Chapter 10
Construction of Combs

Abstract The construction of cells and regulation of the space between combs are separate but related problems. The space between combs, affected by the bees themselves, is the very basis of contemporary practical beekeeping. Within a honeybee multiple comb nest, there are several independent comb starts within the building clusters. Then the "rule of parallelism" comes into play because the building bees modify their constructions to keep equable and parallel spaces between combs. Comb construction is the result of interplay of vertical and lateral forces which lead to many imperfections that are eventually hidden by retouching. A building cluster can exert torsional and tensile loading on a piece of comb. When twisting combs, cell walls become broken; however, the bees rapidly repair them. To achieve parallel combs bees must maintain a tolerance distance between combs which may be due to the detection of gravity. Building bees appear to exploit a sense of gravity which was shown by disrupting the function of sense organs and then observing the effects on comb construction. Bees detect gravity by an unfettered sense organ of the neck and orient themselves during comb construction, based on magnetic material in a band across the abdomen. Different magnetic oxide nanoparticles have been observed in all body parts of honeybees, but greater concentrations occur in their abdomens and antennae.

10.1 Introduction

The construction of cells and the regulation of the space between combs are separate but related problems. The space between combs, affected by the bees themselves, is the very basis of contemporary practical beekeeping. Within a honeybee multiple comb nest there are several independent comb starts within the building cluster and at different attachment sites. Then Darchen's "rule of parallelism" comes into play because the building bees modify their constructions so as to keep a reasonably equable and parallel space between combs. Parallelism overrides other considerations, such as the length of cells.

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Comb construction is the result of interplay of vertical and lateral forces acting on the combs which, over time, lead to many imperfections that are eventually hidden by retouching. A building cluster can independently exert torsional and tensile loading of a piece of comb. In the process of twisting comb, cell walls will inevitably be broken; however, the bees rapidly mend such tears and fractures. Honeybees achieve reasonably parallel sets of combs, but in the end, they have some means both of achieving this and of maintaining the distance between combs within limits that we can recognise as tolerances. This may be due to the detection of the vertical axis of gravity.

Building bees might be able to exploit a sense of gravity that would allow them to build vertical combs. This was shown by disrupting the function of a sense organ and then observing the effects on comb construction. It was shown that an unfettered sense organ of the neck is the instrument by which bees detect gravity and so orient themselves during comb construction. The basis for this ability is supported by the discovery of magnetic material in a transverse band across the abdomen. Indeed, different magnetic oxide nanoparticles, ranging from superparamagnetic to multi-domain particles, are found in all body parts of a honeybee, but greater concentrations occur in their abdomens and antennae.

10.2 Parallelism Between Combs

The building of a honeybee nest involves both the construction of cells and the regulation of the space between combs; separate but related problems. The space between combs, affected by the bees themselves, is the very fundament of practical beekeeping. The realisation of the importance of this space is contained in the correspondence of Langstroth (Naile 1942), but is not explicit in his laborious account of its management (Langstroth 1853). In any event, although Langstroth is usually cited as the ‘discoverer’ of bee space, the first practical application of the principle was that by Dżierzon (1852). The way in which the space between the combs might be regulated by bees occupied Darchen through many years of research on *A. mellifera.* Summarising and expanding on three of his earlier research letters (Darchen 1952a, b, 1954) presages his experimental work with the observation that a straw skep is a more ‘natural’ nest container than a beekeeper’s hive. In the former, the combs curve below and are not constrained by the rectilinear design of the latter. In a skep, or feral nest, the combs are also parallel to one another, even when they curve about a horizontal axis (Fig. 10.1).

Viewed as a crystal, the combs from a skep may contain a dislocation of the lattice (Fig. 10.1). This indicates that there are several independent comb starts within the building cluster and at different attachment sites. Darchen’s “rule of parallelism” then comes into play; the building bees modify their constructions so as to keep a reasonably equable and parallel space between the combs. The finished comb is only the final result of how the bees have reacted to the many stimuli for construction. Interference with the forming nest gives some insight into what

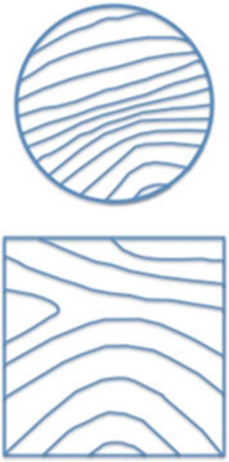

Fig. 10.1 *Top* Disposition of combs naturally built by *A. mellifera* in a skep or a hive without frames; *bottom* bees may interpose an additional comb (on *left*) depending upon constraints of the nest cavity (after Darchen 1954)

stimuli may have influenced the bees. It also provides examples of how bees retouch their constructions to achieve parallelism. In the early stages of construction, a comb is often twisted (Fig. 10.2), but the torsion is obscured by retouching. Similarly, breaches may also be inflicted on combs and these too are quickly repaired with retouching. That parallelism overrides other considerations, such as the length of cells, was shown by juxtaposing two pieces of comb and obtaining the building solution shown in Fig. 10.3.

In another series of tests, Darchen fixed a sheet of wax between two existing combs, but the sheet was abnormally close to one of the combs (Fig. 10.4a, top), with the result that new wax added to the bottom of the given sheet was gradually re-contoured to obtain a parallel result (Fig. 10.4a, bottom). If, however, the comb closest to the inserted sheet of wax was covered with a piece of cardboard, the bees then built so as to connect the sheet of wax (Fig. 10.4b). If the cardboard was placed on the opposite comb, then the new comb built was contoured to lie equidistant between the apparent faces of the two combs (Fig. 10.4c). Darchen (1954) concluded that parallelism operates within a perceptible range of distances, deviations only occurring when a space between two combs is unacceptably small. That the distance between the cell walls themselves is the likely element that bees could measure is shown in Fig. 10.4.

10.3 Festoons and Torsion

The forming combs are generally extended in the vertical plane, but they may well lean to one side and thus grow obliquely. Darchen (1956) suggested that some force might act on the combs during construction, such as a mass of building bees working on only one side of the comb. He concluded that comb construction is the result of interplay of vertical and lateral forces acting on the combs which, over

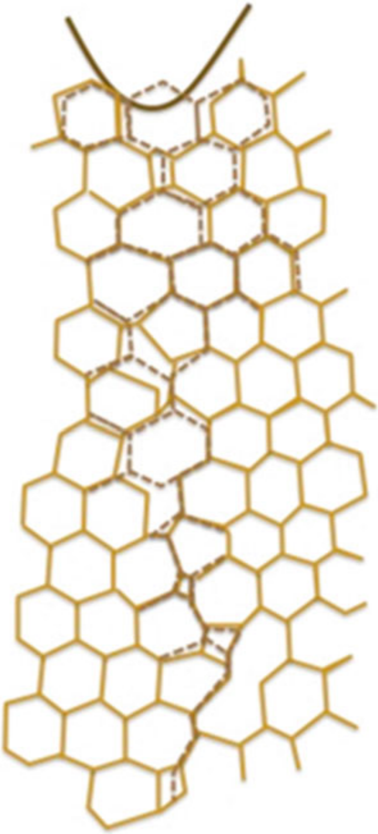

Fig. 10.2 The retouching of cells in the second phase of the construction by *A. mellifera* indicated by the *dark brown* broken line (after Darchen 1954)

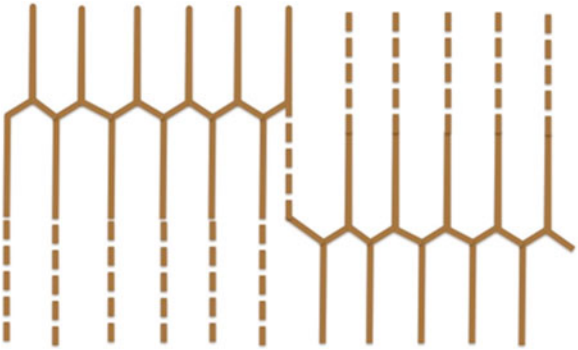

Fig. 10.3 Juxtaposition of two pieces of constructed comb (*solid lines*) results in reconstruction so that parallelism is maintained in *A. mellifera* combs (*dashed line*) (after Darchen 1954)

time, lead to many imperfections that are eventually hidden by retouching (cf. Fig. 10.2). As we shall see, evidence for forces acting on combs during construction comes from several experimental studies on comb-building.

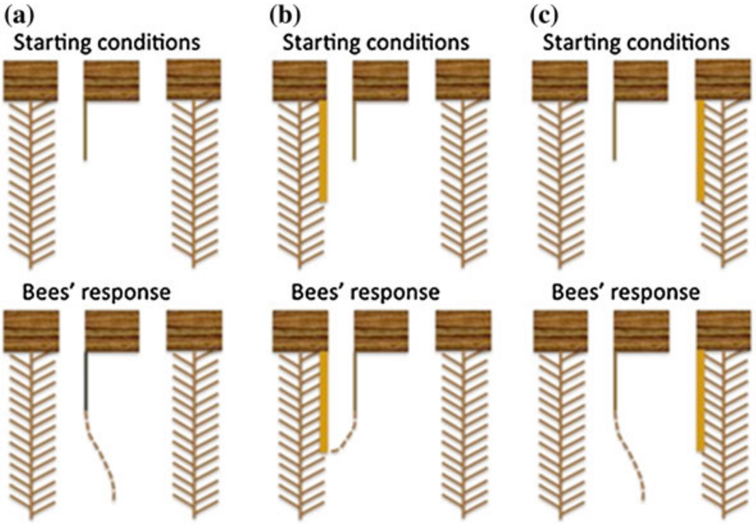

Fig. 10.4 **a** Experimental insertion of a piece of beeswax foundation is placed unacceptably close to an *A. mellifera* comb as the starting condition (*top*) which leads to the bees' response (*bottom*). **b** When the space between the beeswax sheet and an adjacent comb is further reduced by adding a piece of cardboard to the comb face the starting condition (*top*) leads to reconstruction as shown (*below*). **c** In the third sequence, a combination of the interferences shown in (**a**) and (**b**) (*top*) leads to the new construction re-establishing the parallelism between combs (*bottom*) (after Darchen 1954)

In his numerous observations on comb-building, Darchen (1959b) began an analysis of how building festoons congregate on combs and the loading effects the bees may exert on them. Before discussing Darchen's work in any detail, it is important to note that in wild nests, bees make their combs parallel in two ways. They either lengthen the cells of one side of the comb, or they tear down what they have built and reconstruct the comb, the latter tack is imperceptible in the completed combs. In his ingenious experiments, Darchen (1958, 1959b) placed a piece of beeswax foundation normal to and in between two parallel combs (Fig. 10.5). Soon after the bees had settled, this new sheet of wax was gradually twisted about the vertical axis so that the bottom-most portion of the wax sheet was properly aligned to both the adjacent combs as shown in Fig. 10.5. However, the embossed pattern of the middle section of the wax sheet showed that the cells were elongated as well.

In order to separate the torsional effects of the bees from the stretching of the wax, Darchen then introduced a piece of foundation coated with an alcohol extract of propolis (said to inhibit construction). Several hours later, this new piece of wax had been twisted into alignment with the adjacent combs, but the cell embossment showed no stretching at all.

It appears, then, that a building cluster can independently exert torsional and tensile loading of a piece of comb. In the process of twisting comb, cell walls will

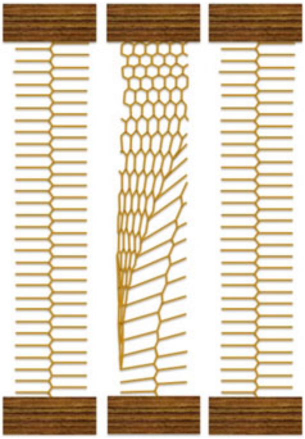

Fig. 10.5 Embossed beeswax foundation inserted in the opposite direction to two adjacent combs, is twisted by the bees into alignment with the pre-existing *A. mellifera* combs (after Darchen 1959a)

inevitably be broken; however, the bees rapidly repair such tears and fractures. These kinds of repairs obscure the fact that bees may well have twisted combs and retouched whatever rents may have appeared. Darchen went on to provide an experimental mechanical model to simulate the torsional deformation of combs, and was able to conclude that simple, horizontal traction, applied to opposite ends of a strip of wax or of a comb, produces sufficient torsion to twist the forming wax of their nests. Since these sheets of wax were twisted, Darchen investigated the chirality of 49 such specimens. He found that 22 of them had a left-handed sense and the other 27 a right-handed sense, results that imply randomness. Similarly, the amplitude or angle of torsion appeared to be related to the distance between the sheet of foundation wax and an adjacent piece of comb. The amplitude of torsion increased with increasing distance between the two combs, in which the experimental sheet of wax was placed.

These simple little experiments of Darchen (1958, 1959b), and his earlier observations on the inter-conversions of worker and drone cells (Darchen et al. 1957), contain a wealth of information and suggestions. They demonstrate considerable plasticity in the building behaviour of bees and show how they effectively ‘hide’ their extensive retouching of nest combs to produce a final product of parallel constructs. In another series of experiments Darchen (1962a) developed further generalisations about nest construction. In essence, his work is really a test of stereotypy, a mechanistic perspective of animal behaviour that dominated ethology over three decades.

By presenting bees with a wide range of different kinds of triangular and several other irregular shapes, Darchen (1955, 1962a) was able to observe how, in such cases, a comb would be constructed. While he regarded the bees’ initial modes of construction as ‘incoherent’, he was able to establish a more orderly second phase of construction in which the wax is gradually drawn and rounded into an ellipsoid body, followed by a rapid vertical increase in comb length, and finally the development of cell walls. This second phase, in fact, reflects exactly what bees do when initiating the building of a nest, as shown by the confirmatory experiments of Naulleau and Montagner (1961).

10.4 Festoons and Comb Growth

Even more comb handling can be directly attributed to the behaviour of festoons of building bees, as Darchen (1962b) learned when he established an observation hive within an incubator held at a temperature of 30 °C. It was under these same conditions that Huber's (1814) thick curtain of bees admitted some light, as the workers began to spread out, and clearly defined chains of bees become visible (Fig. 10.6). (As an aside one must be instantly alerted to the possibility that the extremely dense clustering of bees in an unheated nest is in fact for the production and conservation of heat). Darchen (1962b) found that he could predict the points of growth on the combs from the positions of the festoons. He drew the positions of festoons, or chains of bees, on the glass of his observation hive and, the following day found that the newly constructed comb closely matched the outlines of where the bees had previously hung. Thus the position of the chains of wax-secreting bees could serve as a daily blue-print for comb construction, an idea first suggested by Hubbe (1957) and finally confirmed by Darchen (1962b).

Towards the end of his study, Darchen (1962b) made 12-hourly recordings of the chains and subsequent growth of the combs; the correspondence between the two is evident (Fig. 10.7). Additional information on the chain bees also emerged. Temporarily, the most stable chains were those closest to sites where the comb was actually being extended. Once a chain is formed, other bees rarely join it. Marked bees were observed to remain in a chain for several days. Oddly enough, Darchen could not see wax scales on the bees in a chain, yet when individual bees left the chain there was always a vigorous rubbing of their abdomens, perhaps to loosen scales? We can add confirmation of Darchen's (1962b) observations from very similar observations of our own, on African *A. m. scutellata* and *A. m. capensis,* as well as *A. cerana* in Asia (Hepburn and Duangphakdee, pers. obs.).

Both at the inception of a honeybee nest, or during extensions within an existing nest, groups of wax- bearing worker bees gather in vertical, elongated chains in which individual bees may remain there for some time. These chains of bees, also termed festoons, are easily seen in the frame hives used for *A. cerana* and *A. mellifera*, especially if there are empty frames from which they can be suspended. Often several chains may be seen at different sited and on different frames (cf. Fig. 10.9—Hepburn 1986). Indeed, photographs have been published showing *A. cerana* x *A. mellifera* mixed-species chains of building bees (Yang et al. 2010a, b). To observe chains of building bees in nests of the single comb species is more difficult. The inception of a nest and of a chain of comb-building bees of *A. florea* was recently photographed (Fig. 10.6).

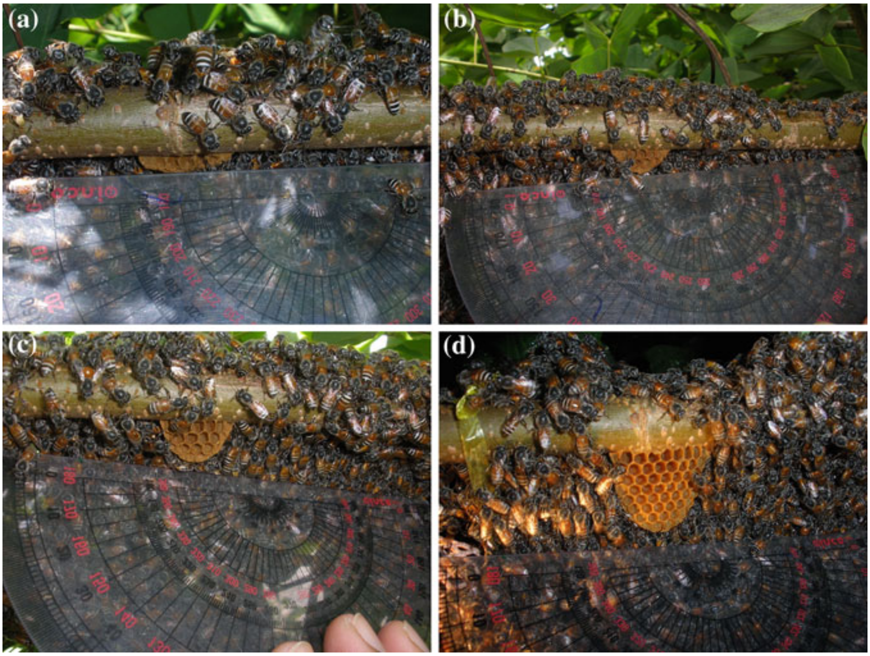

Fig. 10.6 Inception of an *A. florea* nest. **a** shows the worker bees gathering both *above* and *below* the nest twig at 11.31 h after settling on twig; **b** even more bees are present at the site by 12.39 h; **c** distinct chains of workers have constructed a few cells below the twig at 13.54 h; **d** construction is in full swing at 19.56 h and at the same time other bees have begun constructing the crown cob above the twig. Plastic piece with numbering is a protractor

Fig. 10.7 Correspondence between the positions of chains of wax building bees and the construction of new comb by *A. mellifera*. Festoons are represented by *thickened lines*, the thickness of which indicates the density of bees present. *Broken lines* represent additional new comb (after Darchen 1959b)

10.5 Evidence of a Sense of Equilibrium

The thrust of Darchen's many experiments and observations, which he summarised in 1968, is that, through retouching their constructions, honeybees achieve reasonably parallel sets of combs. Bees must, in the end, have some means both of achieving this and of maintaining the distance between combs within limits that we recognise as tolerances. That this may be due to the detection of the vertical axis of gravity was shown by Gontarski (1949), the mechanism investigated by Martin and Lindauer (1966), or rather by a self-organising process related to the substrate (Pratt 2000), and similar to the self-organisation of the hexagonal pattern (Pirk et al. 2004; cf. Chap. 12).

The combined cell bases constitute a mid-wall from which the cells extend perpendicularly. Gontarski (1949) investigated the means by which bees almost invariably achieve a vertical relationship between the vertical axis of the mid-wall and the pull of gravity. In his experiments, Gontarski (1949) placed small queenright colonies (1000 bees) into single-frame hives, which were thermostatically warmed and also kept covered for darkness. Each hive in turn was placed on a rotating stage, with the flight hole in the axis of rotation. By use of a synchronous motor he was able to maintain a constant loading on the combs in a desired axis.

Because the posture of the bees changes depending on their position in relation to the combs, the centre of gravity may act either through the median plane of the animal (dividing a bee into mirror halves when the bee itself is vertical), or through a frontal plane (between top and bottom halves of the bee if it stands on the horizontal). In Gontarksi's first experiment, the bees hung vertically on the combs so that the frontal axis of the bees remained constantly vertical, but there was a continual change about the median axis (Fig. 10.8). Surprisingly, after 10 days or so of continuous rotation, the bees had constructed 'normal' combs. This experiment argues for the mid-wall being constructed in the vertical axis if the frontal plane of the bees building is vertically orientated. It should be noted that the median plane would have been random in this experiment. These results are entirely consistent with natural constructions where the bees build vertically upwards, downwards or even sideways, the mid-wall always being vertical in such cases. A disruption of the median plane does not hinder a bee's ability to build with respect to gravity.

In a second experiment, Gontarski (1949) placed the comb and bees such that they were loaded tangentially on a rotating horizontal plate (Fig. 10.8). In this way centrifugal forces act normal to the broad comb face. In this situation the frontal plane, important for a vertical orientation (see above), is taken out of the vertical mode; likewise, the gravitational and centrifugal forces were not aligned and a resultant was obtained. The median plane of the bees remained vertical. In the configuration of this experiment the mid-wall of the combs would be expected in the direction of the resultant, and this is precisely what Gontarski (1949) obtained. This implies that the bees posturally reorient themselves to obtain a resultant vertical orientation of their frontal plane.

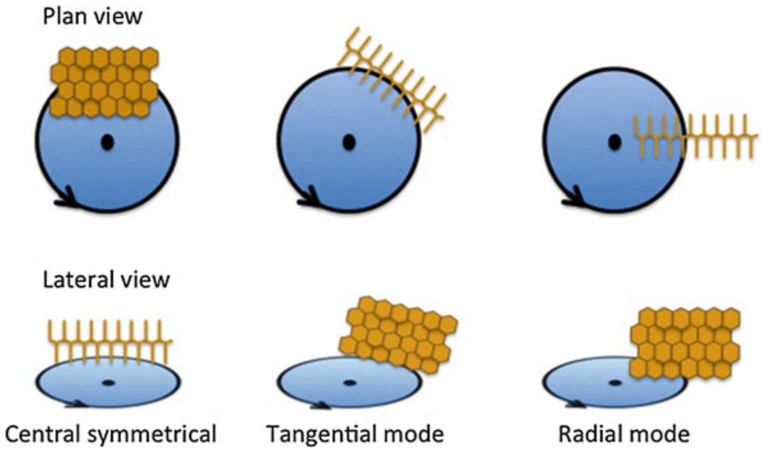

Fig. 10.8 The plane and nearly lateral view of the experimental design of Gontarski (1949) to assess the gravitational sense of bees. The position of the bees in his first experiment was as on the *left*, the tangential mode is shown diagrammatically in the *middle*, and the radial arrangement on the *right*

The role of gravitational forces acting on the median plane was studied in a third experiment. Here the hive was placed radial to the axis of rotation on the horizontal plate (Fig. 10.8). In this case the frontal axis of the bee could remain vertical and its median plane thrown in the direction of the result and of both centrifugal and gravitational forces. Again, the mid-walls of the combs were in the vertical plane.

Thus the bees followed the vertical axis, which must have been perceived through the frontal plane. The orientation of the hexagons themselves appears not to be mediated through a perception of the vertical. The skewed orientations which Gontarski (1949) observed in all his rotating experiments varied with the speed of rotation. He concluded that the degree of skewness results from the vertical orientation of the bees with respect to their median axis. This may be, but this interpretation does not explain the natural occurrences of horizontal, vertical or tilted cells in normal combs.

As a finale to Gontarski's experiments, it is extremely interesting to note that one of his colonies had been rotated continuously for 6 weeks in the radial mode. When removed from the experimental platform, the bees continued building comb. In this new comb the mid-wall was acute to the vertical and opposite in direction from the resultant that had prevailed during 6 weeks of rotation. This obviously implies either an overcompensation on cessation of the stimulus (Hepburn 1986), or an overcompensation during the 6 weeks of constant exposure to the abnormal influence of the hyper-gravitational forces (up to 1.2 g) during the experiment (Pratt 2000).

10.6 Application of the Sense of Equilibrium

In a continuation of their heroic experimental efforts, Martin and Lindauer (1966) further investigated how building bees might be able to exploit a sense of gravity that would allow them to build vertical combsvertical comb. Their experimental approach was to establish small colonies of bees, to disrupt the function of an organ, and then to observe the effects of their various interventions on comb construction. By trial and error, they eliminated surgical ablation as too time-consuming a procedure, and in the end they set about plastering over different sense organs with a wax-resin mixture (how they came about the right proportions is a story in itself). Their procedure was to take 500 to 1000 bees from the building cluster of a strong colony, to anaesthetise every bee and to gum over a sense organ of interest. The bees were then given a queen, put on empty building frames and kept at 25 to 30 °C during the experiments. Since it had previously been shown that bees have sense organs which detect the direction of gravity (Lindauer and Nedel 1959), Martin and Lindauer (1966) performed a series of five experiments to assess the possible role of gravity detection in comb construction.

In their first experiment, Martin and Lindauer (1966) anaesthetised 490 bees and immobilized their heads by gluing them to their thoraces using the wax-resin mixture. These bees were hived and formed a cluster on the building frames. After 8 days there was not a speck of wax on the frames, but wax scales had accumulated on the bottom of the hive. On repeating their experiment using 600 bees there were a few spots of wax here and there on the frames but no combs. The authors noted that the head-thorax join of 121 bees had become loose. Although the setae of the neck hair plates were still gummed over, this may account for the spots of wax. From this we can only conclude that 1090 bees, with their heads glued fast to their thoraces, did construct any comb. The implication is that mobility of the head is somehow necessary for comb construction, but not for wax secretion.

In two more refined, and technically more difficult procedures, Martin and Lindauer (1966) plastered only the sensory plates on the necks of the bees (Fig. 10.9). About 1000 bees in each trial failed to produce proper combs over a two-week period. However, after about two weeks (having checked daily for any loosening of the glue), the first bees were detected in which the glue had become loose. From that time onwards the bees constructed only few erratic triangles. These results are considered sufficient evidence to show that an unfettered neck organ is required for comb construction.

Since bees hold their abdomens in an obliquely downward position when lengthening cell walls (and often when they fly), Martin and Lindauer (1966) decided to assess the possibility that the sense cells of the abdominal petiole (Fig. 10.9) might contribute to comb construction. They performed two trials, with 660 bees in each group. In one group the sensory setae were gummed over, and in the second group the thorax was immobilized and glued to the abdomen to prevent any movement at that joint. Both groups of bees constructed normal combs. The immobility of the abdomen in Martin and Lindauer's (1966) experiment is supportive of a decisive role of

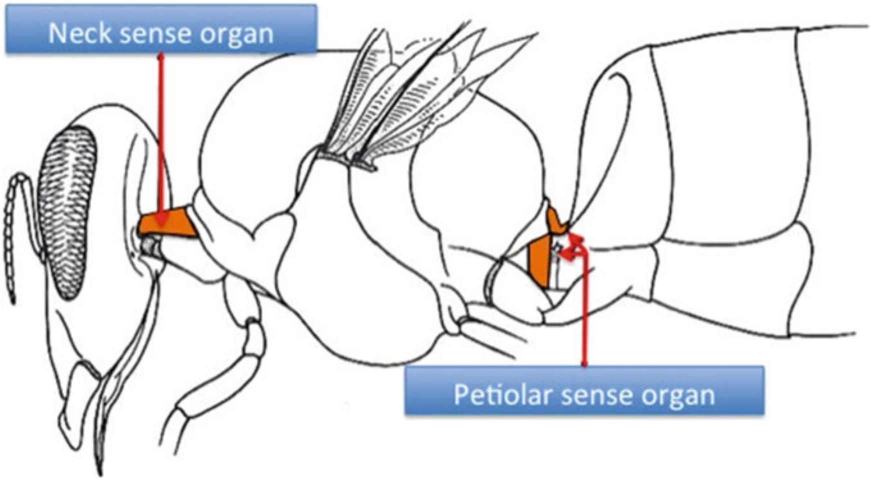

Fig. 10.9 Location of the sense organs of an *A. mellifera* honeybee worker thought capable of perceiving the direction of the force of gravity. Those of the neck (stretched here) are usually covered by the head (after Martin and Lindauer 1966 and modified from Hepburn 1986)

the sensory setae on the neck for comb-building, however they may work. Their results are also consistent with those of Gontarski (1949).

Martin and Lindauer (1966) concluded that an unfettered sense organ of the neck is the instrument by which bees detect gravity and so orient themselves during comb construction. This interpretation is made all the more plausible by the discovery by Gould et al. (1978), that worker bees have magnetic material in a transverse band across the abdomen. This material has been described during the intervening years and was recently reviewed by Wajnberg et al. (2010). To paraphrase these authors, honeybees show sensitivity to small changes in magnetic fields. Different magnetic oxide nanoparticles, ranging from super-paramagnetic to multi-domain particles, were observed in all body parts of honeybees, but relatively greater concentrations occurred in their abdomens and antennae. It is not yet known how magnetic information could be processed by the honeybee nervous system. Nonetheless, results from recent studies on honeybee magnetism published by Hsu et al. (2007) certainly support the original thinking that underlies the experimental work of Martin and Lindauer (1966).

An interesting experiment that relates to their work was the dispatch of a small colony of bees for 6 days on a space-shuttle flight beyond the earth's gravitational pull. It is said that the bees built perfectly normal combs under conditions approximating zero gravity (Vanderberg et al. 1985). This experiment very simply indicates that bees can build normal combs in the absence of gravitational cues. This supports an alternative idea; that not gravity but a substrate-dependent mechanism, because the cell walls are always perpendicular to the substrate (Wedmore 1929; Lau 1959). In comb-building the subsequent rows use the previous row as templates resulting in a cascade of propagating orderliness over the whole comb (Pratt 2000). However, the ultimate test would be to measure the orientation in relation to the substrate and gravity in natural nests of *A. mellifera*, and furthermore in other species to include an evolutionary perspective.

10.7 The Orientation of Combs

The detailed observations of Darchen (1968) clearly show that a newly settled swarm may well begin the construction of combs at several different and apparently independent sites. However, parallel sets of comb are the end result of a building operation that is heavily dependent on retouching. Superimposed upon this parallelism is a planar orientation of combs with respect to compass directions. In one of the very few studies of comb orientation by feral bees, Seeley and Morse (1976) concluded that the arrangement of combs was independent of both the position of the nest entrance (previously noted by Owens and Taber 1973), and the magnetic field of the earth.

When swarms of honeybees are allowed to build combs freely, without the constraints of beekeeping, they build their combs parallel to the same plane and compass direction as were the combs of their mother colonies. Lindauer and Martin (1972, 1973) showed that by taking swarms from hives and placing them in cylindrical containers, these bees built combs of essentially the same orientation that had prevailed in their former nests. The removal of these bees to yet other fresh cartons gave the same results. In some cases, Lindauer and Martin (1972, 1973) placed Helmholtz coils around the second cartons in such a way as to deflect the apparent magnetic field by some 40°. The combs built under these conditions were likewise deflected by 40°. However, several other researchers, including Gould et al. (1978), who established that bees have magnetic remanance in the first place, failed to obtain the same results in similar experiments.

Whether or not bees retain memory of comb orientation in the construction of a new nest, or use the earth's magnetic field for orientation was reinvestigated by de Jong (1982). In his first experiment, he placed 25 swarms, which he had caught in trap boxes (containers with no beekeeping furniture), into specially designed building boxes. He measured the orientation of the combs as they had been constructed in the trap boxes and subsequently in the special building boxes. These bees showed a significant and positive tendency to maintain comb direction. de Jong then proceeded to place five colonies in his special comb-building boxes which were situated within a series of coils designed to generate a magnetic field. When he engaged the coils, the horizontal component of the magnetic field was shifted clockwise through 90°. Every few days the bees were transferred to fresh boxes and the coils engaged or not in alternate trials. He found that the bees had maintained, to a significant degree, their comb construction relative to a shifted magnetic reference. He concluded that the magnetic field of the earth is an important cue utilised by bees in the orientation of their combs during building. Thus, de Jong (1982) was able to confirm the original work of Lindauer and Martin (1972, 1973).

10.8 Behavioural Aspects of Comb Construction

Exposing mixed colonies of the two sister-species of the Western, *A. mellifera*, and the Eastern honeybee, *A. cerana*, to foundations made of pure wax from either species resulted in normal building behaviour, only the number of irregular cells was noticeable. In both pure controls, no worker brood was reared in the cells built on the foundation made of the wax of the opposite species. In the pure *A. mellifera* colonies the cell size was modified, whereas *A. cerana* constructed comb without modification but used the cells based on *A. mellifera* wax only to rear drones or for storage (Yang et al. 2010a, b; cf. Chap. 4).

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