The orientation organs of the hornet

This thesis focuses on a number of orientation organs of the hornet Vi  

esp a orientalis located around the ocelli which, together with  

the latter, comprise part of the hornet’s orientation system. Three ocelli, of which the lateral two have a paraocellar organ attached to each of them, while the medial ocellus bears a coronal suture whose most prominent part, inside, is called the conus. Additionally, there are, on the exterior of the frons and vertex plates, photoreceptor cells, and underneath the plates, there are cilia which are related to the sensory cells of the “Ishay Organ”. This organ is situated underneath the vertex and the frons plates, between the two ocelli and the protocerebrum. The sensory cilia cells are covered by statoliths and a tectorial-like membrane. However, because of the limitations of the preparation and fixation methods for in particular scanning electron microscopy, the tectorial-like membrane appears often as torn away or demolished.

The role of the sensory cells

The sensory cell system is one of the organs of graviception. It is highly sensitive to linear acceleration up to about 0.1 g (Ishay et al, 1989) and to radial acceleration up to 4-5 g. As afore mentioned there are 3 types of cilia with distinct morphology. Although the specific role of each is still unclear at this point, we conjecture that the cilia at the base of the conus and the paraocellar organ are responsible for the detection of linear-horizontal and vertical accelerations. While the cilia on the three periocellar crests probably are responsible for the detection of radial accelerations in all three spatial axes. The sensory information from the “Ishay Organ” is integrated with the input arriving from the peripheral photoreceptors of the frons and vertex. This integration takes place in a special ganglion, near the “Ishay Organ” and is transmitted to the protocerebrum to be further integrated with information coming from the 3 ocelli.

Light absorption by compound eyes and ocelli

As for visual organs intended to absorb light, there are three types, namely, compound eyes (2 of each), ocelli (3 of each) and a large number of extraretinal photoreceptors. The last ones are scattered, both on various regions of the head, as well as on the surface of the body. It is commonly believed that the structure of the compound eye, the ommatidium, enables the detection of a complete image and thus fulfills the normal function of vision. However, the ocellus is constructed to pick up polarized light and also enables seeing in the dark. So, in hornets the compound eye handles the visual needs, while the ocelli serve to locate the direction of the light source and hence is of importance in navigation and orientation. The sensing of dim light and polarized light is also important in the nest where there is relative darkness day and night. Sources of light in the nest are the nest entrance during daytime, the yellow pigment in the adults cuticle, yellow pigment in the larva’s head and the silk of the cocoons, all of which are luminescent and active day and night. In the nest the ocelli might serve for orientation towards
the nest opening, for communication or for various nest activities.

**Micromorphology of the ocelli**

Further investigations on the micromorphology of the ocellus show that the ocellus is composed of numerous functional units. However, essentially each visual unit in the ocellus is comprised of two retinular cells which are joined together at the base by a common rhabdom. The presence of the rhabdom in depth enables vespan sensing polarized light and dim light. In fact, it is a structure typical of a scotopic eye. The dispersal of the pigments (melanin) within the retinular cells promotes the blocking of each unit (in the ocellus) from non-incident light and ensures that each ocellus will respond only to directly incident light.

On the other hand, in the compound eye there is a short conus which transmits light in the direction of the rhabdom, it is composed of an arrangement of 7 retinular cells. Here, the pigment granules are distributed at the bases of the rhabdomeres. Structurally, this can be compared with a photopic eye. Another difference between the simple and compound eyes is that each ommatidium has its own separate cornea, whereas all the ocelli share their cornea. Both, the compound eye and the ocelli are comprised of numerous autonomous units, each of which gives rise to a separate axon. These axons subsequently join to form the optic nerves, one for each compound eye, and one for each ocellus and these ultimately are connected with the protocerebrum.

**Arrangement of the Ocelli in the Hornet’s Head**

The ocelli are situated on the vertex plate in such a fashion that if we draw a straight line through each, we end up with an equilateral triangle (Figs. 1-2). Each ocellus bears a convex cornea shaped as a hemisphere. The tangential planes of each ocellus create in between a pyramid with three equal sides, as shown in Fig. 1. The arrangement of each ocellus on a different plane enables a panoramic visual coverage of practically all the 360° field of vision above and around the head. On our stated assumption that the ocelli pick up polarized light, we surmise that hornets can sense the direction of the sun rays through them. However, to be able to determine the direction and angle of the sun vis-a-vis the zenith which is antipodal to gravity, the hornet needs to orient itself in a position which is absolutely tangential to the earth’s surface. For this purpose, the hornet relies on two organs of equilibrium located at some distance from the two lateral ocelli, and a third, within the coronal suture which extends from the median ocellus. All these elements three are sensitive to linear acceleration.

The two paraocellar organs act like a level with a long arm and between them is the coronal suture, thereby enhancing the sensitivity to every small imbalance (on the part of gravity). With the aid of its equilibrium organs the hornet locates the zenith, while placing itself during flight in a perfectly horizontal position so that it can measure the angle of the sun in respect to the zenith. By way of analogy, we could say that the hornet uses its organs of equilibrium to calibrate its measuring device to the zenith.

**Equilibrium and orientation**

The described system is composed of 3 ocelli and 3 gravity receptors. Such a system has to satisfy two main needs while in flight, namely, equilibrium and orientation. As for equilibrium, there are three axes around which a flying body can move, to wit: roll, pitch and yaw, where roll is the movement around the longitudinal axis of the body, pitch is the movement around the transverse axis of the body and yaw is the movement around the vertical axis.

During hornet flight, which almost invariably takes place in light, the roll movement is mea
sured by the change in the angle formed between the direction of the paraocellar organs and the direction of the gravitational force, as well as by changes in the angle of the conus, Fig.1. The nerve fibers in the conus are oriented parallel to the surface of the earth, while the bobs on the fibers are of course invariably directed downwards, thus indicating the direction of the gravitational pull. On viewing from the outside, what can be deemed a factual change, is that the longitudinal axis of either the flying or walking hornet forms a right angle (90°) with the coronal suture on its frons (i.e. on its face).

As for the pitch movement, each change here results in a change in the orientation in the vespan ocelli vis-a-vis the sun and also changes in the orientation of the paraocellar organs and the paraocellar crest of the lateral ocelli. Finally, with regard to roll movement, this induces changes in the angle between the ocelli and the zenith and that between the gravitic organs and the gravitational force, so a roll to the right causes the left paraocellar organ to orientate more in the direction of gravitation. The right paraocellar organ moves away from the gravitational pull, whereas a roll to the left has the opposite effect.

At the same time, the roll movement is sensed by the median paraocellar organ as well. As for the yaw movement, it apparently helps to retain the existing angle between the gravitic organs and the gravitational pull, while causing change in the angle between the ocelli and the sun.

**Do hornets have a gyro system?**

Is it possible to identify in the Oriental hornet a gyro system? I believe so. Around each ocellus there is a curved, closed canal filled with a liquid, probably hemolymph, and around each canal there is a crista, likewise circular, the mouth of each crista bears a coating of cilia. In the course of rotational movement, a difference is created in the acceleration of the contained hemolympathic fluid vis-a-vis the (solid) crista and its ciliary coating, which results in bending of the cilia in a direction opposite to the rotational movement and thereby to the incipience of radial acceleration.

Insofar, as each of the three crista-equipped ocelli is situated at an inclination of 90° to the other two, it stands to reason that this configuration enables simultaneously determination of the radial acceleration in each of the spatial axes. In fact, each triad of ocellus, canal and crista comprises an independent, self-contained gyro system in which, during flight, the fixed point is situated in the center of the ocellus and determines the linear acceleration of the gravitation which is antipodal to the zenith.

Together, all three ocelli encompass the 360° of spatial panorama and in this respect are analogous to the semicircular canals on both sides of the head of vertebrates, except that in our hornets each ocellus possesses a fully circular canal. The possession of a completely circular canal, apparently, is more advantageous than that of a semicircular canal for insect equilibrium during flight. For example, birds and bats can veer slightly sideways during flight but do not roll over completely as do flying insects attempting to attach to the ceiling. Even in the dark nest the gyro system is apparently operative, mainly to determine the direction of gravity during comb building. In the latter instance the fixed point is determined by the conus in the “Ishay Organ” and the paraocellar organs which are oriented toward the gravitic acceleration which is linear. During comb building, the hornet circles the building site, probably in order to stir and activate the fluid in the gyro system and thereby enable precise determination of the desired direction of building.

**Determination of the zenith**

When the hornet walks in dim or dark surroundings it flips over so that its dorsum and...
the caphalic ocelli are now on the underside and in this fashion the hornet walks on the ceiling which constitutes the zenith. We suspect that in this situation the bond between the ocelli and the gravitic organs is disrupted leaving only the force of gravitation as the dominant factor. The latter are engaged in determining that the nest direction will be toward the gravity detected resultant, while the ocelli in this situation are engaged in other nest mates by their luminescence. As for the hornet’s assessment of the sun’s angle vis-a-vis the zenith, we note that any determination of the zenith is made in the course of rotational movement during ascending flight in the open air. The rate of this rotational movement is at first slow, but it gradually accelerates till the resultant is at the appropriate angle with respect to the angle between the sun and the zenith. In this situation, the radial acceleration, which is measured by the periocellar system, reflects the angle of the resultant vis-a-vis the direction of the gravitational force, which is identical here to the angle of the sun vis-a-vis the zenith. In this situation, also, both sides of the median ocellus are equally lit while the illumination on the lateral ocelli is symmetrical - all this provided the hornet faces the sun.

Orientation and ocelli illumination

When the hornet performs its orientation spin the sun illuminates the ocelli at a varying angle which is dependent on two variables, to wit: (1) the time of the day - in that the earlier or later the hour, the lower the sun’s position in the sky. This means that the more peripheral portions of the lateral ocelli are illuminated along with the central portions of the median ocellus. Whereas the closer the hour to noon is, the more the central portions of the lateral ocelli are illuminated along with the peripheral portions of the median ocellus. (2) the angle of the sun with respect to the zenith. For example, when the sun is in its typical early noon position, its rays impinge on the hornet’s ocelli as the hornet performs its orientation rotatory movement which is counter-clockwise (vide lateral right ocellus in Fig. 3). However as the hornet’s face is directed towards the sun, point A on its right ocellus is illuminated, but as the hornet continues its revolution the point of illumination passes directly through the center of the ocellus to point B which is at 180° to point A. With continuation of the hornet’s rotatory movement to the point of solar illumination it passes through points C and D before returning to point A upon completing one rotation. What we get on the right ocellus, figuratively speaking, is a bow with a single string, where in the angle between the string and an imaginary line transecting the ocellus into an exterior and an interior half is precisely concordant to the angle between the sun and the zenith. (Note that in Fig.3, the lettering pertaining to the ocelli refers either to the early and late hours - the capital letters - or the noon hours - the small letters). Concurrently, movement of illumination occurs also with regard to the left lateral ocellus, except that, now the ocellus remains totally unilluminated throughout the movement from point A to point B (i.e. half of a revolution). The pyramid of the vertex is shading the ocellus, but it starts to be lit on point C and the illuminated point continuous to move towards point D, and then from D back to A. From C to A, as well, one can draw a hypotenuse whose angle vis-a-vis the transector of the ocellus will be congruent with that between the sun and the zenith. Again, at the same time, a similar motion occurs in the median ocellus, only now in the peripheral part of the ocellus. Thus, as we proceed from A to B during the first quarter of the rotation and from B to C during the second quarter we observe illumination of the ocellus but thereafter, during the concluding two quarters of the rotation, there is no illumination of the ocellus. The angle between the hypotenuse drawn between points D and B and an imaginary line transecting the ocellus into front (bottom) and
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back (top) halves is once more concordant with the angle between the sun and the zenith. When the hornet makes its revolution clockwise, the situation is reversed.

The “bee dance” equivalent

In Fig. 3, the path formed by sun rays on the ocellus (right posterior ocellus) is shown as a semicircle with a string in the center pointing to the direction of the sun vis-a-vis the zenith. This circular (or actually semicircular) path bears a resemblance to the circular (and actually semicircular as well) path which a bee follows in the course of the known “bee dance”, whereby the dancing bee transmits information on the path traversed in the field in the way for a food source, intended to recruit other bees to the task of collection (Wilson, 1971).

Of course, in the case of bees, where the combs are vertical, as in the hive of the honeybee *Apis mellifera*, the relevant dance, named the “waggle dance”, translates the direction to or from the sun as the pivotal pathway. In this way movements up or down vis-a-vis direction of the sun, are interpreted as towards or away from gravity. When a bee ‘dances’ at an illuminated site, like the mouth of the hive, or when bees build a horizontal comb, as *Apis florea* does, the relevant dance also becomes a horizontal rather than a vertical one.

In hornets, whose comb is invariably horizontal and the cell outlets face down toward the gravitational force, there is no dance as in bees, but yet the sun rays impinge upon the ocelli in similar fashion. This leads us to speculate that perhaps what the honeybee is actually reconstructing during its dance in the hive proper (vertical) or at the hive entrance (horizontal) is the trajectory of the sun rays upon its ocelli.

The “clock” of the hornet

Where, then, is the ‘clock’ of hornets located? To the best of our knowledge we have to seek for it in the ocelli, which to our mind are the timepiece which lets the hornet know the time of day for as long as the sun is in the sky. By way of explanation the following scenario is offered:

Let us focus on the orientation flight of the hornet, undertaken when it leaves the nest or when it returns to the nest or, at times, also in the midst of regular flight. At that time, the flying hornet faces the sun and in the morning hours, as the hornet rotates counterclockwise, as observable in Fig. 4. Its median ocellus becomes illuminated directly at point (a) subsequently, in the early noon hours (and in the course of its orientation flight), direct illumination of its median ocellus shifts to point (b) and later on to point (c), associated with the late noon hours and finally, toward evening and twilight - to point (d). Note that all the aforesaid pertains also to the two lateral ocelli as well. When the hornet makes its rotation clockwise the situation is reversed, as observable in Fig. 5.

Maturation and first flight movements of the hornet

When a hornet ecloses, it is rather pallid and even its future brown and yellow zones are still pale. This means that the vespan cuticle and perhaps also its sense organ and other organs undergo ‘ripening’ during full maturation of the insect. Neither is the fledgling hornet properly orientated to its environment, so that upon its removal to some distance from the nest, it is incapable of finding its way back. Undoubtedly, for a hornet to fulfill its various tasks, it needs to reach ‘maturity’ in certain functions following its eclosion. Such maturation transpires probably within a few days. In my experience, it is a matter of about five days, during which there is: (1) tanning of the cuticle; (2) maturation of the various sense organs, lending the insect proper orientation to its environment and ensuring that once it leaves the nest it will know how to find its
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way back. My preliminary observations indicate that during the first few days post eclosion, the young hornets venture outside the nest to short distances of several meters only. Their flight during these few days is slow and unsteady, mostly in circles around the nest. It is only gradually that the hornets venture to fly greater distances. I presume that during this interim period the hornet learns to orientate the nest location with the varying direction of the sun in the sky during the changing hours of the day. This learning process is a sine qua non for ultimate orientation of hornets during foraging flights.

![Diagram](https://example.com/diagram.png)

Fig. 1. Scheme showing the location of the ocelli, conus and paraocellar organs on the vertex and frons. Each ocellus is situated on a separate plate, with the angle between the plates being 90°. The three plates thus form a triangular pyramid whose front facet bears the median ocellus and its continuation bears also the frons plate with the coronal suture in its center and behind it the conus and the “Ishay Organ”. At the back of each lateral ocellus there is a paraocellar organ. At the bottom of Fig. 1 can be seen an ocellus with a paraocellar organ behind it. Note that the ocellus is spherical and surrounded by a canal. If one draws an imaginary triangle between the three ocelli, this will be an equilateral triangle with an angle of 60° at each corner.
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Fig. 2. View of the inner sides of the frons and vertex plates. On right, one sees the three ocelli and on the left the conus. The entire surface, barring the ocelli, is covered with hair cells from which protrude the cilia.

Fig. 3. Scheme of the changing trajectory of sunlight on the vespan ocelli during daytime flight. The indicated trajectory corresponds to a counterclockwise rotary movement of the hornet. Capital letters designate the trajectory during the early morning and late evening hours, whereas small letters designate the pattern during the noon hours.
Fig. 4. Scheme depicting the path of the sun rays on the ocelli during daytime hours, with the head of the flying hornet orientated towards the sun. In this situation, the median ocellus is illuminated in symmetrical fashion. As can be seen, the trajectory of the sun rays is from the center in the morning hours to the periphery in the noon hours and back to the center in the late afternoon hours.

Fig. 5. Schematic representation of the vertex with the three ocelli, as it relates to sun direction and the zenith. 1 = sun and 2 = zenith.
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**Summary**

This thesis deals with the structure and the role of the orientation and navigation organs in the Oriental hornet *Vespa orientalis* L. 1771 (Hymenoptera, Vespoidea), with special reference to the ocelli.

The role of the cuticle, acting as a voltaic system providing the energy for the hornet to fly and to navigate has been discussed in chapter 2. The presence of photoreceptors in the cuticular wall with their 3-dimensional appearance and their role in navigation and orientation, have been discussed in chapter 3. The presence of three different types of hair cell structures existing of groups of cilia, around the area of the photoreceptors in the head of the hornet, and their possible role and function in navigation and orientation, as well as their fine structure as far that could be visualized by FE-SEM are discussed in chapter 4.

The main attention in this thesis is given to the role of the ocelli, chapter 5.

The hornet possesses three ocelli, which are situated on the vertex plate. One of those is median and anterior, while the remaining two are lateral and posterior. Each ocellus is covered with a uniform, transparent cornea, which is formed by the corneogenic cells. Underneath the cornea, each ocellus has a single lens composed of an acellular matter.

Further down, below the lens, there are the retinular cells. The arrangement of the latter is such that every two retinular cells create between them, at their deeper parts, the structure known as the rhabdom. This rhabdom is actually formed by the fusion of the membranes of the two adjacent cells. At their upper parts, the two retinular cells are separated by an extension of the superposed corneogenic cell. This separatory extension or process is translucent and serves as a lens that directs and concentrates light toward the deeper lying rhabdom. The retinular cells contain a black pigment which prevents any lateral dispersion of light.

Each rhabdom, with the two retinular cells comprising it, and the corneogenic cell with its extension intruding between the retinular cells, together form an entity analogous to the ommatidium in a compound eye, for which I herein propose the name ocellon.

From each ocellon arises a duplex neural fiber and all the nerve fibers arising from the complete ocellus together comprise the ocellar nerve.

As for the ocellon, its structure is geared for picking up crepuscular light, as does a scotopic eye, and also polarized light. These properties of the ocellon suggest that the ocelli proper have a role in vespan orientation.

The macroscopic structure of the ocelli and their spatial orientation enable the hornet, on the one hand, to determine the sun’s direction during flight, and on the other hand they serve as a clock that lends hornets a temporal orientation.

Returning now to the retinular cell, we note that it is composed of two functional parts, namely, an external sensory portion and an internal neural portion. Between these two parts is located the “neck” of the cell, which passes through the so-called areolar area. The sensory unit creates at its base a rhabdom comprised of the two retinular cells, which are interlinked by a full-fledged desmosome. Microtubuli and microfilaments traverse this region from cell to cell. As already mentioned before, in this upper parts the retinular cells separate to enable intrusion of the process of the corneogenic cell.

Each ocellus is entirely encased in a membrane containing pigmented cells and glia cells. Three ocelli are situated in the vertex plate which is shaped like a three-sided pyramid with a truncated tip. Each side of this pyramid bears one ocellus and of the three sides the anterior one is the longest. Such a configuration of 3 ocelli in fact enables coverage of the entire 360° field of vision, affording a panoramic view.

From the median ocellus, a line descends to the frons plate, forming the coronal suture. In the deepest part of the coronal suture, one
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finds the conus, which is orientated at 90° in- wards to the frons plate. In its interior, the conus shows a complex structure comprised of an envelope of ciliary cells which enclose a system of cords bearing weights. In fact, three types of ciliary cells were encountered in association with the conus. The three types differed morphologically from one another, but whether they also differ functionally remains to be seen.

As for the conus proper it has its inner array of cords which we now recognize as a specialized organ functionally associated with the sensing of gravitation, and we have named this graviceptor the Ishay organ. We have established that all of the frons plate and part of the vertex place are covered with ciliary cells capable of sensing radial acceleration.

In the vicinity of each lateral ocellus is located a structurally unique organ, the so-called paraocellar organ. The organ has at its base ciliary cells, contains a high concentration of Ca-ions and around its middle-setae arranged in rings or circles; structurally it is adapted to sense linear acceleration.

Together the conus with its “Ishay organ”, and the two paraocellar organs have the joint function of determining the angle of each ocellus vis-à-vis the direction of the gravitational force and this at every given moment during hornet flight. This capability figures importantly in vespan determination of the sun’s angle in relation to the zenith. In other words, the hornet flight orientation is achieved by a synthesis of data deriving from the ocelli regarding the direction of the gravitational force. In actuality the vespan flight orientation is accomplished through a stereotypically circular movement of the flying hornet. In the course of this circuitous trajectory, the flying hornet can ascertain the angle of the sun as well as its direction and distance from the nest. Also during such orientation flight, the sun impinges on the hornet’s ocelli, forming a sort of bow with a single string in which the angle between the string and a perpendicular bisecting the ocellus corresponds to the angle of the sun in relation to the zenith, bearing in mind that the zenith is antipodal to the gravitation.

Roughly speaking, this circular flight movement of the hornet and the ancillary string and bow configuration are reminiscent of the waggle dance of the bee, with its orientation towards flowers in the field and the angle between the sun and the field, whose apex indicated the site of the hive.

During flight, the hornet maintains its balance by the use of its equilibrium organs. Specifically, the roll motion is gauged by the paraocellar organs and the conus; the pitch motion by the ocelli, the paraocellar organs and the paraocellar crests (see below) and yaw motion – by the ocelli.

As for the paraocellar crests, these actually function as gyroscopes and consist of a fluid-filled canal encased by a ciliary cells, the whole of which is rather analogous to the semicircular canal in the ear of vertebrates.

Vespan sensing of gravitation (graviception) and sensing of flight (photoreception) are dependent on a suitable temperature level. The maintenance of a steady temperature is relegated in hornets to the cuticle, which acts as an organic semiconductor. At an optimal temperature of 29°C the condition is maximal and the resistance is very low. Under these conditions, the exposure of a hornet to light leads to the appearance of a photovoltaic effect, that is, the accumulation of voltage in the cuticle.

This voltage in the cuticle, coupled probably due to a Seebeck effect, results in cooling or warming of the air in the tracheal loops surrounding in the peripheral photoreceptors. This tracheal air is sucked into the abdominal air sacs, to be blown out, as needed, upon the brood inside the nest. In this fashion, thermoregulation is affected both in the body of the hornet as well as in the entire nest.
Samenvatting

Dit proefschrift behandelt de structuur en de rol van de oriëntatie en navigatie organen in het bijzonder die van de ocelli bij de oriëntaalse hoornaar, Vespa orientalis L., 1771 (Hymenoptera, Vespoidea). De rol van de cuticula, die werkt als een soort accu die de energie leverd voor het vliegen en het navigeren van de wesp, wordt in hoofdstuk 2 behandeld. De aanwezigheid van fotoreceptoren in de cuticula wand wordt besproken in hoofdstuk 3. De aanwezigheid van drie verschillende typen haarcellen, opgebouwd uit groepen cilia, rondom de fotoreceptoren in de kop van de wesp, is elektroonmicroscopisch onderzocht. De mogelijke rol en functie tijdens navigatie en oriëntatie, in samenhang met hun ultrastructuur, wordt behandeld in hoofdstuk 4. De meeste aandacht gaat in dit proefschrift uit naar de ultrastructuur van de ocelli zoals beschreven in hoofdstuk 5.

De wesp heeft drie ocelli of schijnogen, welke geplaatst zijn op de vertex plaat. Eén er van is mediaan geplaatst, de andere twee respectievelijk lateraal en aan de rugzijde. Elke ocellus is bedekt met een uniforme transparante cornea, die door zogenaamde corneogene cellen is gevormd. Direct onder de cornea bevindt zich een enkelvoudige lens met daaronder de retinacellen, die laatste zijn zo gelegen dat tussen twee retinacellen één rhabdium ligt. Dit rhabdium is gevormd door fusie van de membranen van twee naast elkaar liggende cellen. Aan de bovenkant zijn de twee retinacellen gescheiden door een uitloper van de er boven liggende corneogene cel. De retinacellen wijken aan de bovenkant iets uiteen, zodat de uitlopers van de corneogene cel hier tussen passen. Het neurale deel van de retinacel bevat een cellichaam waaruit een axon treedt.

Iedere ocellus is geheel omgeven door een membraan welke pigment en gliacellen bevat. De drie ocelli zijn geplaatst op de vertex plaat die de vorm heeft van een driezijdige pyramidale vorm. De configuratie van de drie ocelli maakt een 360° overzicht en daarmee een panoramische blik mogelijk. Vanaf de mediane ocellus loopt een lijn naar de frons plaat, die de kroonnaad vormt. In het diepste gelegen deel van deze kroonnaad ligt de conus, welke ten opzichte van de fronsplaat 90° naar binnen is georiënteerd. De complexe
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Inwendige structuur van de conus laat een omhulsel van ciliaire cellen zien, dat een systeem van koorden met gewichtjes omgeeft. We hebben eigenlijk drie soorten ciliaire cellen gevonden in combinatie met de conus. Ze zijn morfologisch verschillend, maar of ze functioneel ook verschillend zijn, is op dit moment nog een open vraag.

De eigenlijke conus heeft een intern samenstel van koorden, waarvan we nu denken dat het een speciaal orgaan vormt, dat functioneel geassocieerd is met de detectie van de zwaartekracht. Dit orgaan, de “gravi-ceptor” of zwaartekracht detector, hebben we het “Ishay orgaan” genoemd. We hebben daarnaast gevonden dat de gehele fronsplaat en een deel van de vertexplaat zijn bedekt met ciliaire cellen, die in staat zijn om radiale versnellingen te detecteren.

In de buurt van elke laterale ocellus bevindt zich een qua structuur uniek orgaan, de zogenoemde paraocellus. Dit orgaan heeft aan z’n basis ciliaire cellen die een hoge concentratie aan Ca-ionen bevatten, terwijl rond het centrum setea worden gevonden welke in cirkels liggen. De paraocellus is qua structuur zo opgebouwd dat het lineaire versnellingen kan detecteren. De conus, het “Ishay orgaan” en de twee paraocelli hebben tesamen de functie om de hoek van elke ocellus vis à vis de richting de gravitatie kracht te bepalen, op elk moment tijdens de vlucht van de wesp. De vluchtoriëntatie van de wesp wordt verkregen door samenvoeging van sensorische gegevens van de ocelli met betrekking tot de richting van de zwaartekracht. Dit vermogen om de hoek van de zon te opzichte van het zenith te bepalen is voor de wesp van groot belang.

In werkelijkheid komt de vluchtoriëntatie tot stand door een stereotypisch cirkelvormige beweging van de vliegende wesp. In de loop van deze vliegbeweging, kan de wesp de hoek en de richting van de zon te weten komen, zowel als de afstand tot z’n nest. Gedurende z’n oriëntatievlucht valt het zonlicht op de ocelli, waarbij een soort boog gevormd van één enkele streng, waarbij de hoek tussen de streng en de loodrecht op de ocellus staande bisssectrice correspondeert met de hoek van de zon en het zenith. Vooropgesteld dat het zenith de tegenvoeter van de zwaartekracht is.

Dit rondvliegen van de wesp en de aanvullende streng en boog configuratie doen denken aan de “dans van de honingbij” met z’n oriëntatie ten opzichte van de bloemen in het veld en de hoek tussen de zon en het veld, waarvan de apex de plaats van de korf aan-geeft. Gedurende de vlucht, houdt de wesp z’n balans door het gebruik van verschillende evenwichtsorganen. De rol-beweging wordt gecontroleerd door de paraocellus en de conus; de zijwaardse beweging door de ocelli, de paraocelli en de top van de paraocellus (zie hieronder), en het op koers blijven door de ocelli. De top van de paraocellus werkt als een gyrocooop en bestaat uit een met vloeistof gevuld kanaal dat omgeven is door ciliaire cellen, het geheel is vergelijkbaar met het half-cirkelvormige kanaal in het oor van vertebraten.

De detectie van de zwaartekracht (gravi-ceptie) en die van de vlucht (fotoreceptie) zijn afhankelijk van eengeschikt temperatuurniveau. De handhaving van een vaste temperatuur geschiedt door het cuticulum, dat werkt als een organische halfgeleider. Bij een temperatuur van 29°C zijn de omstandigheden maximaal en is de weerstand zeer laag. Onder deze omstandigheden leidt de blootstelling van de wesp aan licht tot het ontstaan van een foto-voltage effect, er wordt dan elektrische spanning in het cuticulum opgebouwd. Dit voltage in het cuticulum, waarschijnlijk gekoppeld vanwege het Seebeck effect, resulteert in koeling dan wel opwarming van de lucht in de tracheabuizen, die de perifere fotoreceptoren omgeven. De lucht in de trachea buizen wordt in de luchtzakken van het achterlijf gezogen, weer uitgeblazen te worden naar het broedsel in het nest. Op deze wijze wordt de temperatuur geregeld, zowel in het lichaam van de wesp als in het nest.
Vespa orientalis L. 

The compound eyes are the only sensory organs associated with the visual system in Hymenoptera. The eyes consist of 1771 vertex [3 ocelli] and 3 unites. The compound eyes are formed by the fusion of the ocelli and the retina. The compound eyes are sensitive to light and are responsible for the perception of colors and shapes. The corneal region is the outermost layer of the eye and is composed of corneal tissue. The retinula and rhabdom are responsible for the transmission of light information to the nervous system. The ommatidium is the functional unit of the eye and contains the retinula and rhabdom. The retinula is a nerve fiber that transmits the light information to the brain. The retinula is surrounded by a layer of rhabdom that absorbs light information.
Summary

A summary of the text is not provided in the image. The text appears to be in a language other than English, and without proper context or translation, it is challenging to provide a meaningful summary.
waggle dance

Summary

The essence of the dance movements of the parasites and the sensitivity of the host's eyes to these movements. The host's response is mediated by the host's eyes and the parasite's sensory organs. The host's response is further modulated by the parasite's movements and the sensitivity of the host's eyes. The host's response is also influenced by the host's internal environment and the parasite's parasitic lifestyle.

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Curriculum vitae

Eyal Rosenzweig was born 03-07-1960 in Petah Tiqva, Israel to Haim and Hela Rosenzweig; both were born in Poland and immigrants to Israel. Education was received at the Brener primary school and the Kalay high school both at Givataim. After military service (1978-1981) in the Israeli army, he started his medical education at Timisoara in Romania and graduated as an MD in 1988.

From 1989-1990 he was an intern at the Assaf Harofe Hospital in the Tel Aviv area and from 1990-1995 a residence in the Ear, Nose and Throat (E.N.T.). Department of the Tel-Hashomer Medical Center. Since 1996 he is a senior physician specialist at the E.N.T. and Head and Neck surgery Department at Tel-Hashomer Medical Center.

E. Rosenzweig has published close to 20 papers in international scientific journals. He was elected chairperson at the COSPAR Scientific Assembly at Birmingham (U.K), July 1996 and has participated in several international congresses. Currently he is involved in orientation and navigation research of hornets and furthermore in teaching ENT to medical students at the Medical School of the Tel-Aviv University.

E. Rosenzweig is married and father of three children.