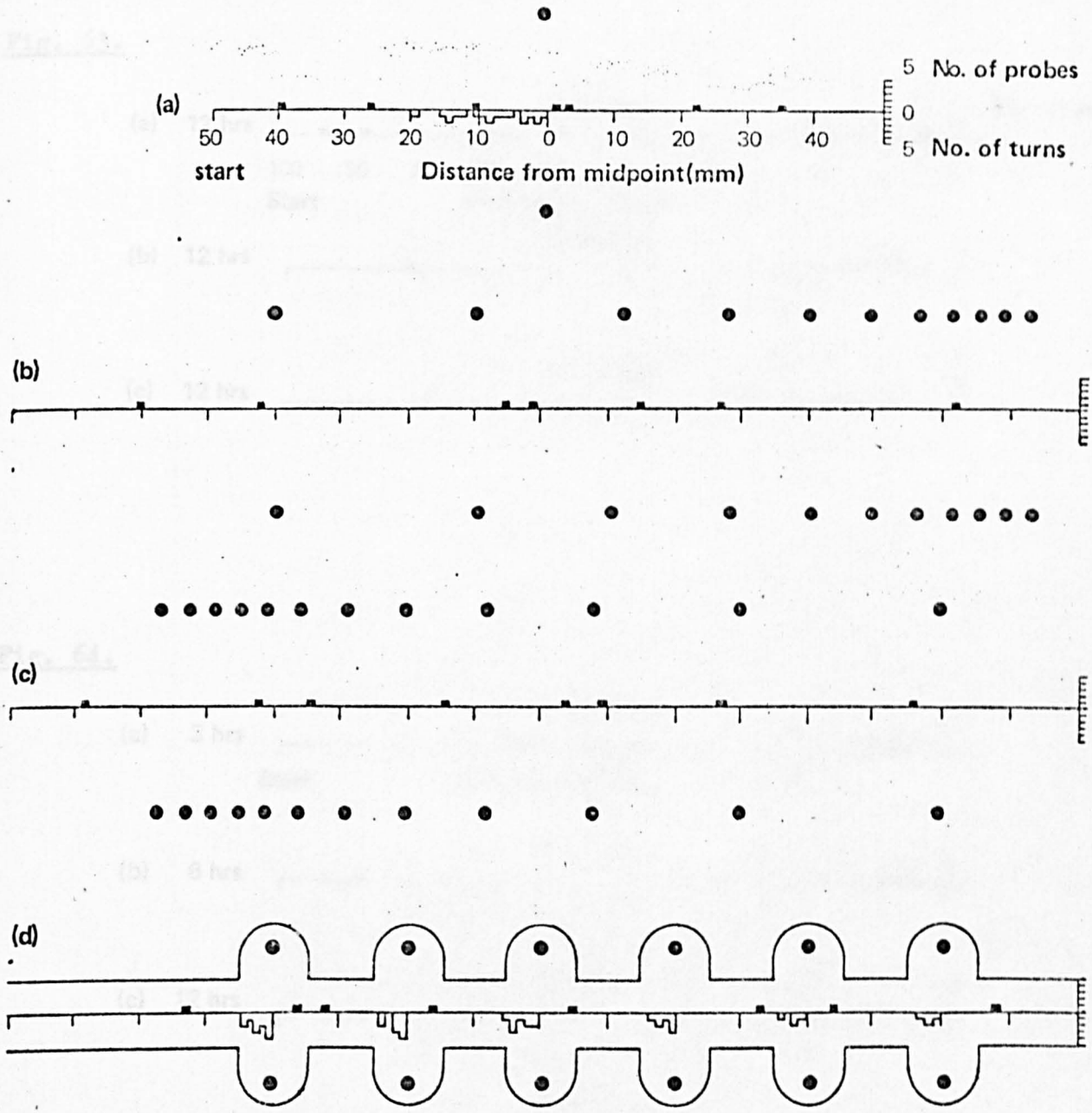


Fig. 62. Distribution along a straight wax ridge of probes and turns made by 30 aphids with triommatidia extirpated, at 12 hours old, walking in turn along the ridge past the pillars indicated and, in (d), white cardboard screens situated as shown.

Fig. 63.

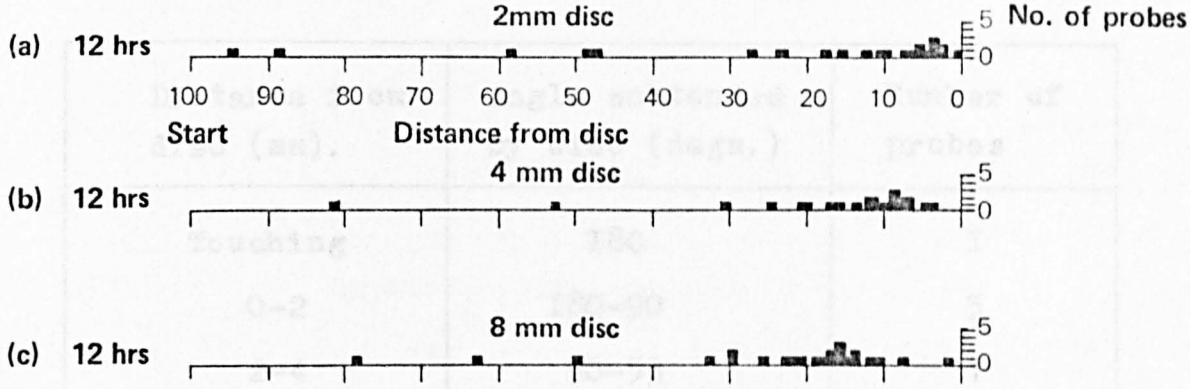
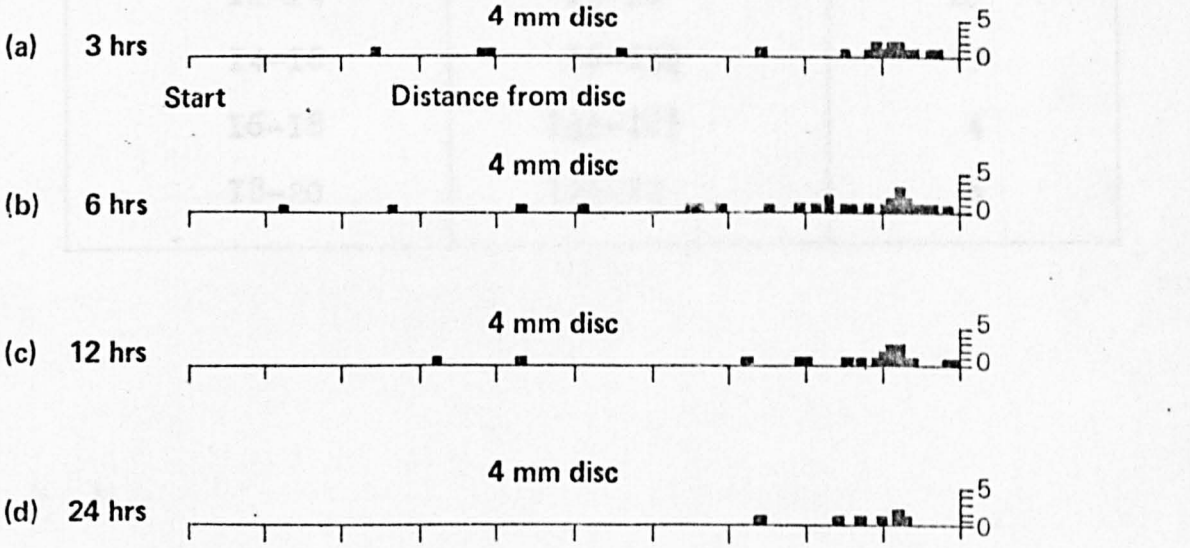


Fig. 64.



Figs. 63a-c & 64a-d Distribution along a straight wax ridge of probes made by 30 aphids of age groups indicated, walking in turn along the ridge towards black discs of various diameters, situated face on and directly ahead.

Distance from disc (mm).	Angle subtended by disc (degs.)	Number of probes
Touching	180	1
0-2	180-90	5
2-4	90-53	7
4-6	53-32	18
6-8	32-28	35
8-10	28-23	20
10-12	23-19	11
12-14	19-16	10
14-16	16-13½	7
16-18	13½-12½	4
18-20	12½-12	6

Table 8. Distribution of probes made by 240 aphids between 3 hours and 24 hours old, walking in turn along a straight wax ridge towards a black disc 4 mm. in diameter situated face on and directly ahead.

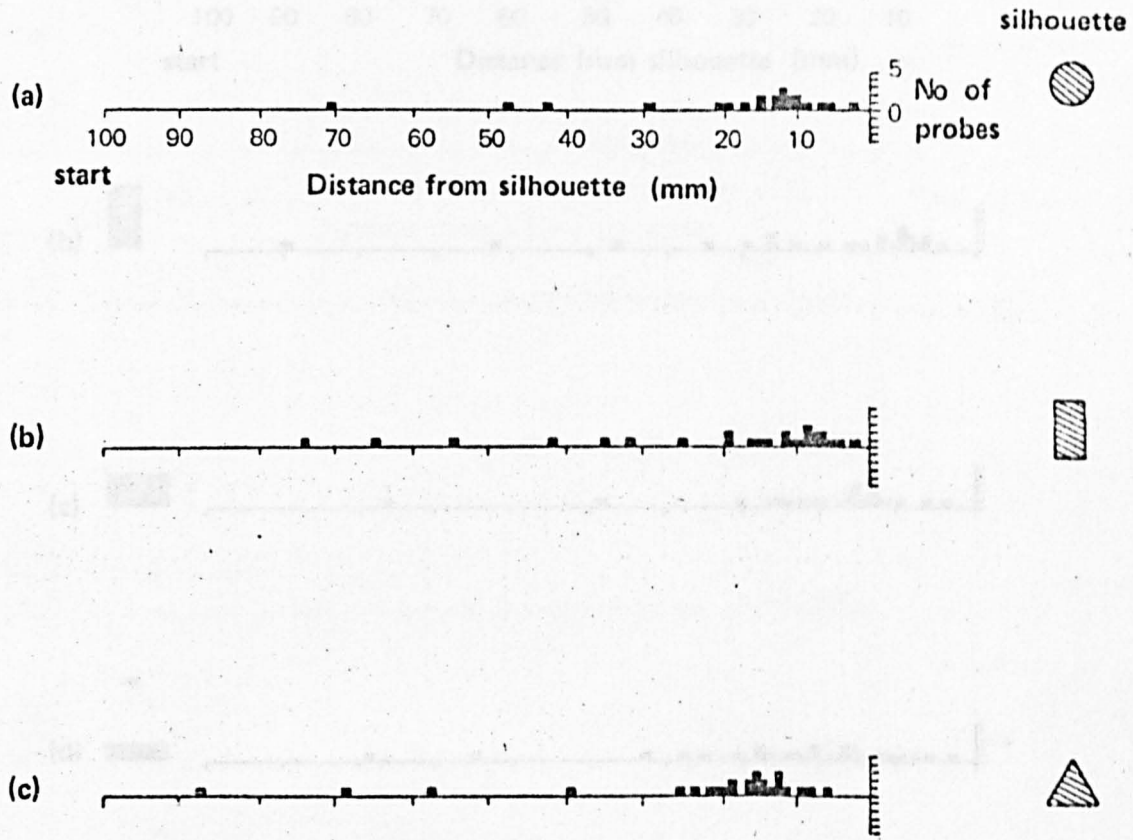


Fig. 65a-c Distribution along a straight wax ridge of probes made by 30 aphids with triommatidia intact at 12 hours old, walking in turn along the ridge towards the silhouttes shown, which were of various shapes but had a common area, situated face on and directly ahead.

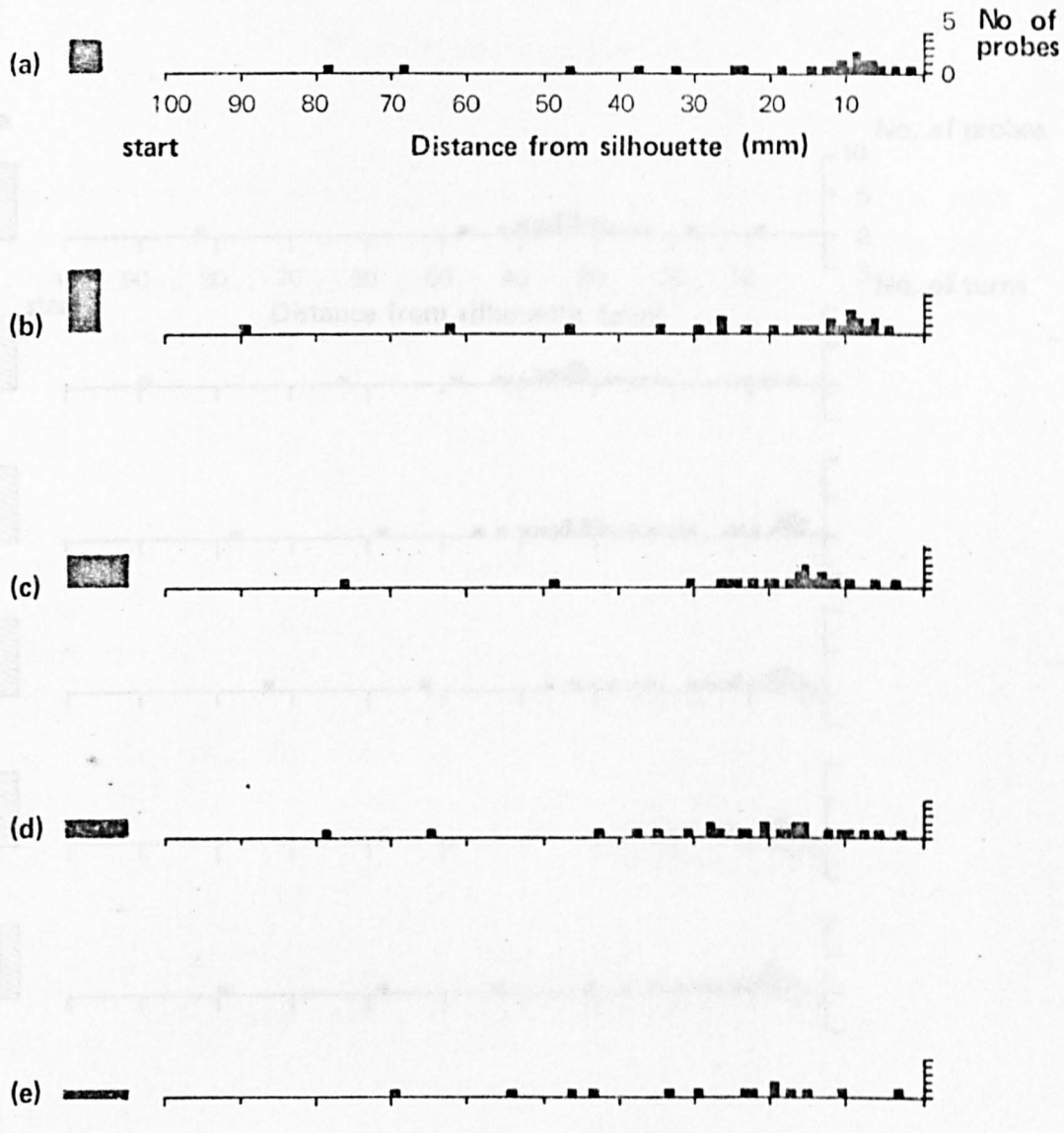


Fig. 66a-e Distribution along a straight wax ridge of probes made by 30 aphids with triommatidia intact at 12 hours old, walking in turn along the ridge towards the following rectangular silhouettes (height x width):

a) 4 mm. x 4 mm., b) 8 mm. x 4 mm., c) 4 mm. x 8 mm., d) 2 mm. x 8 mm., e) 1 mm. x 8 mm.

All silhouettes were situated face on and directly ahead.

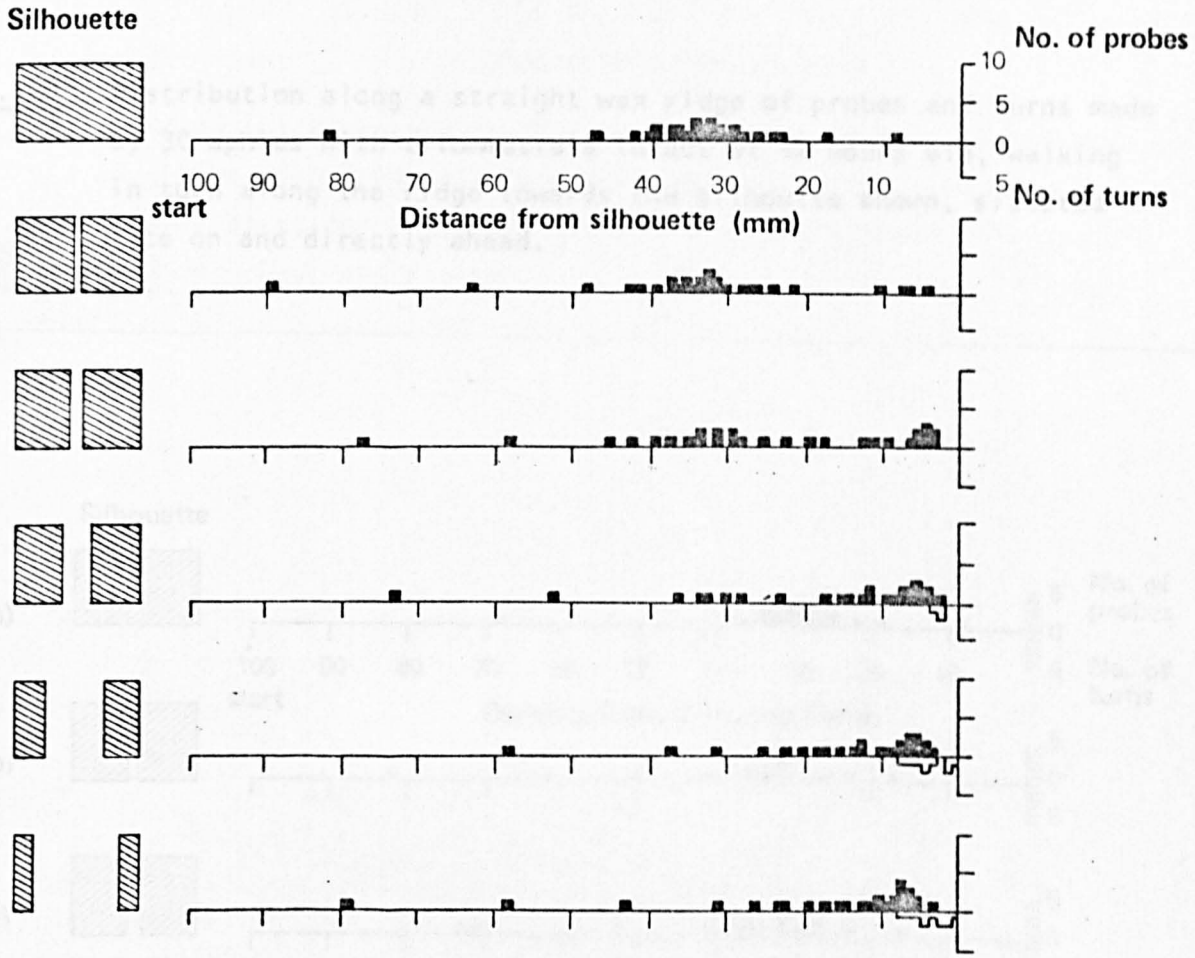


Fig. 67a-f Distribution along a straight wax ridge of probes and turns made by 30 aphids with triommatidia intact at 12 hours old, walking in turn along the ridge towards the silhouettes indicated.

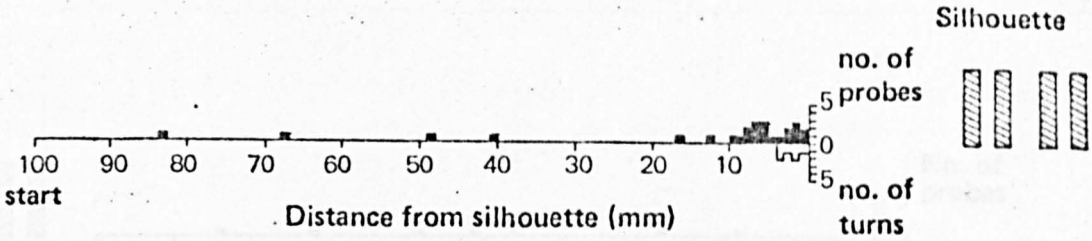


Fig. 68 Distribution along a straight wax ridge of probes and turns made by 30 aphids with triommatidia intact at 12 hours old, walking in turn along the ridge towards the silhoutte shown, situated face on and directly ahead.

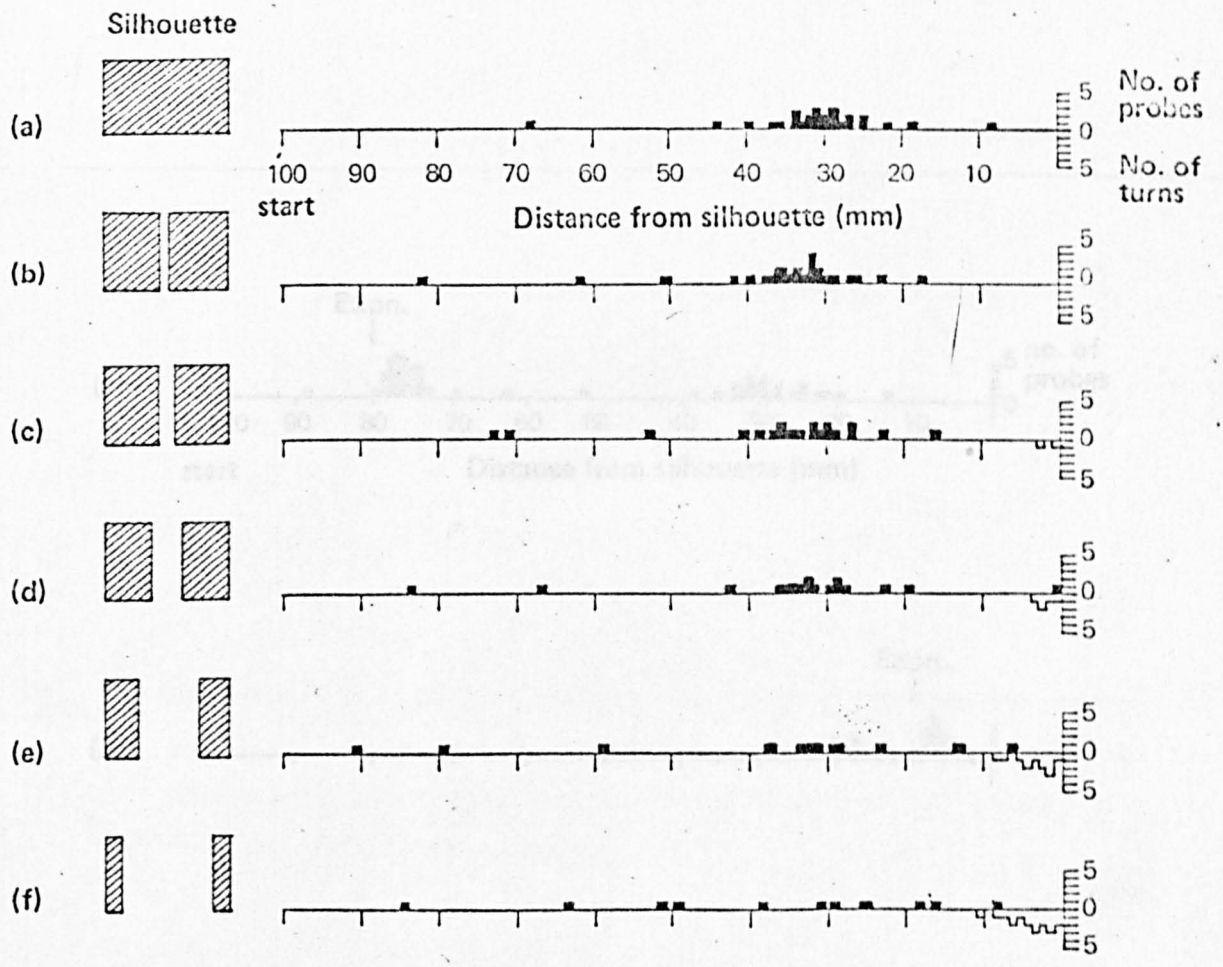


Fig. 69a-f Distribution along a straight wax ridge of probes and turns made by 30 aphids with triommatidia extirpated, at 12 hours old, walking in turn along the ridge towards the silhouttes indicated, situated face on and directly ahead.

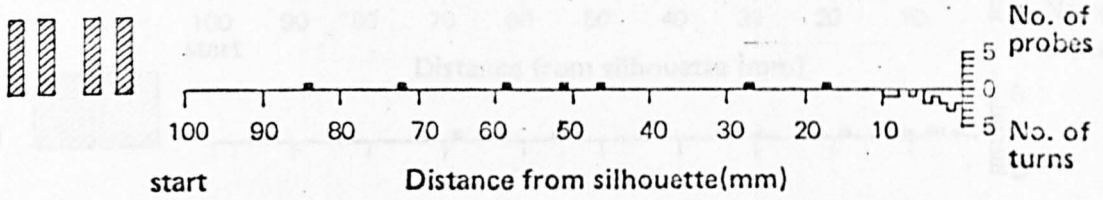


Fig. 70 Distribution along a straight wax ridge of probes and turns made by 30 aphids with triommatidia extirpated, at 12 hours old, walking in turn along the ridge towards the silhouette shown, situated face on and directly ahead.

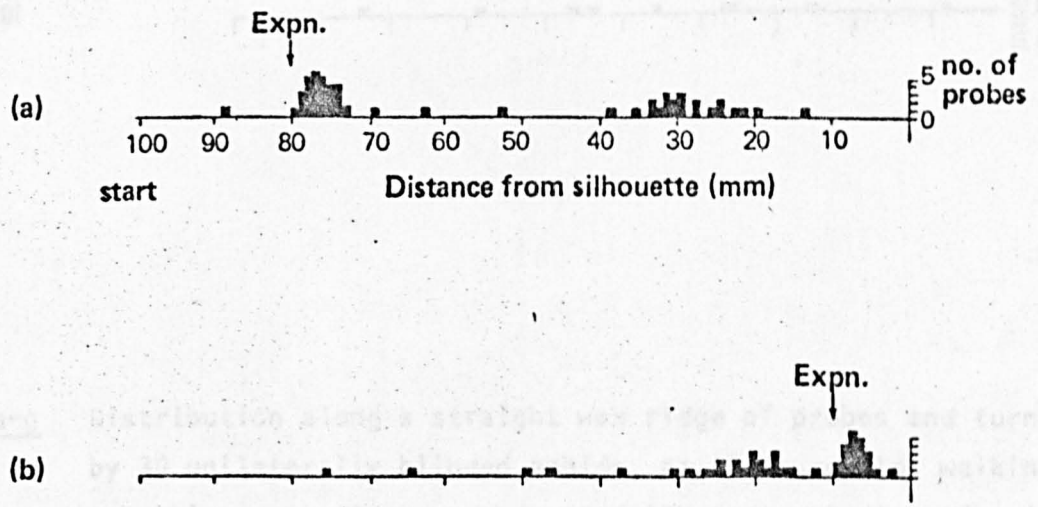


Fig. 71 Distribution along a straight wax ridge of probes and turns made by 30 aphids with triommatidia intact at 12 hours old, walking in turn along the ridge towards a black silhoutte 1cm. high, which expanded suddenly from 1cm. wide to 2cm. wide as the aphid was walking.

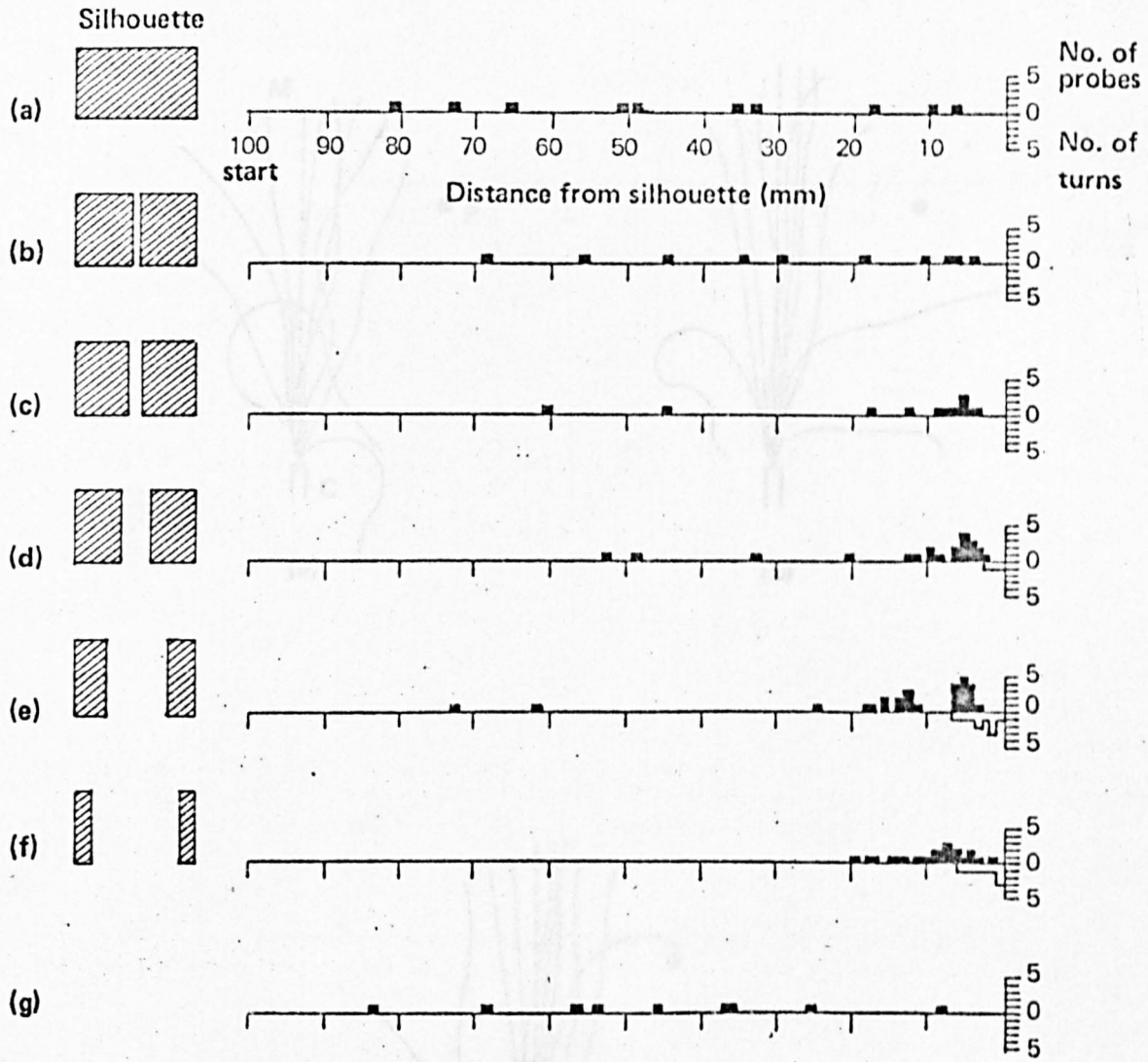


Fig. 72a-g Distribution along a straight wax ridge of probes and turns made by 30 unilaterally blinded aphids, at 12 hours old, walking in turn along the ridge towards the silhouettes indicated, situated face on and directly ahead.

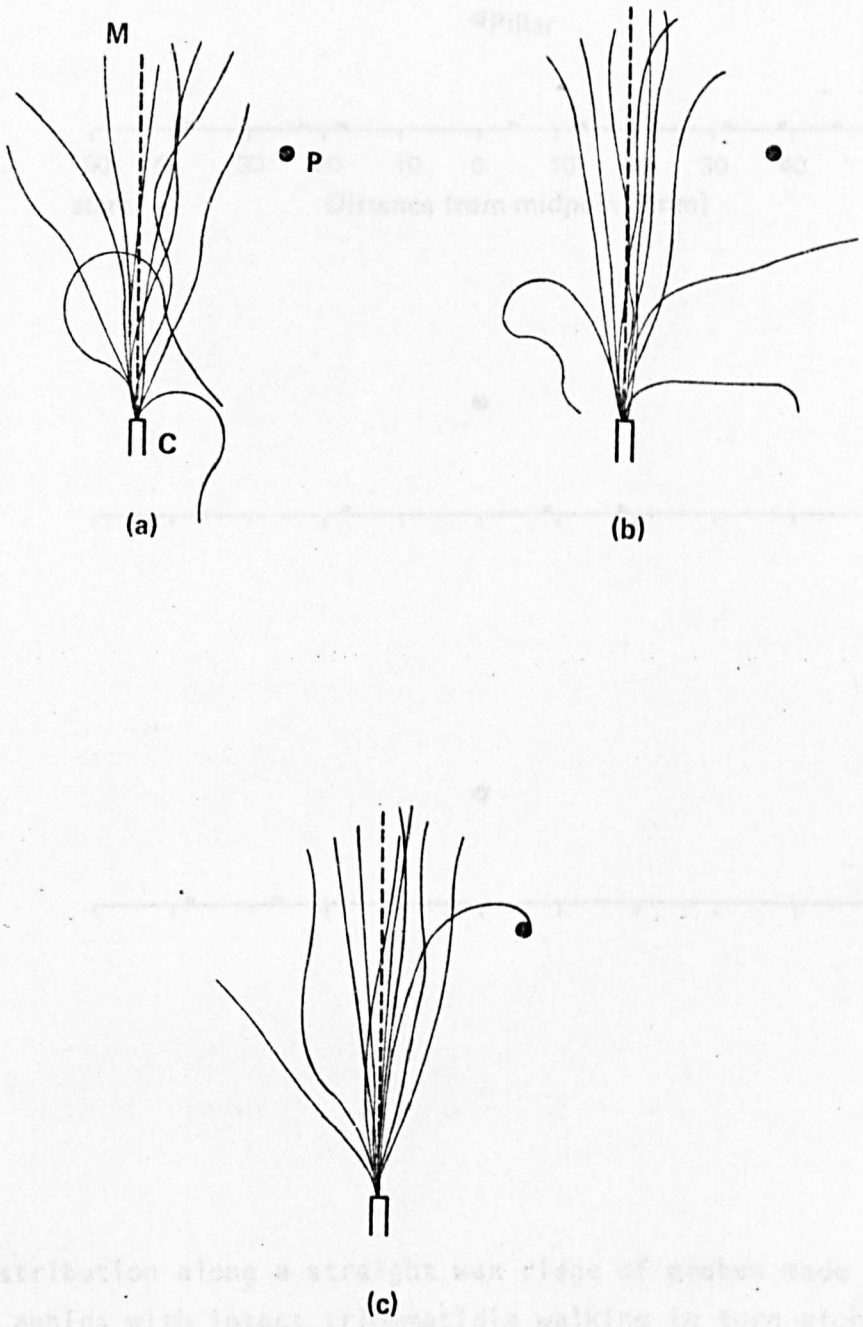


Fig. 73a-c. Tracks made across a flat wax plate by aphids with triommatidia intact, walking in turn towards a black pillar 2 mm. x 30 mm., situated 30 mm. from the point where the aphids left the causeway and at 30° to the median line. Ten representative tracks are shown from a total of thirty recorded in each case, corrected to show the pillar always to the right of the median line. Intensity of incident light 6000 Lux.

a) freshly moulted adults

b) adults 6 hrs. old

c) adults 24 hrs. old

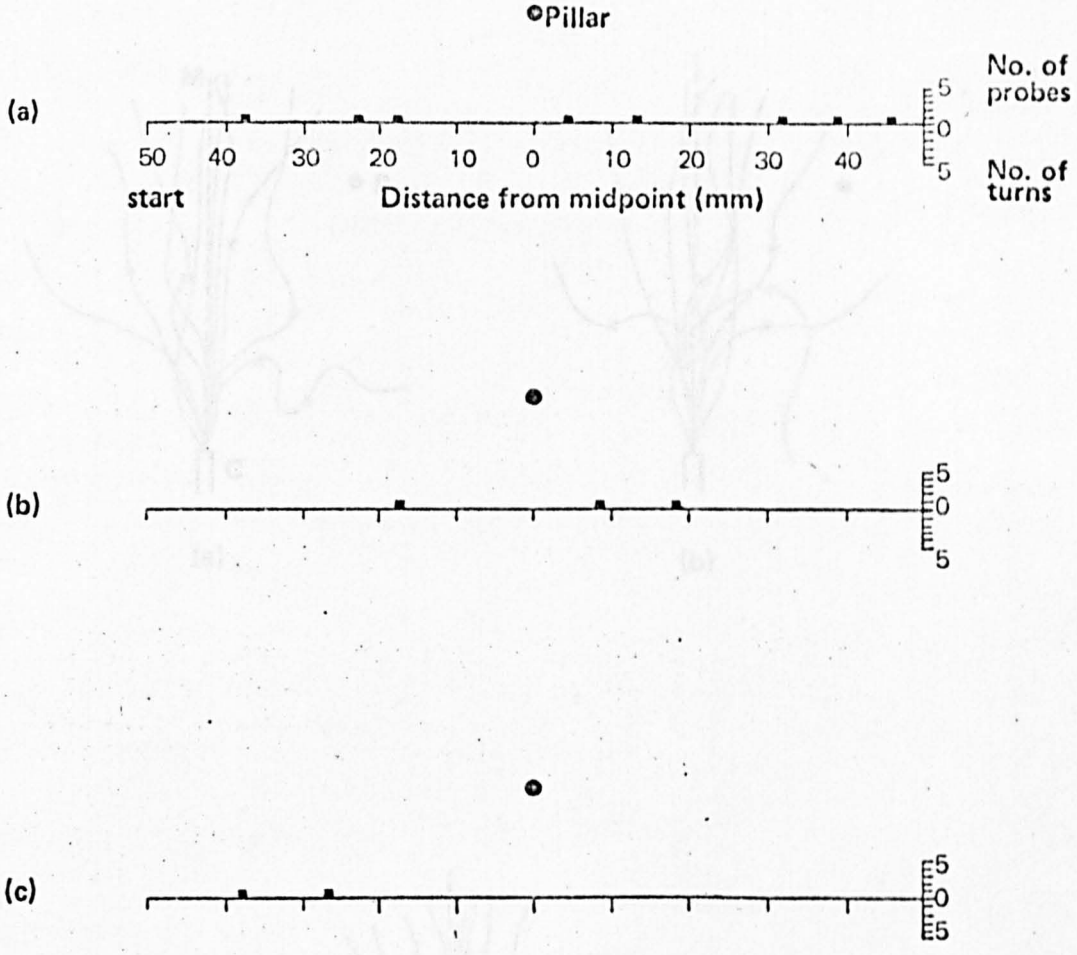


Fig. 74a-c Distribution along a straight wax ridge of probes made by 30 aphids with intact triommatidia walking in turn along the ridge past a single black pillar, 2mm. x 30mm. situated at right angles to the midpoint of the ridge and 1.5cm. from it. Intensity of incident light 6000 Lux.

a) freshly moulted adults

b) adults 6 hours old

c) adults 24 hours old.

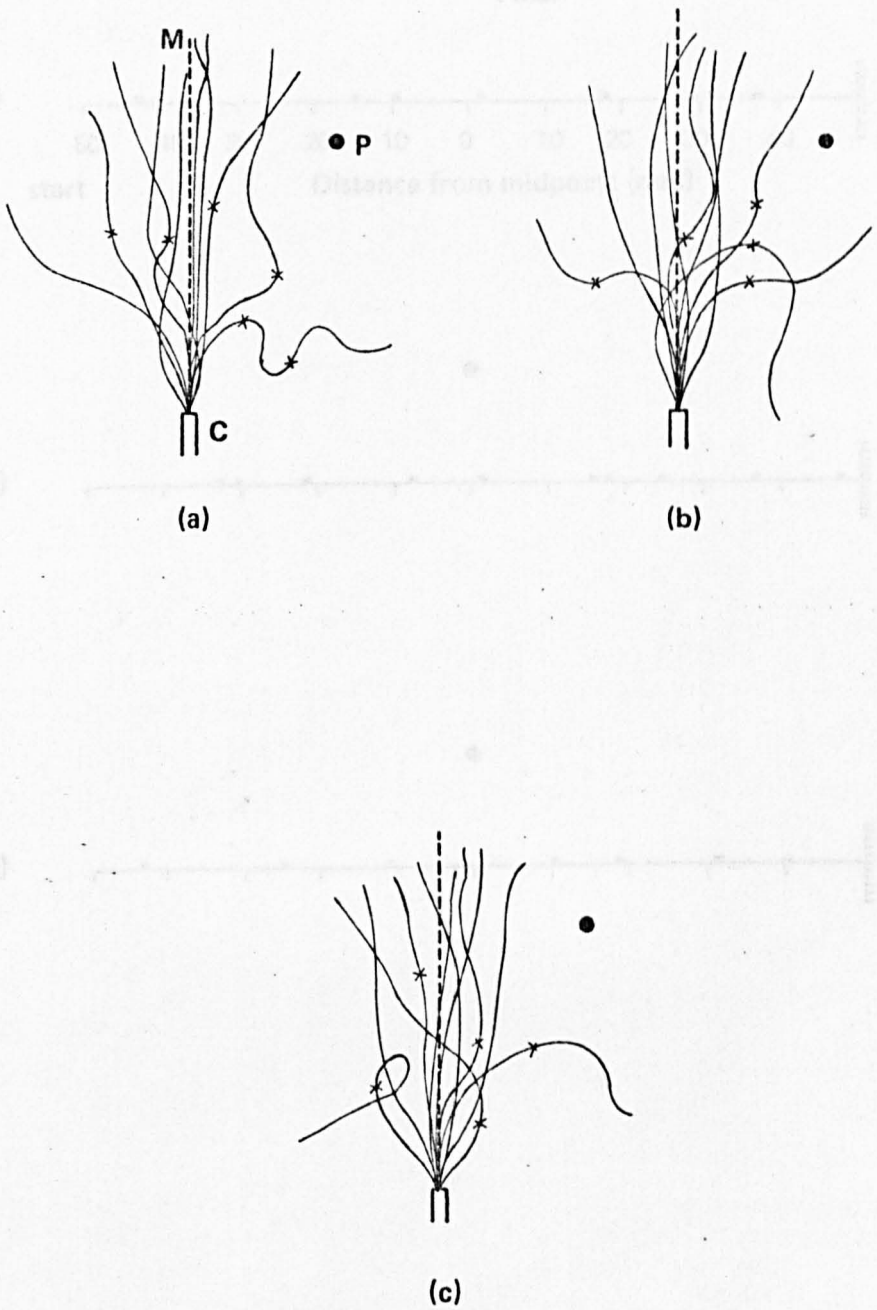


Fig. 75a-c. Experimental conditions as in Fig. 73, except that intensity of incident light 10 Lux.

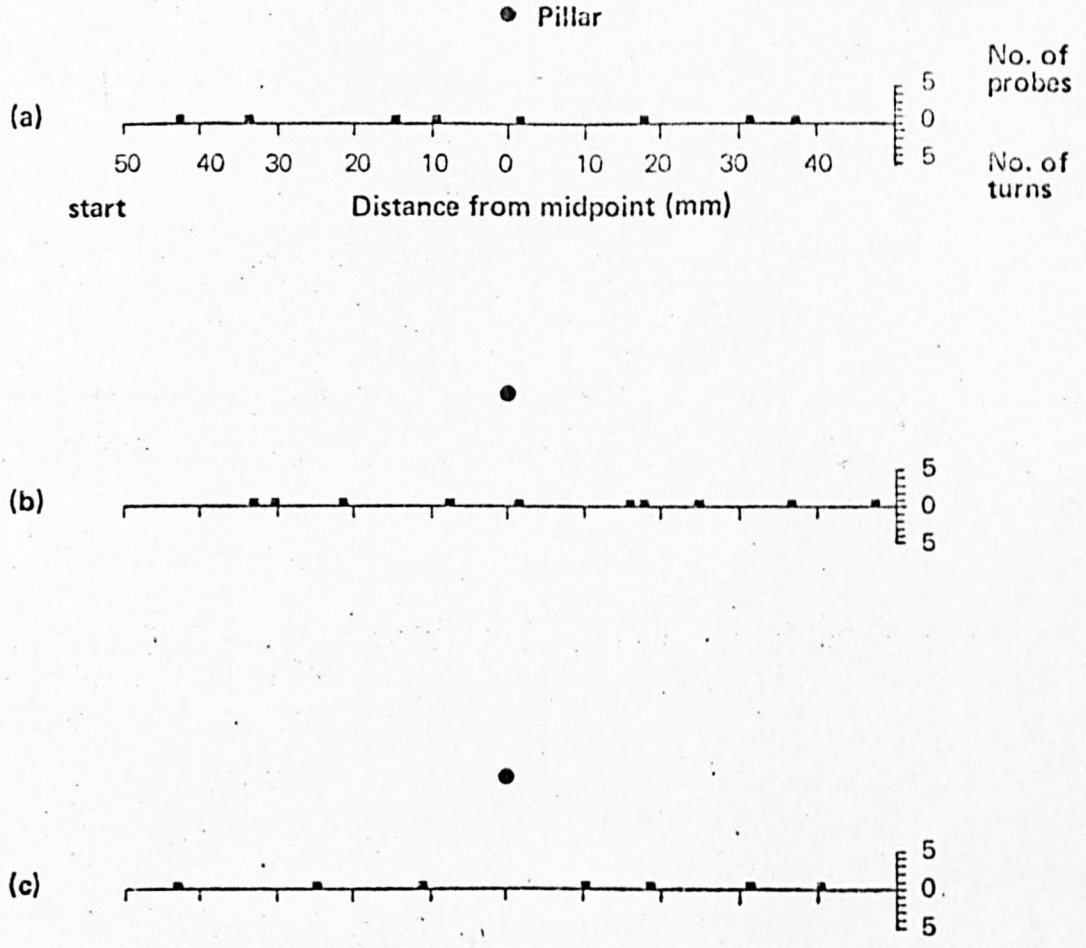


Fig. 76a-c Experimental conditions as in Fig. 74, except that intensity of incident light 10 Lux.