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Neural correlates of symbolic communication in the honeybee dance

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The honeybee can communicate the distance and direction of a food source to its hive mates via a ritualized dance. As far as is currently known, the symbolic nature of this honeybee communication is second only to that of humans. It is currently unknown how the signals contained within the dance are translated into neural activity within the brain of the observing bee. The goal of this proposal is to determine where and how the perception of the dance is encoded within bee brain, and where and how the memory of the information portrayed in the dance is stored. An artificial bee that mimics the dance patterns will be used to stimulate a live, restrained bee while electrical recordings are made from neurons within its brain.

Neural correlates of symbolic communication in the honeybee dance

The honeybee is the only non-human species known for certain to symbolically communicate information displaced in both space and time to other individuals. A bee that has discovered a food source can communicate its direction and distance to other bees in the hive via the honeybee dance to recruit them to the food source. The dance is performed on a vertical plane within the hive, and includes a phase called the wagging run. The angle of the wagging run relative to vertical describes the direction of the food source relative to the sun's azimuth, and the frequency of wing vibrations and duration of the wagging run describe the distance of the food source from the hive. Bees use the sun as a navigational aid during flight and they use optic flow to gauge the distance they have flown. In the darkness of the hive, follower bees closely follow and align with the dancer during the wagging runs. During the wagging run, the dancer generates so-called near-field sound by vibrating her wings. Bees sense both near-field sound and their orientation in gravity via Johnston's organ on their antennae. Near-field sounds carry information about the frequency of wing vibrations and duration of the wagging, which in turn carry somewhat redundant information about the distance to the food source. Gravity sensation tells the bee its orientation relative to vertical, and hence the direction of the food source relative to the sun's azimuth.

The goal of this proposal is to examine how and where information about food source distance and direction is encoded and stored in the brain of the dance follower.

1. I propose that there exists a population of neurons tuned to various ranges of near-field sound frequencies, and that there also exists a population of neurons tuned to various ranges of orientation relative to vertical, as reported by gravity sensation. This will be investigated by stimulating with near-field sound of varying frequency and various bee orientations relative to vertical, while performing electrophysiological recordings from areas of the brain to which Johnston's organ projects.

2. I propose that persistent neural activity is used by the dance follower honeybee to retain in working memory the distance and direction information portrayed to it during the honeybee dance. This will be investigated by examining where the sensory encoding cells described above converge in their projections. Candidate areas of brain will be recorded from during stimulation, as above. I expect to find memory cells that continue encoding distance and direction information even after stimulation ceases. I expect that electrical manipulation of these cells should result in a discernable change in behaviour in subsequently released bees.

A mechanical model of a dancing bee (Michelsen 1992) will be used to communicate distance information to a restrained bee. Extracellular electrodes will be used when searching for the desired cells, while intracellular electrodes will be used to more precisely characterize, locate (via injection of fluorescent dye), and manipulate the cells. Visualization of cells will be done under confocal fluorescence microscopy. Most cells in bee brain are individually identifiable. This will ease the burden of a systematic search for cells with specific physiology.

The honeybee

A marvelously adapted organism, the honeybee has a multitude of fascinating characteristics packed into a body only 1.5 cm long. Bees are sensitive to the diurnal changes of the earth's magnetic field, and concentrations of magnetite have been detected within the bee (Kirschvink, 1981; Martin & Lindauer, 1973). Bees have trichromatic vision (Daumer, 1956), including the ability to detect UV light (Kuhn, 1927). Under UV light, flowers look like targets with radially emanating lines pointing towards a dark centre (Gould & Gould, 1988). Foraging bees orient themselves relative to landmarks and to the sun (von Frisch, 1967). Bees can detect the polarization of light, and when the sun is obscured by clouds, they can use polarized light from patches of blue sky to calculate the position of the sun (von Frisch, 1949). Even at night, bees can use their internal clock, kept accurate by diurnal geomagnetic changes, to calculate the position of the sun below the horizon. Bees use a measure of their optic flow to throttle flight speed in constrained spaces and in preparation for landing, as well as a means of measuring distance flown (Srinivasan et al., 2000). Furthermore, bees exhibit not only Pavlovian and operant conditioning, but also more complex abilities, such as contextual learning and categorization (Giurfa, 2003). All of this is orchestrated by a brain of about 960,000 neurons packed into a volume of about 1 mm³ (Menzel & Giurfa, 2001), orders of magnitude smaller than any mammalian brain.

The honeybee dance

Perhaps most remarkable of all is the honeybee's ability to communicate the distance and direction of a food source to other bees within the hive, via a ritualized dance. Although the honeybee dance does not have syntax or grammar and is therefore not a language *per se*, it is nevertheless a form of symbolic communication between individuals whose message is displaced both in space and time from what it describes. This makes the honeybee the only non-human species currently known to naturally communicate with such versatility.

The honeybee dance is best studied in the European honeybee *Apis mellifera*, introduced worldwide for the purpose of raising honey. The dance is performed on the vertical plane of the beehive by a foraging bee which has returned from successful collection of nectar from a food source. The food source is typically a patch of flowers, or during behavioural experiments, a bath of sugar water. In its broadest form, the dance consists of a repetitive pattern of motion reminiscent of a figure of eight turned on its side, with the dancer facing her direction of motion. Superimposed on top of this, the dancer "wags" her abdomen during the central phase of the figure of eight pattern (Figure 1a). This central phase is called the wagging run, and the frequency of wagging can vary from about 20 to 30 Hz. The other phase of the dance, during which no wagging occurs, is called the return run. The direction of the return run alternates left and right as the bee follows the figure of eight pattern. Other bees typically surround the dancer while the dance is taking place. Some of them sit idly by (dance attenders), while others actively follow the dancer during the wagging run (dance followers). After the dance has been repeated a number of times, one of the dance followers may vibrate the hive floor with her legs. The dancer then stops and regurgitates some of the food she has collected from the food source, allowing the follower to sample it. The follower then typically leaves the hive and flies to the food source from which the dancer collected the food.

Karl von Frisch was the first to notice relationships between certain aspects of the dance, and the distance and direction of the food source being advertised by the dancer (von Frisch, 1967), work for which he shared the Nobel prize. He discovered that the angle relative to vertical at which the dancer performs the wagging run correlates closely with the angle between the projection of the sun's position onto the horizon (the sun's azimuth) and the direction of the food source from the hive. For example, if the food source is located 20° to the left of the sun's azimuth, the dancer rotates her figure of eight dance pattern such that the wagging run points 20° to the left of vertical (Figure 2). What's more, as the dancer continues to perform her dance over time, the angle of the wagging run relative to vertical precesses counterclockwise by precisely the right amount to offset the clockwise motion of the sun's azimuth. Thus, at any point in time the direction to the food source is accurately described by the angle of the dance relative to vertical. Furthermore, von Frisch discovered that the duration of the dancer's wagging run varies linearly with the distance to the food source (Figure 1b).

Because the direction and duration of the wagging run can be varied independently by the dancer, she can independently, yet simultaneously, communicate both the direction and distance of the food source relative to the hive. Since any position on a two dimensional plane is fully described by the values of two independent variables, and by adopting a polar coordinate system with the hive at its origin, the bee is capable of communicating any desired location in two dimensions. Studies have shown that bees do not communicate the height of a food source (von Frisch, 1967).

Skeptics suspected that the honeybee dance is only a way for dancers to capture the attention of other bees in the hive. They argued that there is no clear evidence that follower bees make any use of the information contained within the dance, that they might instead rely exclusively on their sense of smell, matching the scent of the food source on the dancer's body with that of the food source out in the field (Wenner, 2002). Further experiments involving a mechanical model of a dancing bee disproved this alternate hypothesis by showing that followers could find the advertised food source, even though the "dancer" had never visited the food source (Michelsen et al., 1992). A general consensus has emerged that bees use the direction and distance information contained in the dance to guide them to the vicinity of the food source, but after flying the specified distance in the specified direction, they turn to their sense of smell to ultimately pinpoint the food source.

Modality of dance perception

The hives of *Apis mellifera* are enclosed. This means that the dance is performed in complete darkness and follower bees cannot rely on their visual systems to perceive the dance (dance behaviour is traditionally observed by investigators under red light, to which bees are blind). The dancer generates no audible sounds during the dance, and conditioning studies have shown that bees are deaf. The precise modality of information transfer was therefore uncertain. Perhaps information transfer occurs through physical contact between the dancer and the follower, or perhaps the dancer induces vibrations in the "dance floor" which the followers can then feel. The former hypothesis is weak, in that dancer and follower are in physical contact for only brief

periods of time (Michelsen, 2003). The latter hypothesis was disproved by showing that any substrate vibrations generated by the dancer are below the perceptual threshold of bees.

More recent work has shown that the dancer vibrates her wings during the wagging run (Michelsen et al., 1987). These wing vibrations range in frequency from 200 to 300 Hz, and are delivered in pulses of 22 to 35 Hz. Although these wing vibrations do not generate what most animals perceive as sound, they do generate high velocity air-particle oscillations in close proximity to the dancer, so-called near-field sound. Near-field sound falls off quickly with distance, typically going to zero within a fraction of a wavelength of distance from the source. Near-field sound is responsible for the sensation of “feeling” sound in one’s chest, especially if one is close enough to the source (such as a loudspeaker) and if the sound is of low enough frequency (i.e., long enough wavelength). Although deaf to far-field (pressure wave) sound, bees can be conditioned to respond to near-field sound, and the intensity of the near-field sound in the area behind the dancer falls well above their perceptual threshold (Kirchner et al., 1991). Thus, near-field sound is a viable mode of information transfer from dancer to follower.

Further work has revealed that the frequency of the dancer’s wing vibrations during the wagging run, and hence the frequency of the near-field sound generated during the wagging run, varies inversely with the distance to the food source (Spangler, 1991). There is now a general consensus that near-field sound is the primary modality for information transfer from dancer to follower. It has also been accepted that there is redundancy in communication of distance information: both the duration of the near-field sound (which corresponds to the duration of the wagging run as well as the number of wags) and the frequency of the near-field sound describe food source distance. In addition to generating near-field sound, dancer wing vibrations have been shown to also generate jets of air behind the dancer (Michelsen, 2003). Jets of maximum velocity are located directly behind the dancer and fall off smoothly in either direction. It is thought that this velocity profile of air jets allows dance followers to accurately line themselves up with the dancer. This arguably allows the follower to better determine the direction of the wagging run relative to vertical since all that she must do is monitor her own orientation relative to vertical, information she can obtain from her perception of gravity. This line of reasoning is supported by evidence that follower bees are most reliably recruited to the food source when they line up closely with the angle of the dancer (Michelsen, 2003).

Anatomy of dance perception

Bees detect near-field sound via Johnston’s organ, an internal chordotonal organ (i.e. an organ responsive to vibrations) located in the pedicel (base) of the bee’s antenna, which consists of a cluster of sensilla (Figures 3 and 4) (Dreller & Kirchner, 1993). More precisely, Johnston’s organ detects the linear mechanical deflection of antennal movements to near-field sound (Kirchner, 1994). Johnston’s organ has also been implicated in gravity perception (Jeram & Pabst, 1996).

Most investigations of the honeybee nervous system focus on vision and olfaction. Little work has been done to characterize the representation of near-field sound stimuli or gravity perception within the brain of the honeybee. What is known is that antennal mechanoreceptors, including Johnston’s organ, project to three brain areas: the median posterior protocerebrum (MPP), the

lateral posterior protocerebrum (LPP), and the dorsal lobe (DL, also called the antennal mechanosensory and motor center or AMMC) (Maronde, 1991; Homberg et al., 1989; Gewecke, 1979) (Figure 5). All projections remain ipsilateral.

Project hypotheses and experiments

This project will attempt to discern how and where the food source distance and direction information contained in near-field sound stimuli and gravity sensation from Johnston's organ are encoded and stored in the brain of the honeybee dance follower.

Sensory coding

Populations of neurons selectively tuned to ranges of specific features of sensory stimuli have been found across the whole spectrum of animal species, from insects to mammals. Examples include visual cells tuned to specific ranges of stimulus orientation (Hubel & Wiesel, 1959), and auditory cells tuned to specific ranges of sound frequency. **I propose that there exists a population of neurons tuned to various ranges of near-field sound frequencies (Figure 6), and that there also exists a population of neurons tuned to various ranges of bee orientation relative to vertical, as indicated by gravity sensation.** Thus the population responses of such sensory cells would implicitly encode the food source distance and direction information contained in the wagging run.

Captured bees will be mounted vertically and will have their antennae stimulated with near-field sound generated by a mechanical bee constructed and programmed to mimic the honeybee dance as closely as possible (Michelsen et al., 1992) (Figure 7). The mechanical bee will be placed directly in front of and in line with the mounted bee. Extracellular electrophysiological recordings will be used to search the LPP, MPP, and DL for neurons that show a response to the stimulus. Once responsive neurons are found, the mechanical bee will be programmed to generate dance patterns corresponding to a wide range of food source distances via the full spectrum of wing vibration frequencies. If a neuron is found that selectively responds to a certain range of frequencies, its position will be noted and further characterized in subsequent individuals via intracellular sharp electrode recordings. Most neurons in bee brain are individually identifiable (Menzel & Giurfa, 2001). This eases the difficulty of mounting a systematic search, because it can be performed across multiple individuals. The cell will be filled with fluorescent dye and imaged. The frequency tuning of the cell will be compared across individuals. It is likely that the cell will exhibit the same physiology, i.e. the same frequency tuning, across individuals. If sensory coding in other animals can be used as a guide, then on-response, off-response, tonically responding, and phasically responding cells might all be discovered.

A similar experiment will be performed in search of cells tuned to specific positions of bee orientation relative to vertical, although this may prove to be more difficult to accomplish and is therefore only a secondary goal. The setup will be as above, but with the bee held at different orientations relative to vertical. The difficulty will lie in rotating the entire setup with the recording electrode still in the brain. The frequency tuned cells described above will be recorded from and monitored for any modulation of their response as a function of bee orientation.

Otherwise, a search will be undertaken for a population of cells that specifically tune for different ranges of bee orientation angles. As above, first extracellular, and then intracellular recordings will be performed and on-response, off-response, tonically responding, and phasically responding cells might all be expected.

Memory trace

The dance follower must have some way of retaining the distance and direction information communicated to it during the dance. Arguably, this requires some form of working memory. The information is useful to the bee only from the time that it leaves the hive to the time that it has flown to the advertised location, at which point it can “forget” the distance and direction information and switch to olfaction to pinpoint the food source (there is likely a separate parallel system in place that allows the bee to find its way back to the hive). Although it is possible that distance and direction information could be stored via changes in synaptic strengths, such changes would perhaps be more permanent than need be. Recently, neurons in monkey prefrontal cortex have been found whose firing rates not only correlate with stimulus frequency, but continue to do so even after the stimulus is removed (Romo et al., 1999). This so-called monotonic stimulus encoding is thought to be a neural correlate of working memory for one dimensional variables. **I propose that monotonic stimulus encoding is used by the honeybee dance follower to retain in working memory the distance and direction information portrayed to it during the honeybee dance.**

The projections of the frequency and direction tuned sensory coding cells described above will be examined, and areas of convergence that might be candidate locations for memory encoding cells will be identified. Extracellular recordings will be used to search these convergent areas for cells that not only respond to near-field sound frequency or bee orientation, but continue to respond in a discernable manner even after the stimulus is removed. How will direction coding memory cells know when to stop “listening” to bee orientation encoding cells, which are likely always reporting the current orientation of the bee? Perhaps the orientation encoding cells only report their value to direction coding memory cells in conjunction with near-field sound stimuli generated during the wagging run, the exact time at which the follower needs to take note of its orientation. It is thought that repetition of the wagging run allows the follower to more accurately gauge the information being conveyed by the dancer by averaging the stimulus encountered over many wagging runs (Michelsen, 2003). While recording from a putative memory encoding cell, one would expect to see its encoded value fluctuate somewhat after each wagging run by the mechanical bee, but eventually settle down on an average value. The counterpoint to this will be tested by abruptly changing the distance or direction value portrayed by the mechanical bee after several wagging runs at the original value. I expect to find that the firing rate of the memory cell that had settled down will begin changing again as it factors in this new stimulus value into its average firing rate.

Again, once memory encoding cells are found via extracellular recordings, intracellular electrodes will be used to further characterize and visualize such cells. Memory encoding cells may or may not be individually identifiable, depending on whether they fall within or outside of the mushroom bodies, whose cells typically are not individually identifiable (Menzel & Giurfa, 2001). If the memory encoding cells are individually identifiable, a further experiment can be

undertaken. To demonstrate that the memory encoding cells drive behaviour, a bee is caught and temporarily disabled. A small incision in the head capsule is made and an identified cell encoding direction memory is impaled by a sharp electrode, according to external landmarks (this may take some trial and error). The bee will be stimulated with the mechanical bee with a certain pair of distance and direction values, referred to as location 1. The firing rate of the direction memory encoding cell will be recorded. The bee will then be stimulated with the same distance value but with a different direction value, referred to as location 2. Sugar water feeders will be placed at both locations 1 and 2 (this will require large indoor surroundings, perhaps opposite ends of a long hallway with the laboratory in the middle). As a control experiment, the bee at this point is released (its incision is sealed with wax), and it should be found that, with statistical significance, the bee is caught at location 2 more often than at location 1. The experiment is repeated (either with the same bee or a new one), but this time after being stimulated with location 2, the direction memory encoding cell is depolarized or hyperpolarized, whichever is appropriate to bring its firing rate back to the value it had during stimulation of location 1. Persistent neural activity, such as is implicated in working memory, can be manipulated by transient inputs (Seung et al., 2000). Therefore, the memory encoding cell should retain its modified firing rate even after electrode stimulation ceases. Upon release, the expected result this time is that the bee is caught at location 1 more often than at location 2, thus demonstrating that the memory encoding cell drives behaviour. Note that multiple memory cells may need to be manipulated to induce a noticeable change in behaviour, making the experiment technically much more difficult.

Methods

Bees are prepared for recording as described previously (Iwama & Shibuya, 1998). A foraging worker bee is caught at a hive entrance and temporarily immobilized by chilling at 4°C. The bee is mounted in an aluminum tube. The head is held in position with wax. The head capsule is opened and bee saline is added regularly to keep the exposed brain from drying out. Muscles are removed as needed to prevent brain movement. During the release experiments, the muscles will have to be temporarily disabled without affecting neuronal behaviour. This may be possible by local warming of the head while the rest of the body is kept immobilized by chilling.

The mechanical bee model is as described elsewhere (Michelsen et al., 1992) (Figure 7). Briefly, the model is made of brass coated with beeswax, with a razor blade to mimic wings. It is the same size and shape as a bee. The model is connected via a rod to a stepper motor and an X-Y plotter which control the wagging motion and the figure of eight pattern of motion respectively. An electromagnetic driver vibrates the wings. The mechanical bee is fully controlled by computer and its behaviour is recorded in conjunction with a time stamp.

Tetrode electrodes will be used for extracellular recording. Tetrodes can record cells from up to 140 μm away (Henze et al., 2000), making them useful for quickly searching a large volume of brain for cells with specific responses. Electrode position will be marked by passing a lesioning current. Glass capillary sharp electrodes will be used for intracellular recording, electrical stimulation, and fluorescent dye injection. Continuous recordings will be digitized via an analog to digital converter and stored on a personal computer with the same time stamp used for control of the mechanical bee. A cell of interest injected with a fluorescent dye such as lucifer yellow

will be visualized under confocal fluorescent light microscopy. Because of its small size, semi-intact fresh brain can be visualized under the microscope. If the target cell is too deep within the tissue to be adequately viewed, thick tissue slices will be made. To ease its reconstruction, it is desirable to keep the entire cell within a single slice if possible.

Future investigations

The lifespan of a worker bee is typically about 5 weeks. During this time, the responsibilities of a worker bee change. First, she cleans out empty cells in the hive, then, she tends to larvae. Soon, she is collecting food from foragers and storing it in cells. Next, she guards the entrance to the hive. Only after about 3 weeks of age does a worker bee leave the hive for her first orientation flight around the hive. A day or so later, she begins to forage for food and hence participate in and follow the honeybee dance. Future work could examine whether stimulus and memory encoding cells exist and function in less mature worker bees that have yet to begin foraging, in the same way that they do in mature foraging worker bees.

It has been shown that follower bees can correctly interpret the dance even when they are not directly lined up behind the dancer, but off to either side by up to 15° (Michelsen, 2003). Future work could examine the coding of food source direction when follower and dancer are not in line. This would likely involve searching for a neural mechanism that calculates the orientation of the dancer during the wagging run by subtracting the relative angle between the dancer and the follower from the follower's orientation relative to vertical, as determined by gravity sensation.

This proposal focuses on sensory afferents from Johnston's organ. However, there exist various other organs, such as hair plates between the head and thorax, which are also implicated in gravity perception. Future work could examine the contribution of these organs to the coding of bee orientation relative to vertical.

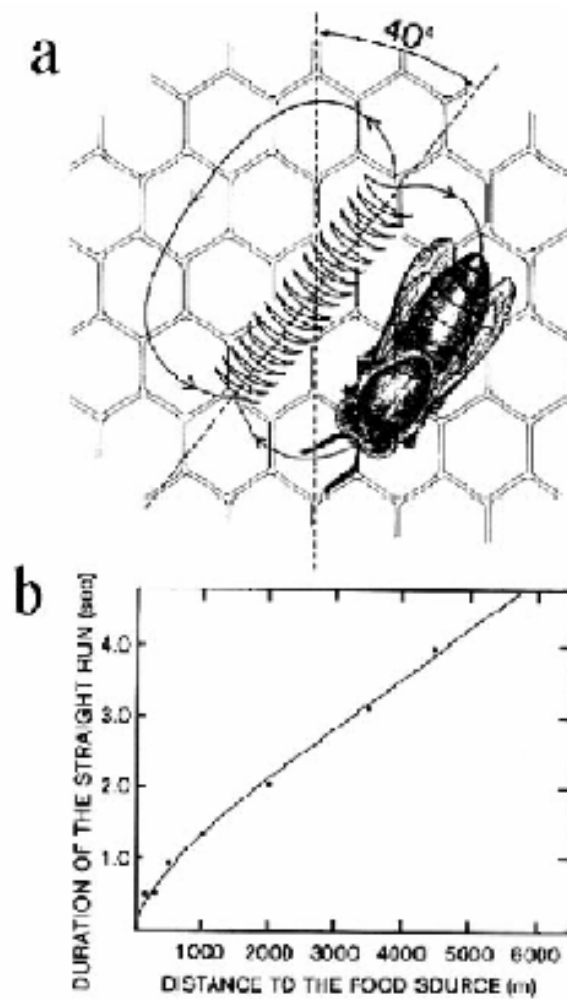
As the recruited dance follower is flying out to the advertised food source, she must keep track of the distance she has flown. It is conceivable that the value of the bee's optic flow "odometer" is constantly being compared to the target distance stored in working memory, and that when the two values are equal, a change in flight behaviour is triggered, from long distance flight to a searching flight pattern with greater activity of the olfactory system. The mushroom bodies in the insect brain are a centre for multimodal integration (Menzel & Giurfa, 2001). Perhaps this comparison of optic flow information with near-field sound memory trace occurs in the mushroom bodies during flight to the food source. This might be investigated with a mounted bee in a laboratory environment by first stimulating the bee with the appropriate dance, and then presenting it with optic flow from a fly visual stimulation system such as *FliMax* (Lindemann et al., 2002). A bright light could be used to simulate the sun. When the bee has been "flown" the appropriate distance, one might expect to see a change in wing muscle activity in conjunction with a neural event in the mushroom bodies.

Perhaps the redundancy in the information describing food source distance (wagging duration, number of wags, frequency of wing vibrations) is not as redundant as is thought. These apparently redundant aspects of the dance might separately describe the optic flow experienced

by the dancer on her return flight to the hive in different parts of her field of vision. Since sky is usually above the bee and ground below, the ratios of optic flow of different parts of the visual field may in a natural setting stay generally constant, and therefore their description in the dance appears to be redundant. Behavioural studies could be performed that manipulated the level of optic flow experience by a forager in different parts of its visual field during her return flight to the hive. This could be accomplished by placing the bee in an artificial environment (such as the patterned tubes used by Srinivasan et al., 2000), and then monitoring how or if the apparently redundant characteristics of the dance varied.

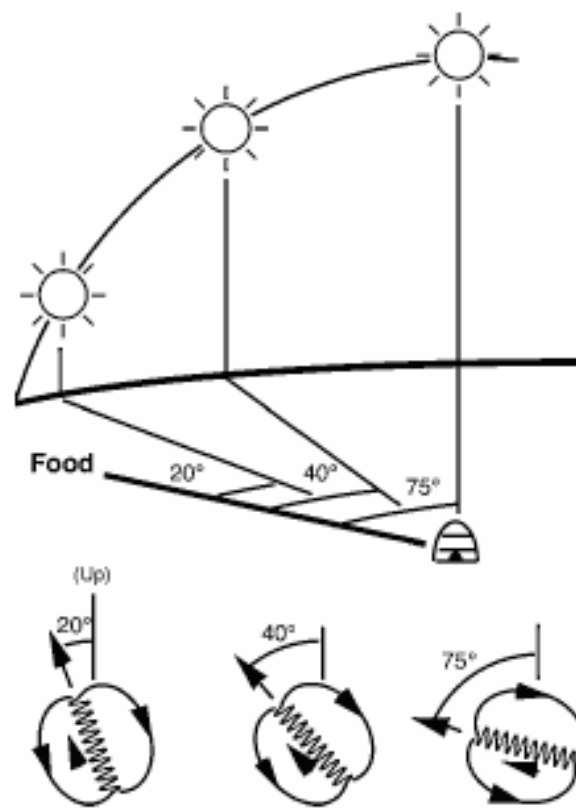
When the hive grows overpopulated and it is time for some of the hive to separate and form a separate hive, individual bees fly off in search of an ideal new nesting site. When a bee finds a potential site, she returns to the hive and performs a dance similar to that described here. It typically takes about 48 hours of nonstop activity before all of the bees come to a consensus and suddenly leave the hive in a swarm. The neural correlates of honeybee communication in swarming behaviour would be a ripe area of investigation.

Figure 1



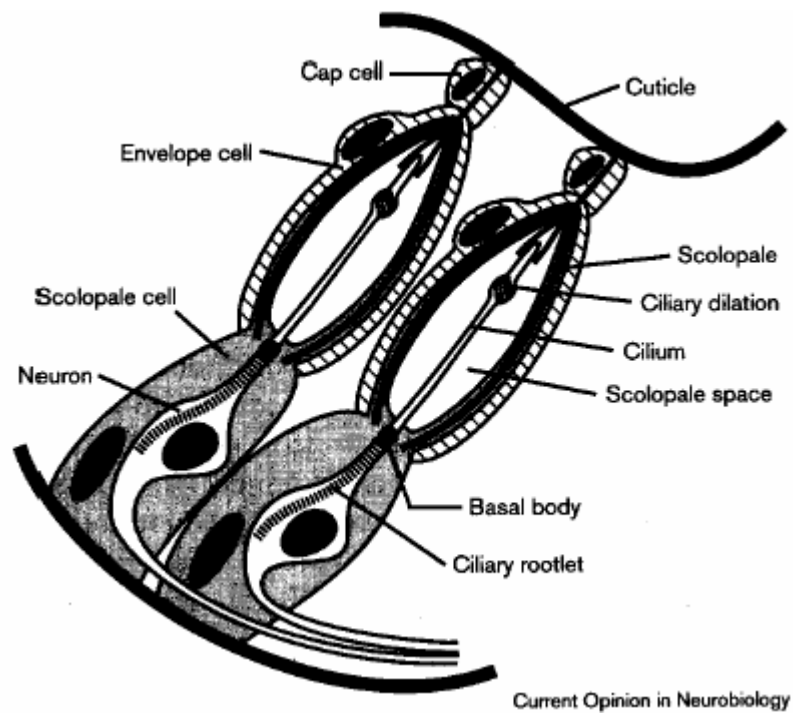
A: The bee wagging dance. The bee is shown during the return run of the dance. B: The correlation of wagging duration with food source distance. From Dyer, 2002.

Figure 2



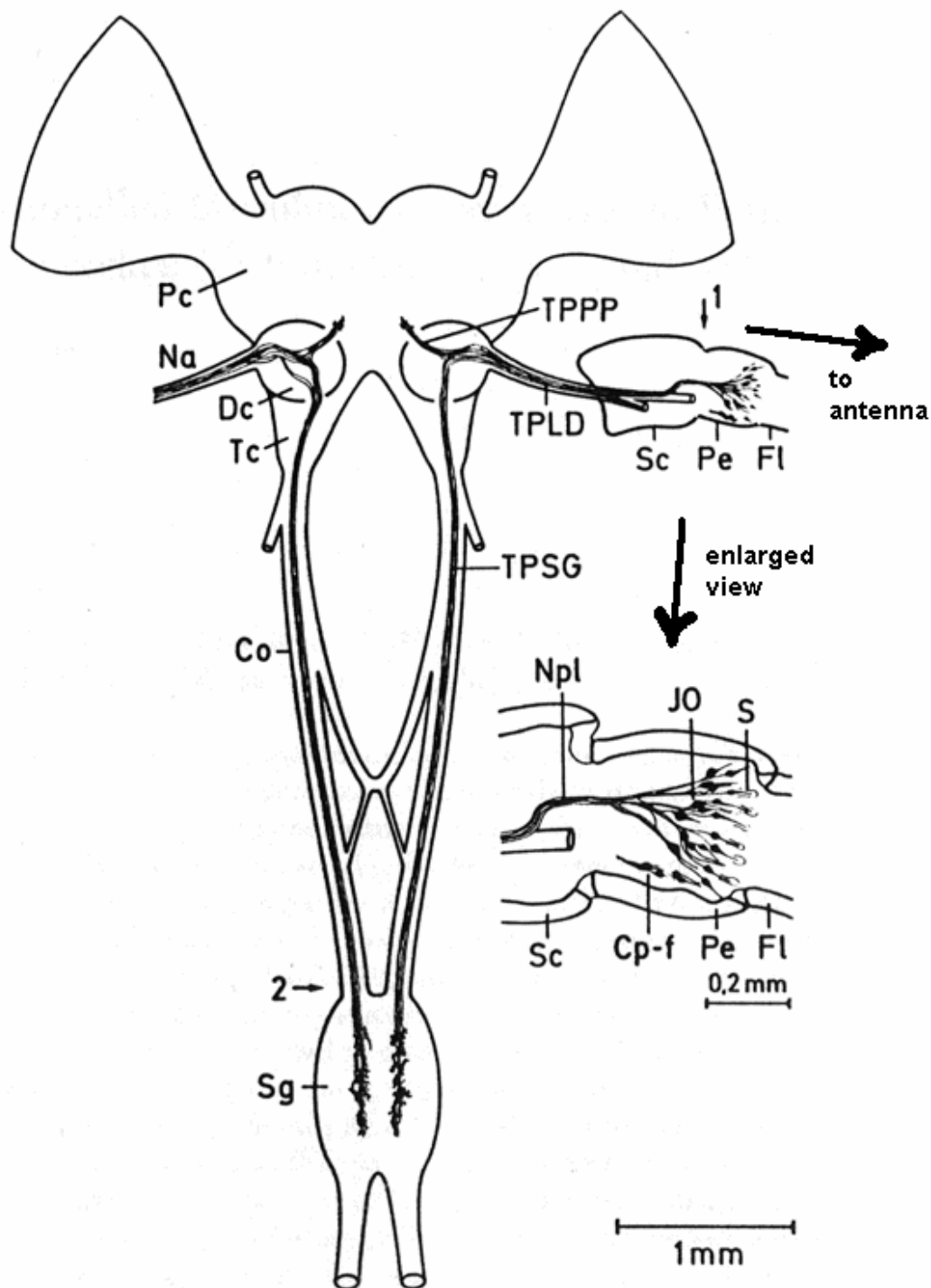
The angle between food source location and the sun's azimuth corresponds to the angle of the wagging run relative to vertical. From Dyer, 2002.

Figure 3



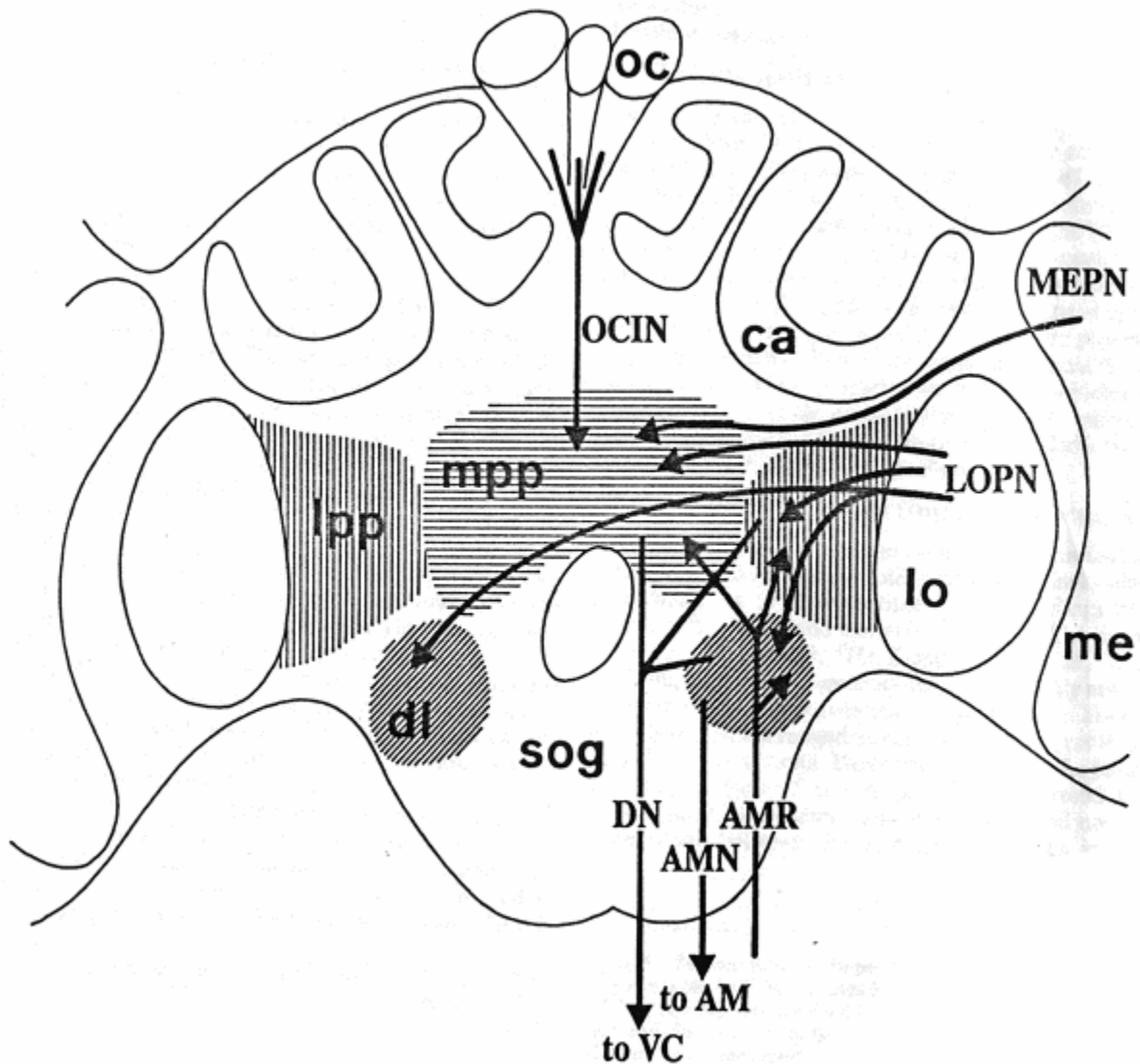
General structure of Johnston's organ. From Eberl, 1999

Figure 4



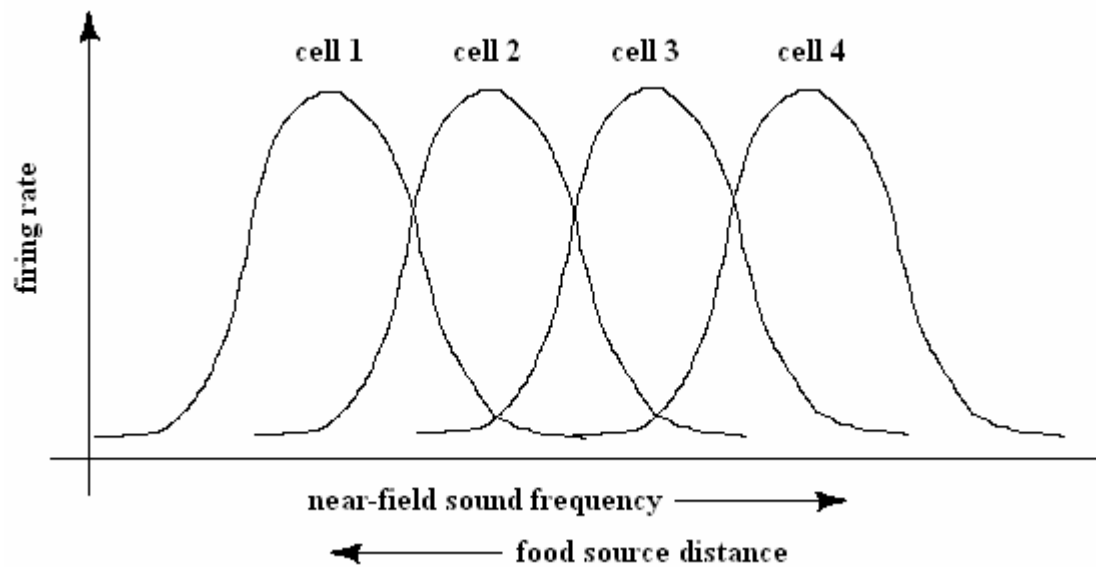
Schematic frontal view of *Locusta migratoria* showing the location of Johnston's organ (JO) in the pedicel (Pe) of the antenna, near its base. The sensilla (S) of Johnston's organ, which detect the actual vibrations, are shown. Adapted from Gewecke, 1979.

Figure 5



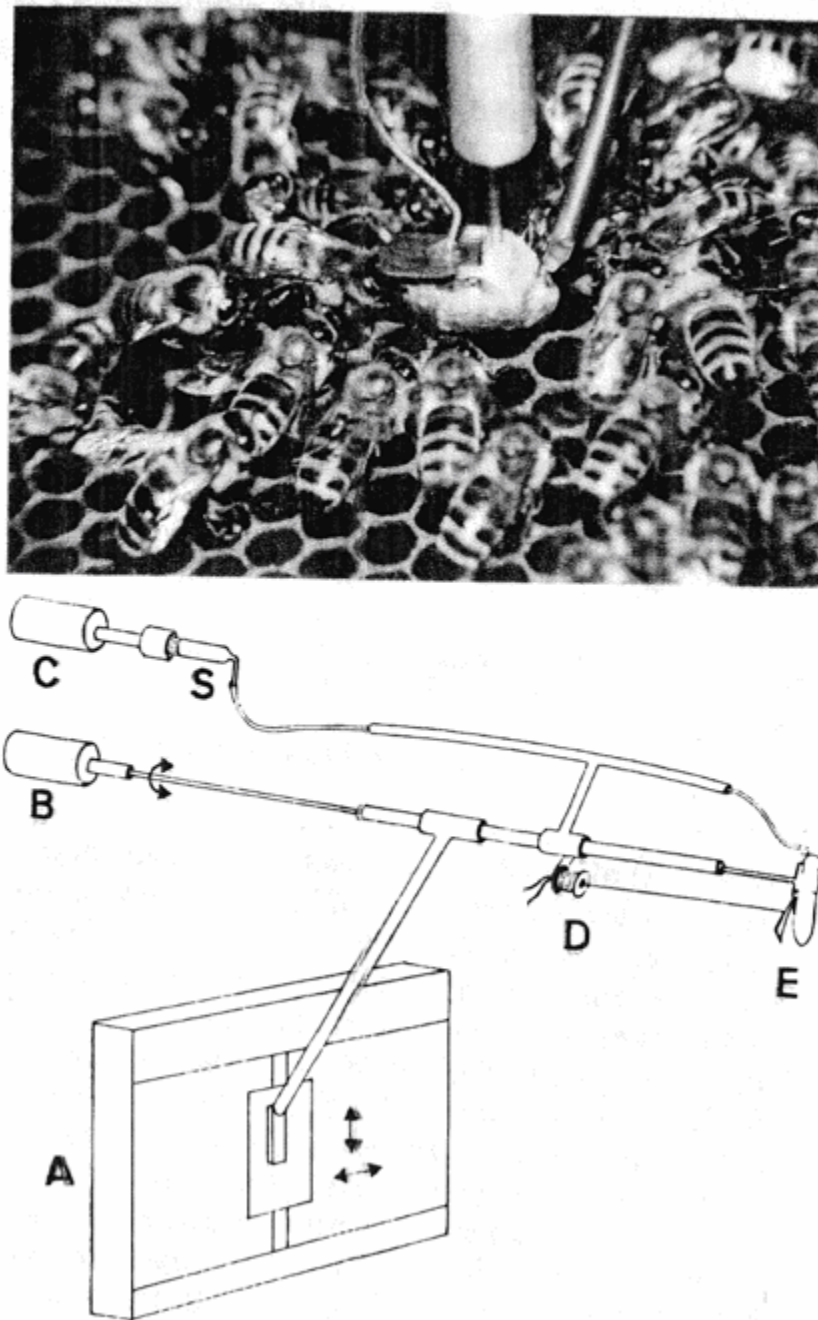
Schematic frontal view of the bee brain. The antennal mechanosensory fibres (AMR), which include fibres from Johnston's organ, project to the median posterior protocerebrum (mpp), the lateral posterior protocerebrum (lpp), and the dorsal lobe (dl). From Maronde, 1991.

Figure 6



The response distribution of a hypothesized population of on-response neurons tuned to the frequency of near-field sound stimuli.

Figure 7



Top: The mechanical model bee surrounded by follower bees and attending bees during a wagging run. Bottom: A schematic of the mechanical model. The X-Y plotter (A) controls the figure of eight pattern. A stepper motor (B) turns the model during the figure of eight pattern, and also controls the wagging motion. Another stepper motor (C) pumps sugar water to the front of the model (to allow follower bees to sample the food). An electromagnetic driver (D) vibrates the model's wings (E). From Michelsen et al., 1992.

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